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Land Snail Diversity and Community Assemblage in Biak-Na-Bato National Park, San Miguel, Bulacan, Philippines

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Karst ecosystems are critical refugia for various invertebrates including land snails. In the Philippines, data on these mollusks are insufficient amidst wide-scale habitat destruction due to uncurbed tourism and mineral extraction activities. To address this research gap, land snail diversity and community assemblage in the historic Biak-Na-Bato National Park (BNBNP), San Miguel, Bulacan were examined. A total of 32 5x5m quadrats were randomly set around the vicinity of four accessible caves: Santol, Bahay Paniki, Cuarto-Cuarto, and Aguinaldo, during dry and wet seasons. Environmental variables including altitude, temperature, relative humidity, soil moisture, soil pH, soil exchangeable calcium, number of trees, diameter of trees, canopy cover, and leaf litter depth were measured. From a total of 2,834 land snails sampled, 42 species and 14 families were identified. From these, 23 were classified as macro (> 5 mm) and 18 as micro (< 5 mm) land snails, and one as a slug. Moreover, 37 (88.10%) were native species while 5 (11.90%) were non-native. Bahay Paniki recorded the highest species richness but lowest diversity (27 species/qD = 5) whereas Aguinaldo exhibited the highest overall diversity (23 species/qD = 12). Relatively high sample coverage values (> 0.95) suggest increasing sampling effort to detect rare species. PERMANOVA and NMDS showed significant difference in community assemblage between sites. *Cyclophorus appendiculatus* attained the highest contribution (34.01%) to site dissimilarity. Land snail assemblages were influenced by temperature, soil pH, soil calcium, number of trees, tree diameter at breast height, and soil moisture based on CCA. The GLMM identified soil pH as the strongest predictor of species richness, while abundance was best explained by a combination of canopy cover, number of trees, soil moisture, soil pH, and temperature. This study reveals BNBNP's distinct malacofaunal diversity, underscoring its significance as a karst ecosystem that warrants continued conservation.

Keywords: Biak-Na-Bato National Park, Malacofauna, Karst, Caves, Macro land snail, Micro land snail

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BACKGROUND

In the Philippines, karst terrains contribute to approximately 35,000 km^2 or 11.7% of its total land area (DENR-BMB 2019). Among the recognized karsts in the country is the Biak-Na-Bato National Park (BNBNP), one of the first declared protected areas known for its significant role in the Philippine history, and wildlife and floral diversity. Located between the boundaries of three municipalities of Bulacan Province: San Miguel, San Ildefonso, and Doña Remedios Trinidad, the protected landscape has karst forests with two rivers, Balaong and Madlum, as well as cave systems including unexplored tunnels and caverns (Manipon and Mesina 2009). Years after the declaration, 70% of its original land size was excluded for mineral extraction following a presidential proclamation (FPE 2004). In 2010, House Bill 2677 was filed to reinstate BNBNP's original land area but was not approved. Over the years, the impacts of man-made threats including marble quarrying, wildlife poaching, and illegal logging are still evident (Eballo 2019). Therefore, as an eco-historical destination, conservation projects and initiatives are further promoted to preserve its biological integrity while boosting economic opportunities (DENR 2022)

The BNBNP harbors unique biodiversity including cave-dwelling arthropods (Hinolan et al. 2018; Cristales 2019). However, there are no studies available on its malacofaunal diversity, particularly on land snails despite their abundance in karst habitats. Land snails are also efficient indicators and predictors of environmental health (Salih et al. 2021). Hence, the assessment of land snail diversity and community assemblage is crucial in strengthening the biodiversity status of this protected area. Moreover, this study can contribute to designing a more inclusive science-based conservation and management plans and policies amidst threats involving invasive species, destructive activities, i.e., illegal quarrying and mining, and unregulated collection and consumption of endemic and endangered fauna and flora. Thus, the main objective of this study is to determine the diversity and community assemblage of land snails in the BNBNP, Bulacan. Specifically, to determine the diversity and abundance of macro and micro land snails around the vicinity surrounding the four caves (Santol, Bahay Paniki, Cuarto-Cuarto, and Aguinaldo) in the BNBNP, compare community assemblage of land snails during dry and wet seasons, and analyze the relationship between selected environmental variables and the species richness and abundance of land snails.

MATERIALS AND METHODS

Sampling Area

Biak-Na-Bato National Park (121°05'06"E, 15°07'08"N) is situated in Barangay Biak-Na-Bato, San Miguel, Bulacan, and stretches out to nearby municipalities of San Ildefonso and Doña Remedios Trinidad. The park is 80 km northeast of Manila and lies on the southern boundary of the 540-km Sierra Madre mountain range (Fig. 1). It constitutes a portion of the base of Angat Dam watershed. Its total land area is 3,030.56 ha with only few caves being explored out of hundreds scattered across cave systems with various limestone formations and river systems. Flat and steep concrete to rugged trails and hanging bridges connect various caves and picnic spots. For this study, the vicinity surrounding the four caves, namely Santol (121°04'15.55"E, 15°06'43.6"N), Bahay Paniki (121°4'33.33"E, 15°06'28.91"N), Cuarto-Cuarto (121°04'19.5"E, 15°06'28.1"N), and Aguinaldo (121°04'18.0"E, 15°06'31.3"N), were designated as sampling sites due to their accessibility (Fig. 2).

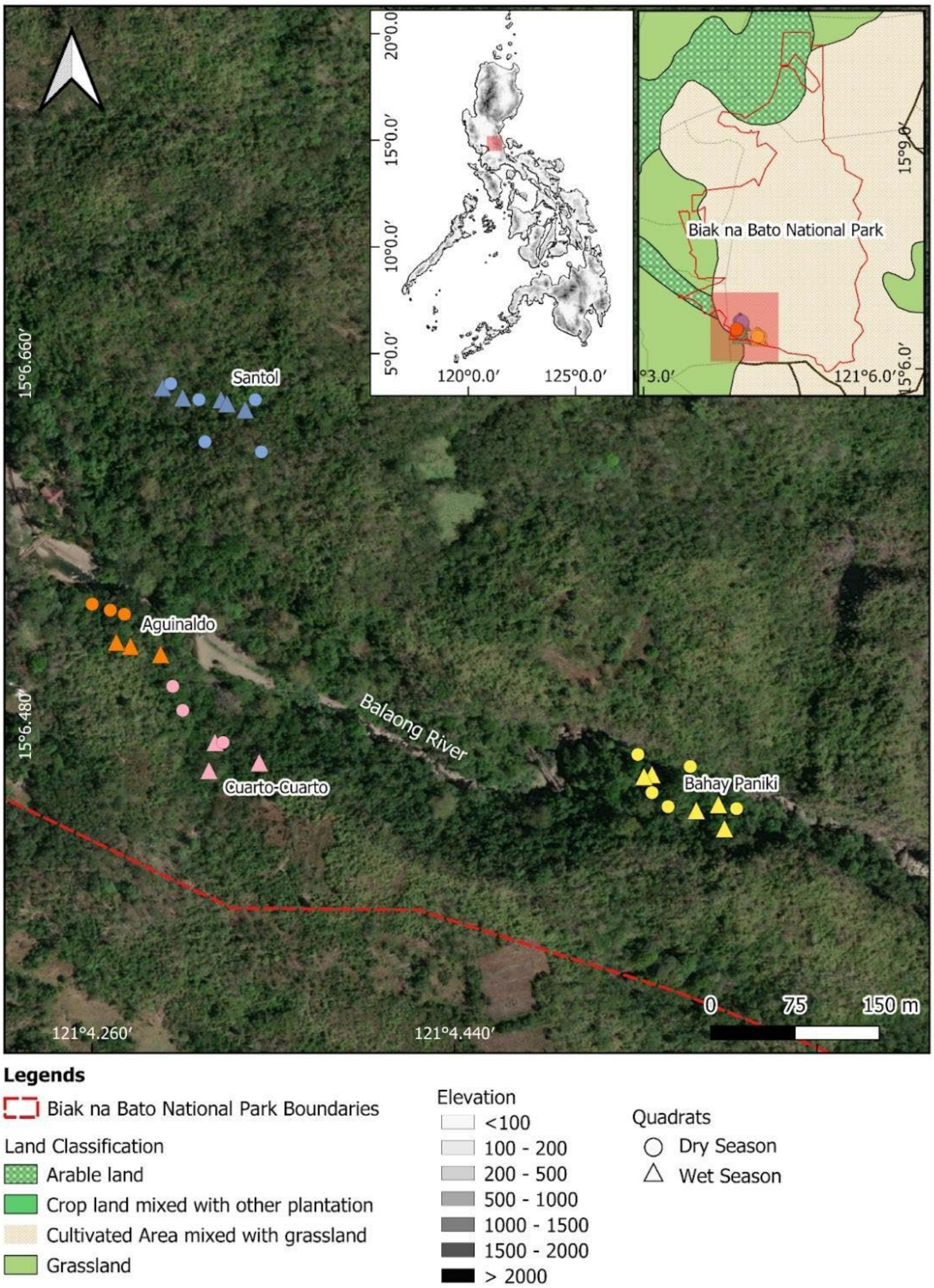

Fig. 1. Sampling sites around the vicinity of the four caves (Santol, Bahay Paniki, Cuarto- Cuarto and Aguinaldo) in the Biak-Na-Bato National Park.

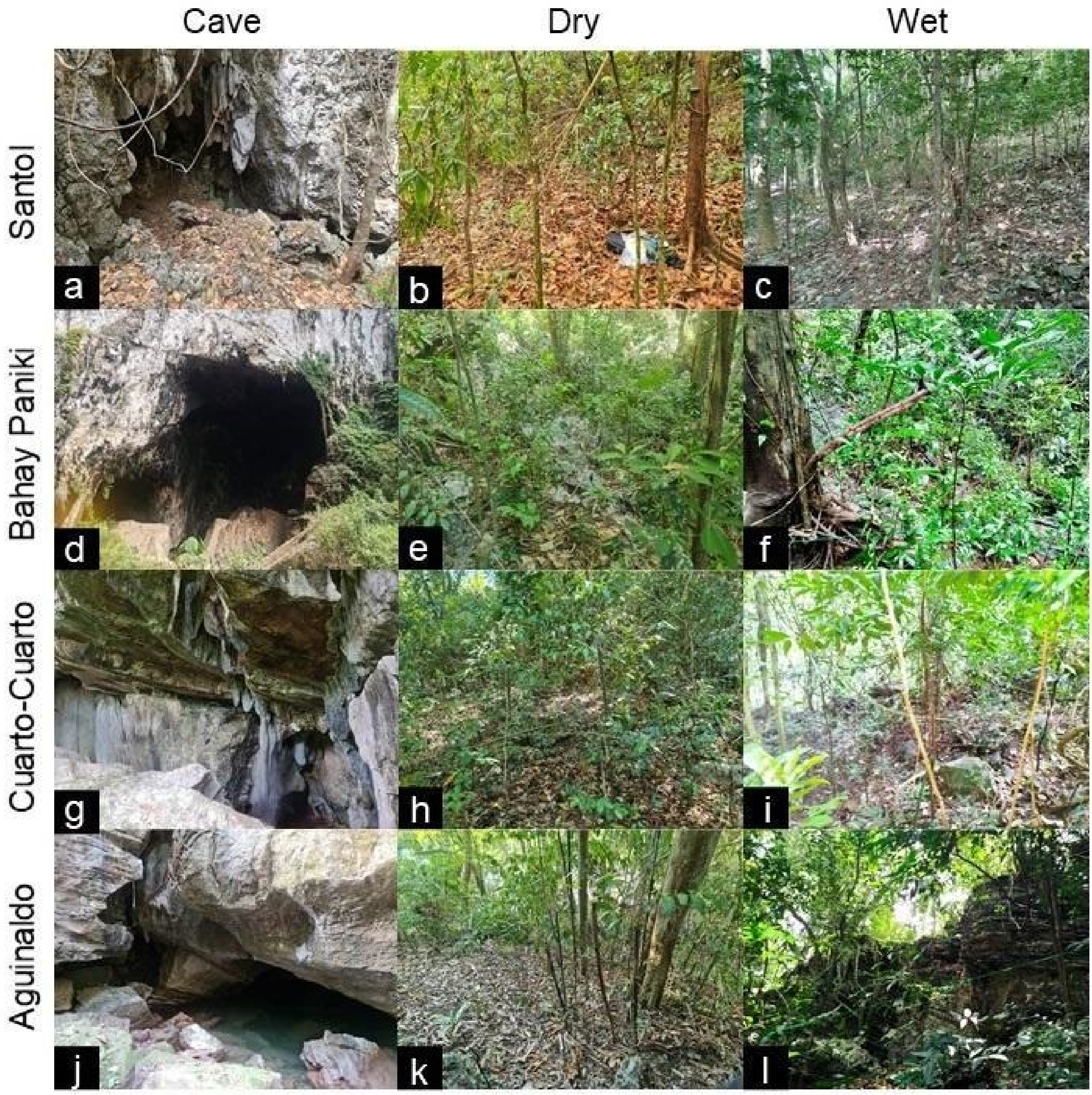

Fig. 2. Sampling sites around the vicinity of Biak-Na-Bato National Park caves during dry and wet seasons. a–c, Santol; d–f, Bahay Paniki; g–i, Cuarto-Cuarto; and j–l, Aguinaldo.

Sampling Protocol

Sampling protocol for the collection of macro and micro land snails were modified from Schilthuizen (2004), Clements et al. (2006), de Chavez and de Lara (2011), and Valdez et al. (2021). It incorporated visual and soil survey techniques to enhance sampling efficiency. Accessible locations at each cave entrance and surrounding vicinity were identified. Five quadrats were set in Santol and Bahay Paniki and only three Cuarto-Cuarto and Aguinaldo due to their small and inaccessible areas. In total, sixteen 5x5m quadrats were set at random locations at least 10 m away from the cave entrance, from each other to avoid pseudoreplication, and from the trail to reduce edge effect. Different sampling quadrats for each season take account the patchy distribution of land snail communities in karst areas.This captures spatial interspersion and broader range of microhabitats and reduces bias. Quadrats were set around the four caves during the dry season (May 2024) and wet season (October 2024). Overall, 32 quadrats were established for the entire sample collection.

Measurement of Environmental Variables

The geographic coordinates of each quadrat were determined using Garmin 12 Hand-held Global Positioning System (Garmin International, Inc., USA).The vegetation was described using the relative distribution of trees, grasses, and other plant representatives in each quadrat. To measure the vegetative canopy, a concave spherical densiometer (Forest Suppliers, Inc., USA) was used. The number of trees was recorded followed by measurement of the diameter at breast height (dbh). The leaf litter depth was measured using a 12-inch ruler inserted into five points in forest detritus (corners and center of each quadrat). A digital thermometer (Uni-T, Model UT333, China) recorded air temperature and relative humidity. A soil tester meter (Alotpower Soil Tester Meter) was inserted (corners and center of each quadrat) into the forest substrate to measure soil moisture. Soil pH from the collected soil samples was measured using a water quality tester pen. For soil exchangeable calcium, sieved soil samples using 0.5 mm-aperture metal mesh were subjected to ethylenediaminetetraacetic acid (EDTA) titration ammonium acetate extraction at the Analytical Services Laboratory, University of the Philippines Los Baños.

Land snail Collection and Identification

A standard 30-minute sampling effort per person was followed in each quadrat. For macro land snails, live and undamaged, non-eroded empty shells along the trail and quadrats outside the caves were collected through visual search and handpicking focusing on microhabitats. The undamaged and non-eroded empty shells represent recently deceased individuals which may still reflect the species diversity of an area due to its limited dispersion ability and distribution. Live samples were photographed and returned to their natural location afterward. In addition, five live individuals per species per site were collected as voucher specimens, and for further morphological and molecular analysis. Micro land snails were collected via direct hand-picking on limestone surfaces and crevices. In addition, 25 kg of topsoil were collected from each quadrat. Soil samples were placed in aluminum trays and oven dried at 90°C for 7 hours. Dried samples were sifted through metal mesh (cascade sieving).Sieved samples were collected and observed under a stereomicroscope for micro land snails. Specimens were identified up to genus and species level using published literature (Faustino 1930; Bartsch 1932; Springsteen and Leobrera 1986; Hemmen et al. 1987; Poppe et al. 2022a b) The updated taxonomic names of identified samples were verified in MolluscaBase (www.molluscabase.org).

Data Analyses

Species abundance data of both live and empty shells were tested for normality using Shapiro-Wilk test while homogeneity of variance was examined using Permutational Multivariate Analysis of Dispersion (PERMDISP). A two-way Permutational Analysis of Variance (PERMANOVA) was used to assess difference in community composition based on two factors: sites and sampling periods. One-way PERMANOVA was then performed to determinethe effect of significant factors. All tests were run using Paleontological Statistics Software (PAST) v. 5.2.1 (Hammer et al. 2001).

Species Diversity

The individual counts for a species determined the species abundance while the number of species per site defined species richness. Species acquired from incidental collection (samples collected along the trails, and beyond the established quadrats) were recorded but excluded in the ecological analysis to avoid statistical bias.The species diversity and sampling completeness at each site were evaluated using Hill numbers, which were visualized through rarefaction and extrapolation (RE) curves generated with iNEXT Online (Chao et al. 2014 2016). Conventional diversity indices such as Shannon's and Simpson's were not suitable in comparing diversities in each site due to differences in sampling intensities and inherent ecological variations (Staudhammer et al. 2018; Batomalaque et al. 2025).

Multivariate Ordination Analyses

Non-metric multidimensional scaling (NMDS) was utilized to assess and visualize community assemblage patterns among the sampling sites. Bray-Curtis similarity index was used to exclude the influence of joint absences. The computed stress value in two or three dimensions (2D or 3D) reflect the goodness of fit among samples (Clarke 1993). In NMDS scatterplot, sampling sites were represented by varying points and visualized by 95% ellipses. To identity the species that highly influence these variations, similarity percentage (SIMPER) analysis was performed.

Canonical correspondence analysis (CCA) was employed to identify the distinct relationship of environmental parameters to the abundance data of species in different sampling sites. This method presents the microhabitat preference of land snails based on habitat types. Inputs from species matrix include the abundance of species while the environmental matrix comprise of different environmental conditions. Some of environmental variables that were highly correlated and had weak influence were excluded to enhance ordination. To visualize CCA results, a biplot was generated using type 2 scaling which presented the environmental variables as vectors, species as points, and sites as symbols or legends. To test its statistical significance, Monte Carlo Permutation (with 1000 iterations) was performed. All multivariate analyses were generated and plotted using PAST v. 5.2.1.

Generalized Linear Mixed Model

Generalized linear mixed modelling (GLMM) by model averaging was conducted to determine the optimal parameters and identify the key predictors of species richness and abundance. All measured environmental variables were tested for correlation to remove highly collinear factors. Thus, the remaining variables were attributed as fixed factors. The quadrat in each site was determined as random factor. Predictors were standardized using the two-standard-deviation method (SD) of Gelman (2008) to make effect sizes directly comparable across variables. Corrected Akaike information criterion (AICc) was applied to compare model performance, considering limitations due to small sample sizes. Models were ranked based on their ΔAICc values to determine the level of support for each. Models with the lowest ΔAICc and highest AICc weight (wAICc) after excluding values with < 0.10 were identified as the most parsimonious. The GLMM was ran in RStudio v. 2024.12.1+563 with *lme4* and *MuMIn* packages (Bates et al. 2015; R Core Team 2025; Bartoń 2026).

RESULTS

Characteristics of Sampling Sites

The study areas, namely Santol, Bahay Paniki, Cuarto-Cuarto, and Aguinaldo exhibit moderate soil fertility and distinct vegetation structures (Fig. 2, Table 1). Tree density across the sites was generally low, ranging from one to seven individuals, with mean diameters at breast height (dbh) between 6.62 and 25.85 centimeters. Canopy cover was relatively high, ranging from

93.08% to 97.57%, while leaf litter depth varied from 1.88 to 2.92 centimeters. Soil exchangeable calcium concentrations were moderate, ranging from 13.70 to 21.11 $cmol_c/kg$, and soil pH values were comparatively neutral (6.79–7.10). Vegetation was dominated by shrubs, herbs, vines, and bamboo groves, with the presence of tall tree species such as mahogany (*Swietenia macrophylla*) and Tree bean (*Parkia timoriana*). The terrain was characterized by limestone formations, including boulders, pavements, and outcrops, along with artificial features such as concrete steps and trails. Evidence of anthropogenic disturbance, including garbage accumulation, concrete fragments, and burnt waste, was observed particularly in Cuarto-Cuarto and Aguinaldo. Both Bahay Paniki and Aguinaldo contained subterranean and surface waterways connected to the Balaong River, providing habitats for various fauna but was currently restricted to minimize human interference and protect wildlife populations. Overall, the sites represent moderately disturbed yet ecologically diverse karst forest environments with complex vegetation structures, moderate nutrient availability, and conservation relevance.

Table 1. Mean environmental variables (± SE) recorded in each sampling site in Biak-Na-Bato National Park

Environmental variables	Sampling sites			
	ST	BP	CC	AG
Altitude (masl)	109.30 (± 4.68)	80.00 (± 10.72)	61.33 (± 11.02)	75.33 (± 3.43)
Temperature (ºC)	28.86 (± 0.61)	29.63 (± 1.02)	31.20 (± 1.28)	31.58 (± 0.29)
Relative humidity (%)	76.31 (± 1.90)	76.24 (± 0.69)	70.83 (± 0.44)	67.87 (± 0.24)
Canopy cover (%)	93.08 (± 6.67)	96.70 (± 6.82)	97.57 (± 7.26)	97.49 (± 2.69)
Leaf litter depth (cm)	2.01 (± 0.70)	1.88 (± 0.75)	2.92 (± 0.72)	1.96 (± 0.40)
Number of trees/quadrats	1 – 6 (± 0.70)	1 -7 (± 0.75)	1 – 5 (± 0.72)	1 – 5 (± 0.40)
Dbh (cm)	6.62 (± 1.38)	25.85 (± 3.94)	10.01 (± 6.50)	11.86 (± 1.23)
Soil moisture	4.86 (± 1.09)	5.15 (± 1.22)	3.92 (± 1.28)	4.57 (± 0.91)
Soil pH	7.10 (± 0.21)	6.88 (± 0.14)	6.79 (± 0.28)	6.98 (± 0.07)
Soil calcium ($cmol_c/kg$ soil)	13.70 (± 2.94)	16.42 (± 3.41)	20.82 (± 0.95)	21.11 (± 1.47)

ST, Santol; BP, Bahay Paniki; CC, Cuarto-Cuarto; AG, Aguinaldo.

Species Diversity, Abundance, and Distribution

A total of 42 land snail species, comprising 2,834 individuals, were sampled in BNBNP (Table 2). Altogether, 37 species were found in standard sampling quadrats, while the remaining five were observed during incidental collection. Of these, 23 were categorized as macro land snails (> 5 mm), 18 as micro land snails (< 5 mm), and one as a slug (shell-less gastropod) (Figs. 3, 4). These were represented by 14 families: Achatinidae (3 species), Ariophantidae (4 species), Assimineidae (4 species), Camaenidae (7 species), Chronidae (6 species), Cyclophoridae (5 species), Diapheridae (1 species), Diplommatinidae (3 species), Helicarionidae (1 species), Helicinidae (1 species), Pomatiidae (1 species), Trochomorphidae (3 species), Veronicellidae (1 species), and Vertiginidae (1 species). Among these species, five (11.90%) were invasive under Achatinidae, Camaenidae, and Veronicellidae which were based on existing studies on introduced and pest species in the Philippines. The rest of the recorded species (88.10%) were either native or endemic in the country. In all sampling sites, *Cyclophorus appendiculatus* recorded the highest number of individuals (594) followed by *Lamarkiella nigrescens* (272) and *Orthostylus metaformis* (239). In contrast, species with the lowest individual count that were considered as singletons (only 1 individual for entire sample) were *Allopeas gracile*, *Diplommatina megaloptyx*, *Helicarion* sp., *Geophorus pseudomphalus*, *Bradybaena similaris*, *Obba bulacanensis*, *Gastrocopta* sp., and *Acmella* mp. 2.

Table 2. Land snails sampled in Biak-Na-Bato National Park

Family	Species Name	CCA Code	Site				Total	IC
			ST	BP	CC	AG		
Superfamily Achatinoidea								
Achatinidae	*Allopeas clavulinum* (Potiez & Michaud, 1838)**$^{+}$	Alc	1	1	2	11	15	0
	Allopeas gracile (Hutton, 1834)**$^{+}$	Alg	0	0	0	1	1	0
	Lissachatina fulica (Bowdich, 1822)**$^{+}$	Lif	1	7	4	3	15	30
Superfamily Cyclophoroidea								
Cyclophoridae	*Cyclophorus appendiculatus* (Pfeiffer, 1854)$^{+}$	Cyp	16	513	35	30	594	219
	Cyclophorus reevei (Hidalgo, 1888)$^{+}$	Cyr	10	10	6	1	27	48
	Japonia sp.$^{+}$	Jap	0	1	1	0	2	0
	Platyrhaphe anthopoma (Möllendorff, 1895)*	Pla	4	3	0	2	9	31
	Platyraphe sp.$^{+}$	-	0	0	0	0	0	10
Diplomatinidae	*Diplommatina boettgeri accedens* (Möllendorff, 1887)$^{+}$	Dpb	0	3	0	51	54	0
	Diplommatina megaloptyx (Möllendorff, 1894)*	Dpm	0	0	0	1	1	0
	Palaina quadrasi (Möllendorff, 1887)$^{+}$	Paq	0	0	1	35	36	0
Superfamily Helicarionoidea								
Ariophantidae	*Macrochlamys* sp.$^{+}$	Mac	1	4	0	0	5	8
	Lamprocystis crystallina (Möllendorff, 1887)$^{+}$	Lac	2	3	1	21	27	0
	Microcystina mp. 1^{+}	Mi1	6	7	4	14	31	0
	Microcystina mp. 2^{+}	Mi2	0	2	2	3	7	
Helicarionidae	*Helicarion* sp.$^{+}$	Hel	1	0	0	0	1	2
Superfamily Helicinoidea								
Helicinidae	*Geophorus pseudomphalus* (Möllendorff, 1894)*	Gep	0	1	0	0	1	0
Superfamily Helicoidea								
Camaenidae	*Bradybaena similaris* (Férussac, 1822)**$^{+}$	Brs	1	0	0	0	1	0
	Chloraea dryope (Broderip, 1841)$^{+}$	Chd	5	0	0	0	5	3
	Helicostyla rufogaster (Lesson,1832)$^{+}$	-	0	0	0	0	0	1
	Helicostyla woodiana	Hlw	7	4	0	0	11	46

	(Lea, 1840)[+]							
	Obba bulacanensis (Hidalgo, 1888)*	Obu	0	1	0	0	1	2
	Obba marmorata (Möllendorff, 1898)[+]	Oba	0	1	2	0	3	6
	Obba morongensis (Möllendorff, 1889)[+]	Obo	0	2	0	0	2	2
	Orthostylus metaformis (Férussac, 1821)[+]	Orm	50	119	29	41	239	279
Superfamily Cyclophoroidea								
Cyclophoridae	*Leptopoma* sp.[+]	-	0	0	0	0	0	1
Superfamily Pupilloidea								
Gastrocoptidae	*Gastrocopta* sp.[+]	Gas	0	1	0	0	1	0
Superfamily Streptaxoidea								
Diapheridae	*Diaphera hidalgoi hidalgoi* (Möllendorff, 1888)*	Dhh	0	0	1	1	2	0
Superfamily Trochomorphoidea								
Chronidae	*Hemiglypta fulvida semiglobosa* (Pfeiffer, 1845)[+]	Hfs	1	96	12	0	109	110
	Hemitrichiella sp.[+]	-	0	0	0	0		4
	Lamarckiella nigrescens (Möllendorff, 1888)[+]	Lan	24	189	39	20	272	317
	Kaliella micropetasus (Möllendorff, 1893)[+]	Kam	0	0	0	2	2	0
	Kaliella mp. 1[+]	Ka1	0	1	0	5	6	0
	Kaliella mp. 2[+]	Ka2	0	1	1	5	7	0
Trochomorphidae	*Trochomorpha* sp.[+]	-	0	0	0	0	0	1
	Videna sibuyanica (Hidalgo, 1887)[+]	Vis	16	7	1	17	41	32
	Videna crassula (Möllendorff, 1898)*[+]	Vic	4	3	0	1	8	7
Superfamily Truncatelloidea								
Assimineidae	*Acmella polita* (Möllendorff, 1887)[+]	Acp	46	9	25	43	123	0
	Acmella mp. 1[+]	Ac1	0	1	0	0	1	0
	Acmella mp. 2[+]	Ac2	0	0	0	2	2	0
	Omphalotropis columellaris (Quadras & Möllendorff, 1893)[+]	Omc	0	0	0	3	3	0
Superfamily Veronicelloidea								
Veronicellidae	*Laevicaulis alte* (Férussac, 1822)**[+]	Laa	0	10	0	0	10	0
Total number of individuals			196	1000	166	313	1675	1149
Overall total number of individuals								2834

CCA, Canonical correspondence analysis; ST, Santol; BP, Bahay Paniki; CC, Cuarto-Cuarto; AG, Aguinaldo; SC, Systematic collection; IC, Incidental collection; *endemic species; **invasive species; [+] new recorded species in Bulacan.

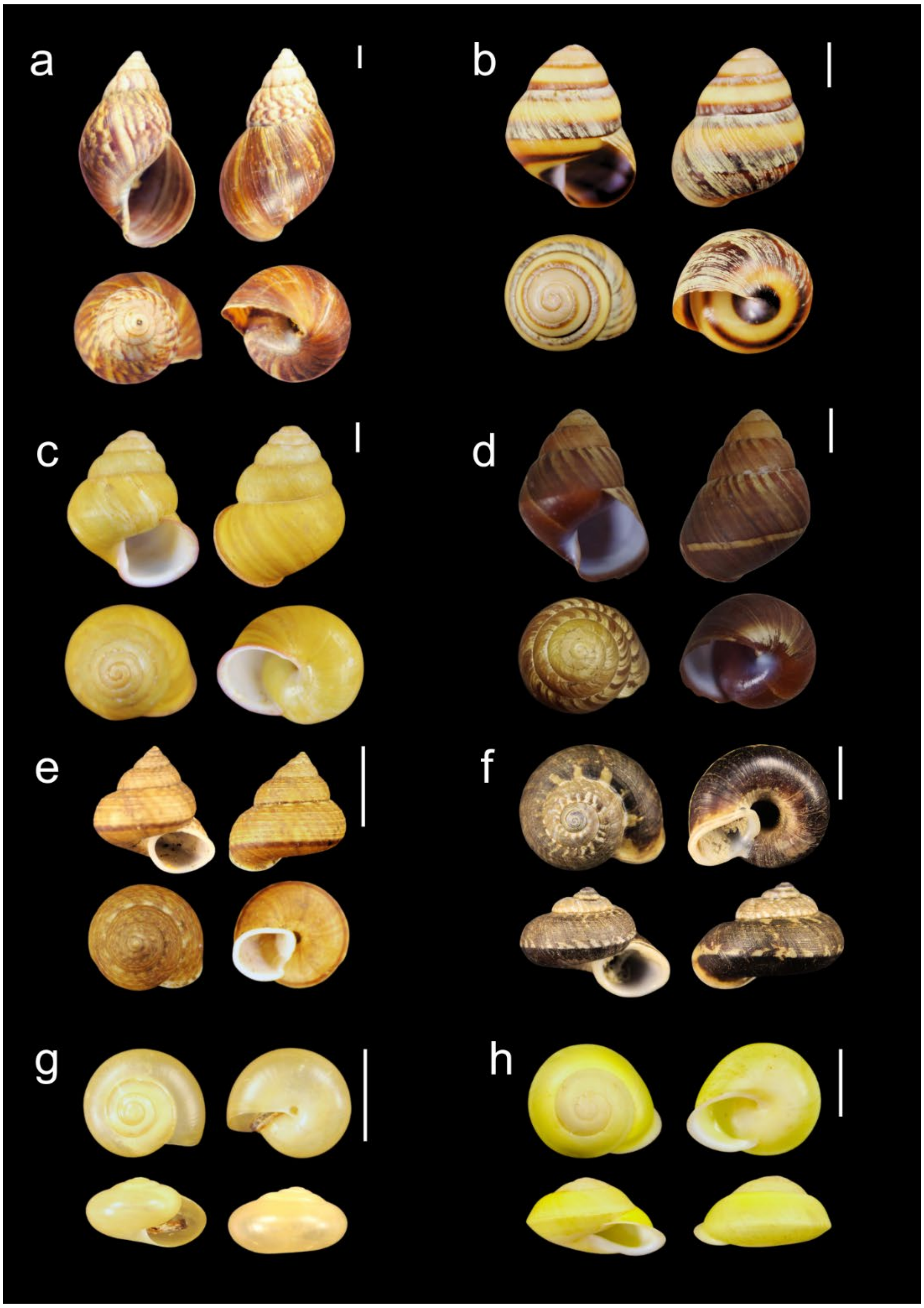

Fig. 3a–h. Land snails of Biak-Na-Bato National Park: a, *Lissachatina fulica*; b, *Orthostylus metaformis*; c, *Helicostyla woodiana*; d, *Helicostyla rufogaster*; e, *Cyclophorus reevei*; f, *Cyclophorus appendiculatus*; g, *Macrochlamys* sp.; h, *Chloraea dryope*. Scale bar = 10 mm.

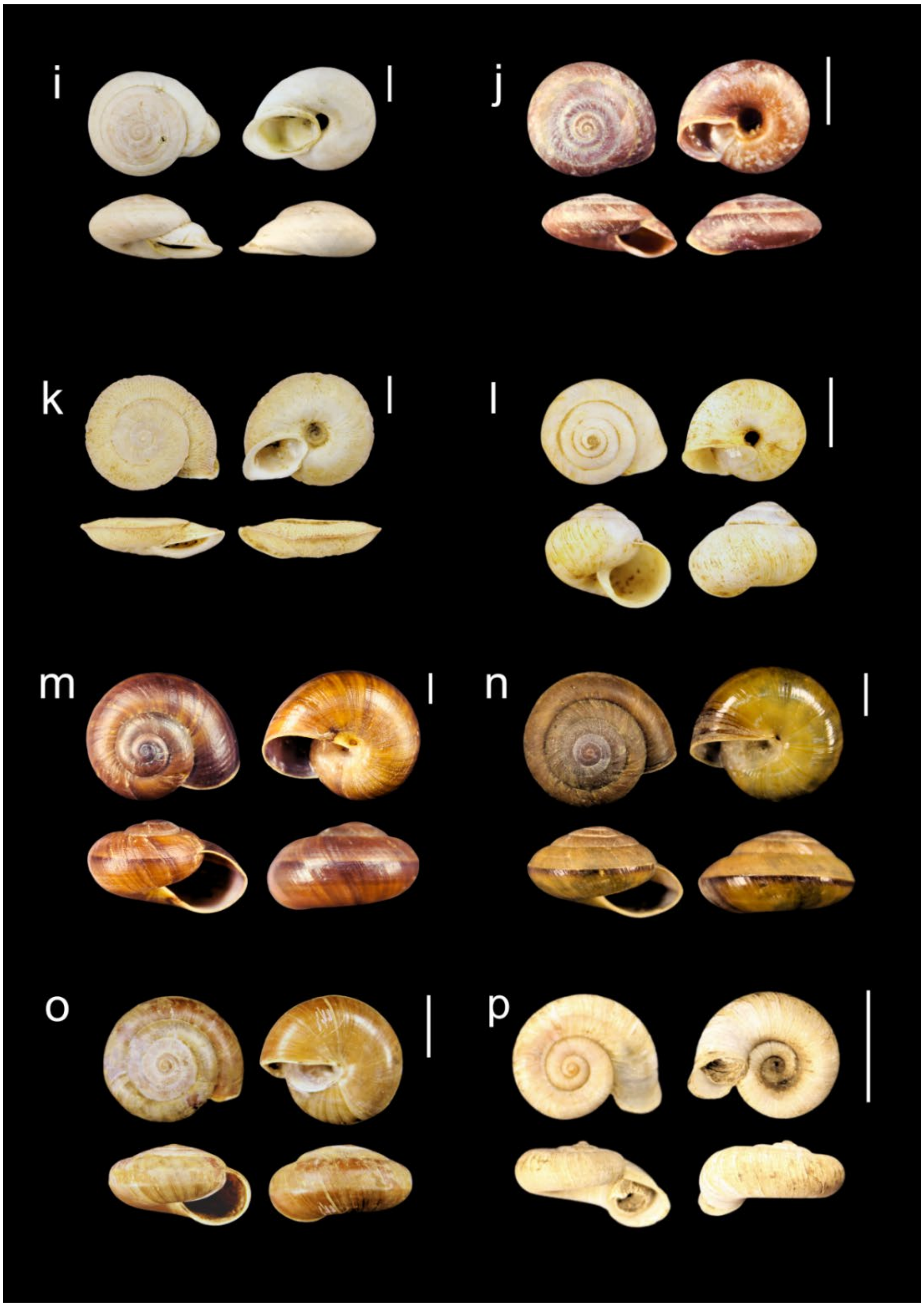

Fig. 3i–p. Land snails of Biak-Na-Bato National Park: i, *Obba marmorata*; j, *Obba morongensis*; k, *Obba bulacanensis*; l, *Bradybaena similaris*; m, *Lamarckiella nigrescens*; n, *Hemiglypta fulvida semiglobossa*; o, *Hemitrichiella* sp.; p, *Platyraphe anthopoma*. Scale bar = 10 mm.

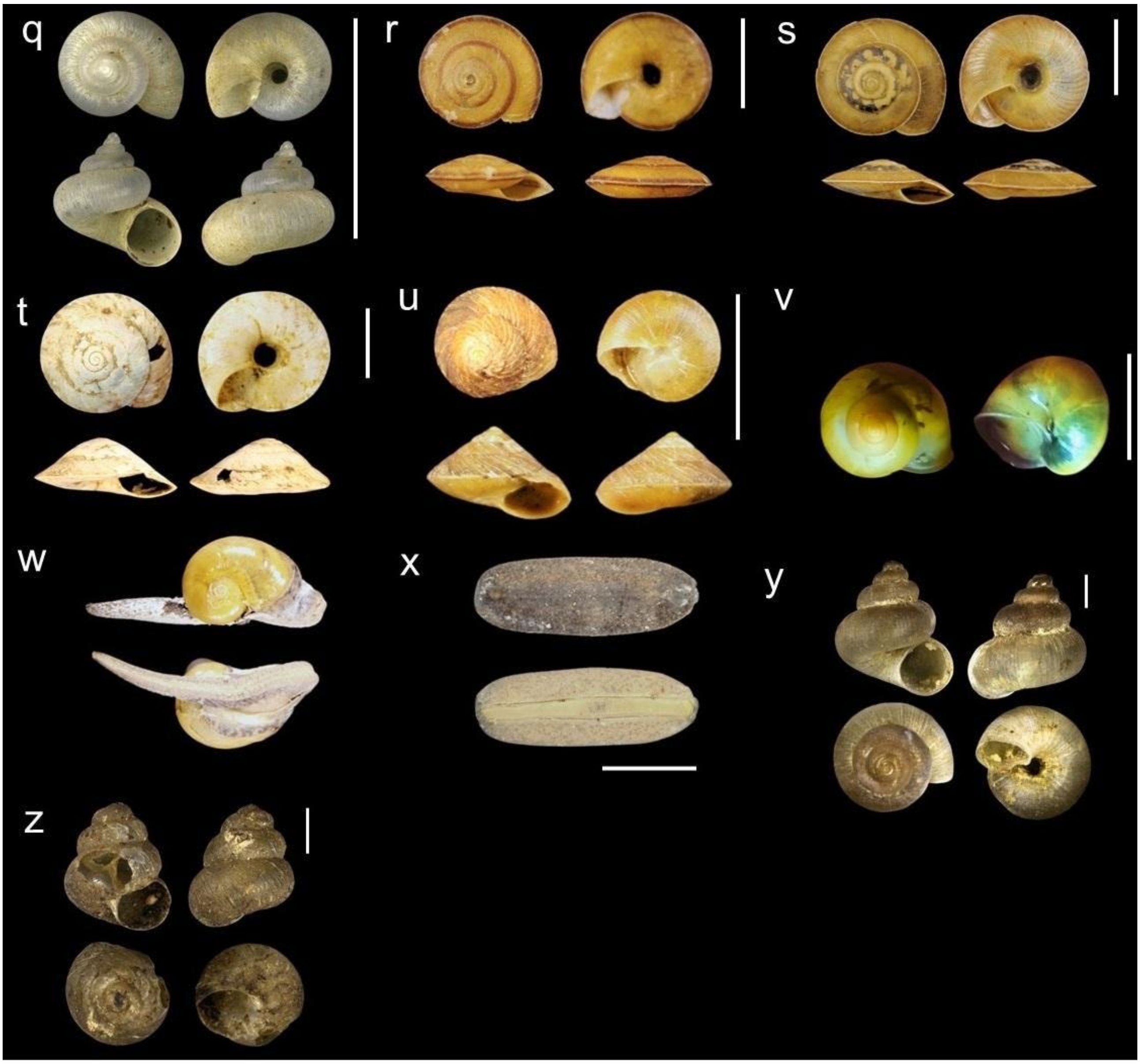

Fig. 3q–x. Land snails of Biak-Na-Bato National Park: q, *Platyraphe* sp.; r, *Videna crassula*; s, *Videna sibuyanica*; t, *Trochomorpha* sp.; u, *Geophorus pseudomphalus*; v, *Leptopoma* sp.; w, *Helicarion* sp.; x, *Laevicaulis alte.* Scale bar = 10 mm. y, *Acmella polita*; z, *Acmella* mp.1. Scale bar = 0.1 mm.

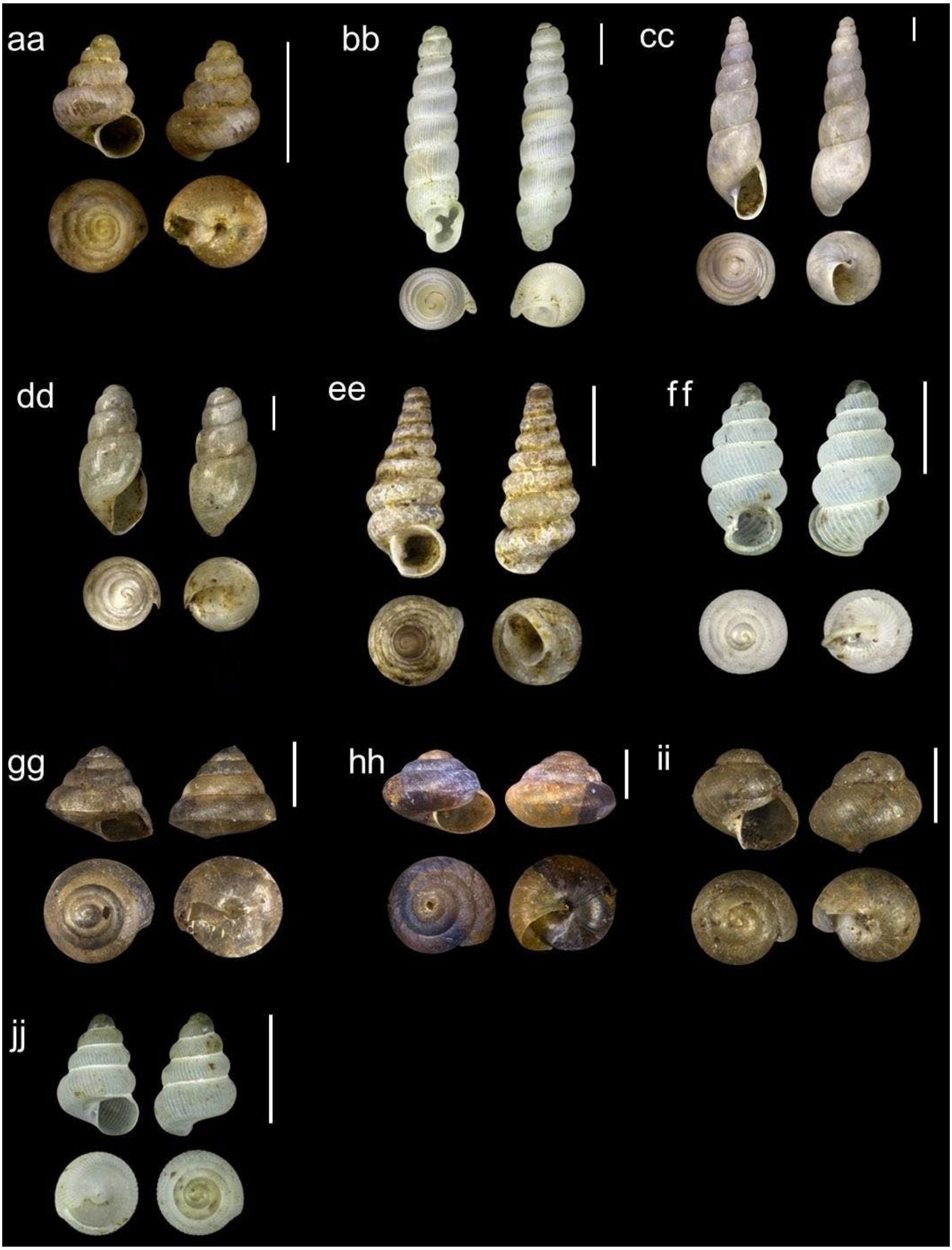

Fig. 3aa–jj. Land snails of Biak-Na-Bato National Park: aa, *Acmella* mp.2; bb, *Diaphera hidalgoi hidalgoi*; cc, *Allopeas gracile*; dd, *Allopeas clavulinum*; ee, *Diplommatina megaloptyx*; ff, *Diplommatina boettgeri accedens*; gg, *Kaliella micropetasus*; hh, *Kaliella* mp.1; ii, *Kaliella* mp.2; jj, *Palaina quadrasi*; kk, *Lamprocystis crystallina*; ll, *Microcystina* mp.1; mm, *Microcystina* mp.2; nn, *Omphalotropis columellaris*; oo, *Gastrocopta* sp.; pp, *Japonia* sp. Scale bar = 0.1 mm.

Fig. 3kk-pp. Land snails of Biak-Na-Bato National Park: kk, *Lamprocystis crystallina*; ll, *Microcystina* mp.1; mm; *Microcystina* mp.2; nn, *Omphalotropis columellaris*; oo, *Gastrocopta* sp.; pp, *Japonia* sp. Scale bar = 0.1 m.

Fig. 4. Live macro land snails in Biak-Na-Bato National Park: a, *Lissachatina fulica*; b, *Orthostylus metaformis*; c, *Helicostyla woodiana*; d, *Cyclophorus appendiculatus*; e, *Cyclophorus reevei*; f, *Macrochlamys* sp.; g, *Chloraea dryope*; h, *Lamarkiella nigrescens*; i, *Platyraphe anthopoma;* j, *Videna sibuyanica*; k, Hammerhead flatworm feeding on *V. sibuyanica*; l, *Geophorus pseudomphalus*; m, *Leptopoma* sp.; n, *Helicarion* sp.; o, *Laevicaulis alte.*

Overall, Aguinaldo had the highest species diversity (AG, qD = 12) with 313 individuals belonging to 23 species (Fig. 5a). This is followed by Santol (ST, qD = 9) with 196 individuals belonging to 18 species and Cuarto-Cuarto (CC, qD = 8) with 166 individuals belonging to 17 species. However, Bahay Paniki had the lowest species diversity (BP, qD = 5) with 1000 individuals belonging to 27 species. Rarefaction and extrapolation curves did not plateau while sample coverage in each cave were high (0.98, 0.97, 0.96, 0.99) but did not approach the value of 1.00 (Fig. 5b, 5c).

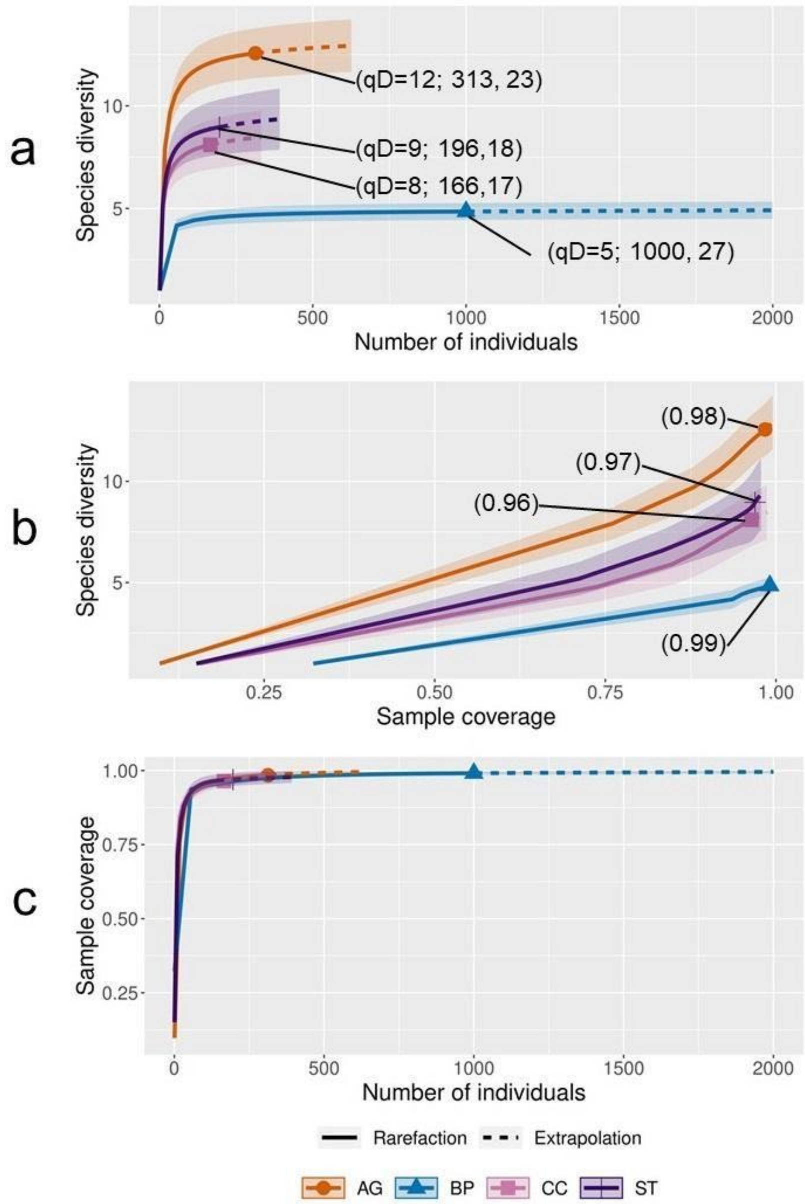

Fig. 5. Diversity in each cave in the Biak-Na-Bato National Park represented in rarefaction and extrapolation (RE) sampling curves based on a) sample size and b) coverage with c) completeness of sampling. Symbols denote the end point of the respective datasets. Solid lines show the rarefaction curves, while broken lines represent the extrapolation. Hill numbers (of the order q = 1) are represented in parentheses, while shadows on each curve represent the 95% confidence interval generated from 1000 bootstrap replicates. AG – Aguinaldo, BP – Bahay Paniki, CC – Cuarto-Cuarto, ST – Santol.

Six of 17 species recorded by Faustino (1930) in Bulacan were identified in BNBNP. These were *Videna crassula*, *Obba bulacanensis*, *Diplommatina megaloptyx*, *Diaphera hidalgoi hidalgoi*, *Geophorus pseudomphalus*, and *Platyraphe anthopoma*. The remaining 11 that were not observed in BNBNP were *Vitrinula carinaria*, *Coneuplecta convexospira*, *Coneuplecta costulata, Macroceras fasciata*, *Lamprocystis leucodiscus*, *Pseudohelicarion subcarinatus*, *Chloraea caerulea*, *Helicostyla boettgeriana*, *Orthostylus metaformis rusticus*, *Helicostyla juglans solai*, and

Gastrocopta servilis. However, due to outdated and limited data on their conchology and distribution, identification of their presence in the sampled specimens was limited. Of the 42 land snail species observed, 36 represent possible new records compared to the list of Faustino (1930). Thus, the documented lands snails in Bulacan increased by 211.76% from 17 to 53 species.

Land Snail Community Assemblages

Two-way PERMANOVA showed that there was no significant difference in community assemblage during dry and wet seasons (F = 0.97, $p = 0.2994$) while significant difference was observed between sites (F = 3.11, $p = 0.0001$). One-way PERMANOVA revealed moderate variation in assemblages across sampling sites (Table 3). In pairwise analysis, Bahay Paniki conveyed significant difference in community assemblage compared to Santol, Cuarto-Cuarto and Aguinaldo. Specifically, Bahay Paniki and Santol showed the highest separation.

Table 3. One-way permutational analysis of variance test for significant differences between sampling sites in Biak-Na-Bato National Park

Site	F	*p*	Total quadrats (n)
Overall	3.40	0.0001***	32
Pairwise			
BP, ST	6.72	0.0006***	10, 10
BP, CC	4.11	0.0054**	10, 6
BP, AG	5.30	0.003**	10, 6
ST, CC	2.01	0.3396	10, 6
ST, AG	1.34	1	10, 6
CC, AG	1.64	0.8586	10, 6

Significance: *** $p < 0.001$, ** $p < 0.01$; ST, Santol; BP, Bahay Paniki; CC, Cuarto-Cuarto; AG, Aguinaldo.

The NMDS ordination of four caves exhibited differences in species composition (Fig. 6). The three dimension stress value of 0.1293 (> 0.1) indicated potentially useful representation. The computed value is interpretable, but higher values within this range may compromise accuracy. Across all sites, samples from Bahay Paniki were separated in the multidimensional space compared to overlapped Santol, Aguinaldo, and Cuarto-Cuarto.This implies that species composition in Bahay Paniki is relatively distinct from the other caves. Santol, Cuarto-Cuarto, and Aguinaldo, on the other hand, showed overlapping samples and relatively similar centroids which suggest more related community compositions. Moreover, samples of Aguinaldo are highly dispersed, suggesting more divergent assemblage.

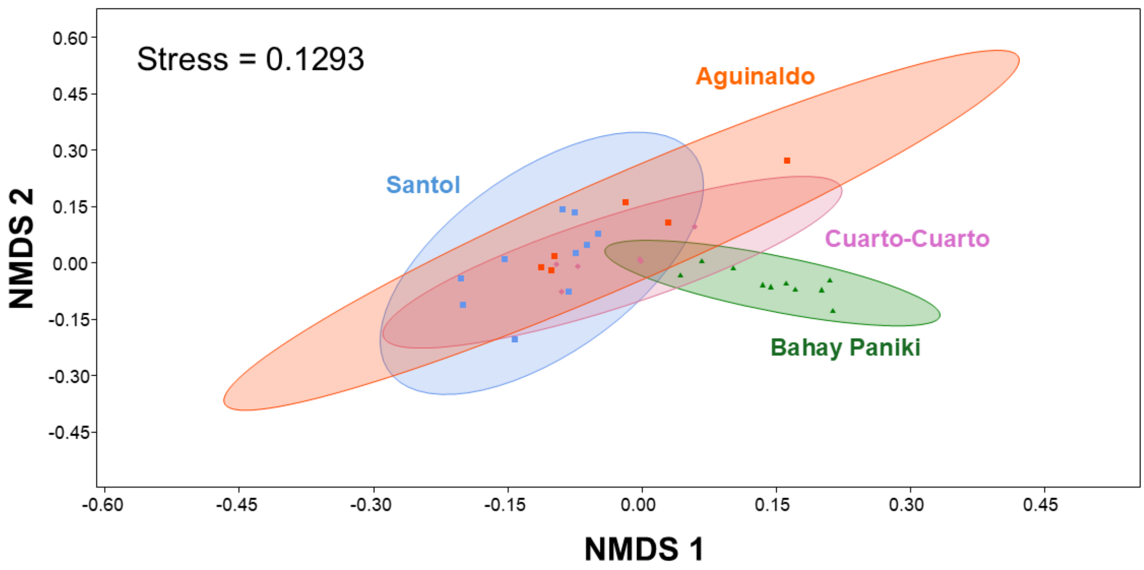

Fig. 6. Non-metric multidimensional scaling plot using Bray-Curtis similarity index of species abundance in sampling sites in Biak-Na-Bato National Park (n = 32).

SIMPER analysis discriminated the top ten land snails that showed most of the dissimilarity (Table 4). The overall dissimilarity of the sites was 69.82%, which indicate that the areas indeed harbor different terrestrial gastropod communities. In descending order, species with the highest percent contribution were *Cyclophorus appendiculatus* (34.03%), *Lamarkiella nigrescens* (13.78%), and *Orthostylus metaformis* (9.80%). These species, which explains 57% of total variation, were most abundant in Bahay Paniki.

Table 4. Similarity percentage analysis of the top ten land snail species contributing to community assemblage variation among sampling sites in the Biak-Na-Bato National Park

Species	Average dissimilarity	Contribution (%)	Cumulative (%)	Mean abundance			
				ST	BP	CC	AG
1. *Cyclophorus appendiculatus*	23.76	34.03	34.03	3	103	12	10
2. *Lamarkiella nigrescens*	9.62	13.78	47.81	5	38	13	7
3. *Orthostylus metaformis*	6.84	9.80	57.61	10	24	10	14
4. *Acmella polita*	6.44	9.23	66.83	9	2	8	14
5. *Hemiglypta fulvida semiglobosa*	5.23	7.49	74.32	0	19	4	0
6. *Diplommatina boettgeri accedens*	3.27	4.68	79	0	1	0	17
7. *Videna sibuyanica*	2.11	3.02	82.01	3	1	0	6
8. *Palaina quadrasi*	1.91	2.74	84.76	0	0	0	12
9. *Lamprocystis crystallina*	1.32	1.89	86.64	0	1	0	7
10. *Microcystina* mp. 1	1.23	1.78	88.43	1	1	1	5

ST, Santol; BP, Bahay Paniki; CC, Cuarto-Cuarto; AG, Aguinaldo.

The CCA ordination of species, environmental variables, and sites exhibited variation in community assemblage patterns (Fig. 7). The first two axes contributed to 65.29% of variation but there was no significant relationship observed ($p > 0.05$). Nevertheless, dominant environmental variables appeared to influence the distribution of land snail communities. Micro land snails including *Diplommatina megaloptyx*, *Omphalotropis columellaris*, *Diaphera hidalgoi hidalgoi*, *Acmella polita, Diplommatina boettgeri accedens, Acmella* mp. 1, *Kaliella* spp., *Allopeas* spp. *Microcystina* spp., *Lamcrocystis crystallina*, and *Palaina quadrasi* were potentially distributed in areas with relatively high temperature, soil pH, and soil calcium but low number of trees, tree diameter at breast height, and soil moisture, together with macro land snails *Videna sibuyanica*, *Obba marmorata* and *Lissachatina fulica*. Areas with wider tree diameter at breast height, high number of trees, and moist soil but with low temperature, soil pH and soil calcium, may harbor macro land snails *Macrochlamys* sp., *Geophorus pseudomphalus*, *Cyclophorus appendiculatus, Hemiglyptafulvida semiglobossa*, *Obba morongensis*, and slug *Laevicaulis alte* as well as micro land snails *Japonia* sp., *Acmella* mp. 2, and *Gastrocopta* sp. In addition, macro land snails, *Bradybaena similaris*, *Obba bulacanensis*, *Helicostyla woodiana*, *Chloraea dryope*, *Cyclophorus reevei*, and *Orthostylus metaformis* were associated to areas with high temperature and low number of trees, tree diameter at breast height, and soil moisture. Furthermore, species near the origin including *Lamarkiella nigrescens*, *Videna crassula*, *Helicarion* sp. and *Platyraphe anthopoma* were broadly distributed which suggest poor association to environmental variables.

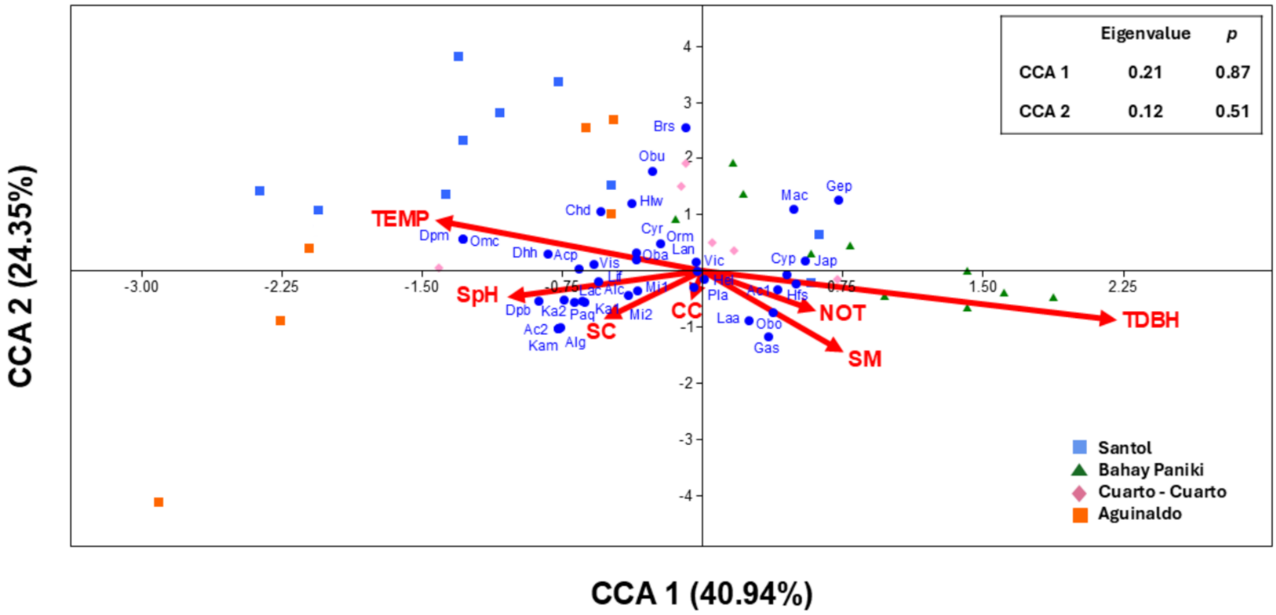

Fig. 7. Canonical correspondence analysis of land snail species and environmental variables of sampling sites in Biak-Na-Bato National Park ($n = 32$). Biplot represents land snails (blue letters and points), continuous environmental variables (vectors), and sites (legends). ALT, Altitude, TEMP, Temperature; CC, Canopy cover; LLD, Leaf litter depth; TDBH, Tree diameter at breast height; SM, Soil moisture; SpH, Soil pH; SCA, Soil calcium.

Sampling sites also showed variation based on environmental variables. Bahay Paniki had habitats with high number of trees, tree diameter at breast heigh, soil moisture and low temperature, soil pH, and soil calcium. Aguinaldo and Santol, on the other hand, have areas with high temperature, soil pH, and soil calcium and low number of trees, tree diameter at breast height, and soil moisture. Moreover, sampling sites of Cuarto-Cuarto were dispersed and less associated to dominant environmental factors.

GLMM identified optimal models that affect species richness and abundance (Table 5). Forspecies richness, soil pH emerged as the most parsimonious model (ΔAICc = 0.00, wAICc = 0.53). In terms of abundance, four strongly supported models with ΔAICc values below two were revealed. Among these, the combination of canopy cover, number of trees, soil moisture, soil pH, and temperature was the most significant model ($\Delta AIC_c = 0.00$, $wAIC_c = 0.36$). Although none of the environmental variables showed statistically significant effects ($p > 0.05$), several predictors exhibited high relative importance values (Table 6). For species richness, soil pH had a positive relationship and a moderate relative importance value (E = 1.02, RI = 0.53). For abundance, the number of trees, soil moisture, and soil pH all had the highest relative importance, with the first two positively associated with the parameter (E = 4.75, 6.01, -20.71; RI = 1). This is followed by temperature (E = -0.50; RI = 0.70) and canopy cover (E = 0.72; RI = 0.51).

Table 5. Summary statistics of model averaging for species richness and abundance of land snail across the study sites in Biak-Na-Bato National Park

Model component*	*k*	AIC_c	ΔAIC_c	$wAIC_c$
Species richness				
SpH	1	167.03	0.00	0.53
Abundance				
CC, NOT, SM, SpH, TEMP	5	317.67	0.00	0.36
NOT, SM, SpH, TEMP	4	317.79	0.12	0.34
CC, NOT, SM, SpH	4	319.34	1.67	0.16
NOT, SM, SpH	3	319.47	1.79	0.15

*Models are ranked based on Akaike's information criterion corrected for small sample size (AIC_c) where AIC_c weights ($wAIC_c$) < 0.10 are excluded; *k*, number of parameters; CC, canopy cover; NOT, number of trees; SM, soil moisture; SN, season; SpH, soil pH; TEMP, temperature.

Table 6. Generalized linear mixed model testing each environmental variables on the species richness and abundance of land snails across the study sites in Biak-Na-Bato National Park

Parameter	Estimate (E)*	SE	*p*	Relative importance (RI)
Species richness				
Intercept	3.96	6.23	0.54	
Soil pH	1.02	1.01	0.56	0.53
Abundance				
Intercept	102.89	194.30	0.61	
Canopy cover	0.72	1.67	0.68	0.51
Number of trees	4.75	4.20	0.28	1.00
Soil moisture	6.01	3.95	0.15	1.00
Soil pH	-20.71	18.44	0.29	1.00
Temperature	-0.50	4.37	0.91	0.70

*effect sizes have been standardized on two SD following Gelman (2008).

DISCUSSION

Malacofaunal Diversity in BNBNP

BNBNP (42 species and 14 families) is comparable to the karsts in Sta Teresita, Cagayan (45 species and 17 families), and Masungi Georeserve, Rizal (45 species and 12 families) (Valdez et al. 2021; Parcon et al. 2021). It also exhibits higher diversity in some karst-rich locations such as Batanes Group of Islands (38 species and 19 families),Pamitinan Protected Landscape, Rizal (29 species and 9 families) and primarily in non-karst areas of southern Luzon such as Mt. Makiling (24 species from 9 families) and Mt. Banahaw (34 species and 9 families) as well as in Leyte in eastern Visayas (22 species and 5 families) (de Chavez and de Lara 2011; Agudo 2017; Mendoza 2017; Uy et al. 2018; Pogado et al. 2022; Perez et al. 2023; Batomalaque et al. 2025). However, differences in species richness and diversity may partly reflect variation in sampling protocols (e.g., quadrat number, size, or placement) rather than true ecological differences. Richness comparisons should be interpreted cautiously unless sampling effort is standardized or adjusted statistically. These data nevertheless suggest karsts as malacofauna-rich areas compared to non-karstic forest ecosystems (Valdez et al. 2021).

Site-level Diversity and Assemblage Patterns

Aguinaldo exhibited the highest diversity regardless of its proximity to human settlements and man-made infrastructures despite ranking second in terms of species richness and abundance. This can be due to even distribution of species, particularly the abundance of micro land snails as 13 out of 19 species sampled were observed in the area. Extremely small land snails may have specialized in ecological niches such as limestone outcrops, crevices, and walls as well as soil detritus found in Aguinaldo. However, future malacofaunal studies should explore possible influence of anthropogenic disturbances including ecotourism activities and human encroachment on the diversity of land snails as well as other wildlife in BNBNP. On the contrary, Bahay Paniki showed the lowest diversity but highest species richness and abundance which can be due to the presence of dominant species such as *Cyclophorus appendiculatus*, *Lamarckiella nigrescens*, and *Orthostylus metaformis*. There were 513 and 189 individuals of *C. appendiculatus* and *L. nigrescens* observed in Bahay Paniki which were significantly greater than the combined counts in other cave areas. Meanwhile, 119 individuals of *O. metaformis* were sampled. Proliferation and distribution of these species can be attributed to their shell morphology and habitat preference adapted for various external conditions (Shen et al. 2025). *Cyclophorus appediculatus* has a thick discoidal shell and operculum that protects its soft and moist body from desiccation. Relatively, *L. nigrescens* has a large, thick, non-operculated shell adapted in humid tropical forests. As grazers and detritus feeders, these characteristics may protect them from harsh conditions and terrestrial predators. On the contrary, *O. metaformis* is an arboreal snail with a dark-banded, bright shell. Its elevated habitat on leaf surface and tree bark enables it to bypass land predators while its banding pattern acts as camouflage. Across all sites, RE curves did not plateau while the sample coverage, despite having high values, did not approach the value of 1. These imply that increasing sampling effort is necessary to capture rare species and completely examine the diversity of land snails in BNBNP. Nevertheless, this provides a reliable estimate of malacofaunal diversity in the area.

Two-way PERMANOVA revealed that community assemblages only differed between sites and not during dry and wet seasons. However, the inclusion of empty shells may have partially obscured the impact of seasonal variation. Thus, it is suggested for future investigations to only include live land snails in examining differences in community compositions between the two sampling periods. In terms of differences in land snail assemblages between sites, NMDS supported by one-way PERMANOVA showed that species composition in Bahay Paniki is distinct as opposed to Santol, Cuarto-Cuarto, and Aguinaldo. SIMPER also denoted dominant species such as *C.appendiculatus* which was primarily abundant in the area. In karsts of northern Vietnam, it was revealed that competition among various *Cyclophorus* species shape community structures through ecological adaptations (Von Oheimb et al. 2018). Similarly, its high abundance in Bahay Paniki may have influenced interspecific interaction and its overall community composition. According to Clements et al. (2006), isolated karst landscapes such as caves and limestone outcrops usually restrict species gene flow especially in organisms with low mobility which will likely foster high levels of endemism. In addition, Khac and Binh (2024) suggest that microclimatic conditions such as temperature, humidity, and soil type can affect habitat preference of snail in cave areas. Relatively, Bahay Paniki exhibited the greatest spatial separation from the other caves. It also has distinct ecological features such as limestone outcrops, loose soil, and thick vegetation capable of altering microclimatic parameters. On the contrary, few and smaller outcrops and extensive limestone pavements were prevalent in Santol, Cuarto, Cuarto, and Aguinaldo.

Environmental Drivers of Assemblages

The results of CCA further supported the influence of environmental factors in distinct assemblages between sites. Most of micro land snails were distributed in Aguinaldo and Santol wherein habitats had higher temperature, soil pH, and soil calcium. Temperature is usually correlated with the mortality of land mollusk. As temperature increases, snails become prone to desiccation and death. However, studies reveal that related species exhibit adaptive physiological strategies and occupation of microclimate niches in response to extreme temperatures (Lucid et al. 2021). Hence, micro land snails in BNBNP despite being exposed to higher temperature possibly prefer microhabitats to regulate heat and moisture. These microecosystems include rock surfaces, limestone crevices, litter, and vegetation which were evident in karst areas (Hernández and Reyes-Tur 2017). In addition, anatomical structures such as operculum particularly in the most abundant micro snail, *Acmella polita*, may have contributed to temperature tolerance. According to Páll-Gergely et al. (2016), the operculum in terrestrial snails provides protection, prevents body-water loss, and improves respiration. Soil pH and soil calcium, on the contrary, are positively correlated to land snail viability particularly in micro land snails. This is observed by Uy et al. (2018), wherein soil pH and soil calcium significantly affect their assemblages. High pH level in soil increases the bioavailability of soil calcium as the latter is integral in egg and shell formation of terrestrial gastropods (Rygało-Galewska et al. 2023). Moreover, most micro land snails including endemic species are known to be exclusive in karst habitats with high levels of calcium (Lipae et al. 2020). The unique preference of micro land snails to ecological niches and minute conditions describes them as habitat specialists (Myšák et al. 2013).

Most of macro land snails had an affinity to areas with high number of trees, larger tree diameter at breast height, and moist soil that were most evident in Bahay Paniki. Old growth forests marked by mature trees provide extensive canopy cover and organic layer from woody debris which establish moist soil suitable for land snail communities (Kappes 2006). As documented by Athukorala et al. (2019), soil moisture is an integral determinant of density and richness of land snail in forest ecosystems. In the current study, large trees including the native Trea bean (*Parkia timoriana*) and forest floor covered by moderate loose soil were observed around the vicinity of Bahay Paniki. Moreover, large terrestrial mollusks are often associated in habitats that support their detritus feeding and arboreal lifestyle (Saeki et al. 2017). Unlike their micro counterparts, macro land snails are regarded as generalists due to their higher dispersal ability and tolerance to broader ecological conditions (Dahirel et al. 2014). For species that were poorly associated with environmental vectors, it is possible that either none or a combination of environmental factors influence their distribution and habitat preference across sampling sites.

Among all the dominant environmental factors, GLMM revealed that soil pH was the best predictor for species richness and combination of canopy cover, number of trees, soil moisture, soil pH, and temperature for abundance. Similar observations were reported by de Chavez and de Lara (2011) and Uy et al. (2018), wherein soil pH was the most plausible determinant of species richness due to its positive influence on soil calcium, a known key limiting factor of land snails. In karst landscapes, calcium availability promotes growth and reproduction of various land snails as opposed to non-karstic areas where low levels limit species richness (Nurinsiyah and Hausdorf 2020; Valdez et al. 2021). In addition, karst formations such as caves constitute localized ecosystems with stable calcium source (Meng and Fan 2022), making them foci and refugia of land snail diversity (Petrovová et al. 2024). On the other hand, canopy cover and number of trees go together in enhancing ecological continuity which creates essential microhabitats (*e.g.*, wood debris and litter) that ensure optimal habitat quality for land snail proliferation (Gheoca et al. 2021). Suitable microclimate (temperature and relative humidity) and habitat (soil pH and moisture) conditions as parameters of environmental health also increase land snail diversity (Martinez-De León et al. 2022; Esteves et al. 2025).

New Records, Invasisve Species, and Conservation Strategies

New species records increase the overall data in Bulacan province after 95 years since the study of Faustino (1930). However, these new discoveries noted the presence ofintroduced and invasive species that were not documented in the past which may be linked to current human disturbances in the BNBNP. This is consistent with Goh et al. (2025) who noted the presence of non-native species near anthropogenic structures and altered vegetation that are non-existent from historical records. Furthermore, interference of invasive and predatory hammerhead flatworms was also observed wherein its exclusive raptorial behavior against native land snails may pose an adverse ecological impact (Ducey 2007). Despite having a history of habitat degradation mainly due to mineral extraction, the national park still exhibited lower number of invasive species (5 species; 11.90%) which is less compared to Masungi Georeserve, Rizal (7 species: 15%) (Valdez et al. 2021). Thus, the malacofauna-rich status of BNBNP requires inclusive conservation strategies that include consistent malacological surveillance and local ecological knowledge-based assessments (Perez et al. 2024). Local awareness may also be strengthened through public exhibitions and dissemination of related materials. Moreover, it is recommended to conduct future malacofaunal studies in the areas covering non-tourism caves and distinct karst formations within BNBNP as well as other karst landscapes in the Philippines to further validate the findings of this study.

CONCLUSIONS

Biak-Na-Bato National Park (BNBNP) represents a significant reservoir of land snail diversity, with 42 species across 14 families recorded. This richness is comparable to, and in some cases exceeds, that of other karst and non-karst ecosystems in the Philippines. The park's complex karst geology, characterized by limestone outcrops, caves, and variable microhabitats, contributes to the high species diversity observed. Despite ongoing anthropogenic pressures, including illegal quarrying, habitat degradation, and the introduction of non-native species, the park continues to support a diverse malacofaunal community, including several endemic and potentially undescribed taxa. Community assemblages varied significantly between sites, driven primarily by environmental factors such as soil pH, calcium content, canopy cover, tree density, soil moisture, and temperature. Soil pH emerged as the strongest predictor of species richness, while a combination of edaphic and vegetation-related variables best explained species abundance. Micro land snails were associated with warmer, calcium-rich microhabitats, whereas macro species were more abundant in moist, forested areas with mature vegetation. Notably, Bahay Paniki cave exhibited a distinct assemblage structure, potentially shaped by dominant species, habitat specialization, and biotic interactions. These findings underscore the ecological importance of BNBNP as a karst biodiversity refuge and highlight the critical need for sustained conservation efforts. Future research should prioritize standardized sampling across karst and non-karst systems, investigation of species–environment relationships, and monitoring of invasive species and anthropogenic impacts. Conservation strategies must incorporate habitat protection, community engagement, and environmental education to safeguard the park's unique malacofaunal diversity.

List of abbreviations

AG, Aguinaldo cave.
BNBNP, Biak-Na-Bato National Park.
BP, Bahay Paniki cave.
CC, Cuarto-Cuarto cave.
CCA, Canonical correspondence analysis.
DENR, Department of Environment and Natural Resources.
EDTA, Ethylenediaminetetraacetic acid titration ammonium acetate.
GLMM, Generalized linear mixed modelling.
IC, Incidental collection.
NMDS, Non-metric multidimensional scaling.
PAMB, Protected Area Management Board.
PAST, Paleontological Statistics Software Package.

PERMANOVA, Permutational analysis of variance.
RE, Rarefaction and extrapolation.
ST, Santol cave.

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Authors' contributions: JJCC, MKMC, and ERCD conducted field work involving site inspection, ecological assessment, and specimen collection and identification. JJCC and MKMC processed soil samples and organized shell specimens. JJCC performed statistical analyses and wrote the manuscript. All authors were involved in revising, reading, and approving the final manuscript.

Competing interests: JJCC, MKMC, and ERCD declare that they have no competing interests.

Availability of data and materials: The original samples are deposited as voucher specimens of the Malacology Laboratory, Animal Biology Division, Institute of Biological Sciences, University of the Philippines Los Baños.

Consent for publication: Not applicable.

Ethics approval consent to participate: Acquisition of wildlife was approved and permitted by the PAMB-BNBNP and DENR Region III (Central Luzon) under wildlife gratuitous permit number: III-2024-012.

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