Rapid ecological assessment of land snails (Gastropoda) across a disturbance continuum in a southern Belize lowland rainforest

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ABSTRACT. A rapid ecological survey for land snails was conducted in September 2009 in a lowland rainforest in southern Belize, Central America. Systematic, opportunistic, and timed collection methodologies were used to sample land snails in six plots placed within three ecological forest community types distinguished by disturbance histories. Land snail richness (36 species) and diversity were high within the narrow elevation gradient sampled. Several species new to science can likely be recovered from the region since nearly half of the recovered taxa were unable to be assigned to a described species. The forest community types were characterized by distinct assemblages of land snails as assessed by Sørensen coefficient of community, percent similarity, and the interpretation of a nonmetric multidimensional scaling ordination (NMS). The environmental parameters of canopy cover, coarse woody debris, and shrub cover were significantly correlated with species richness, diversity, and the total number of snails collected. The analyses suggested that overall forest structure influenced the assemblages of land snails present in a given forest community.

RESUMEN. Un muestreo ecológico rápido de caracoles terrestres fue llevado a cabo en setiembre de 2009 en un bosque lluvioso en el sur de Belice, América Central. Una serie de metodologías que incluyen muestreo sistemático, oportunístico y de recolección temporal fueron usadas para registrar los caracoles terrestres en seis parcelas localizadas dentro de tres tipos de comunidades forestales que se distinguen por su historia de disturbios. La riqueza de caracoles terrestres (36 especies) y la diversidad fueron altas dentro del angosto gradiente de elevación que fue muestreado. Algunas especies nuevas para la ciencia pueden ser recuperadas de la región debido a que en casi la mitad de los taxones registrados fue imposible la asignación de una especie conocida. Los tipos de comunidades forestales fueron caracterizados por diferentes grupos de especies de caracoles terrestres de acuerdo con el coeficiente de comunidad de Sørensen, el porcentaje de similitud y la interpretación de una ordenación del tipo no métrico multidimensional de escala (NMS). Los parámetros ambientales de cobertura de dosel, material lignícola grueso y cobertura de arbustos estuvieron significativamente correlacionados con la riqueza y la diversidad de especies así como con el número total de caracoles terrestres recolectados. Los análisis sugieren que la estructura boscosa ejerce una influencia sobre los grupos de caracoles terrestres presentes en una comunidad boscosa dada.

KEY WORDS. biological monitoring, biodiversity, Mollusca ecology, Neotropics, tropical biology.

It is not clear if land snails follow the trend of decreasing species richness with increasing latitude as has been documented for many other groups of organisms. It has been suggested that tropical land snail fauna are less abundant and diverse when compared to temperate regions (Solem 1982); however, others have found rather diverse land snail faunas in tropical areas (Emberton 1995). High land snail species richness may be masked by an apparently low abundance of individuals within a given tropical habitat (de Winter & Gittenberger 1998). Regardless of the true global biogeographic patterns of land snails, it is certain that the diversity and ecology of these organisms are severely understudied in tropical ecosystems worldwide. This is particularly true in the Neotropics where it has been estimated that only approximately 35% of the land snail species have been discovered and formally described (Thompson 2011).

Snails carry out a variety of important roles in terrestrial ecosystems such as serving as food for other organisms (Robinson 1994), acting as vectors to disperse other organisms such as fungi (Caldwell 1993), nutrient cycling (Dallinger *et al.* 2001), and overall ecosystem functioning and health (Graveland *et al.* 1994). Snails have been documented to respond to environmental gradients (Tattersfield *et al.* 2001) and anthropogenic disturbance (Nekola 2003). As such, land snails may represent suitable model organisms to monitor forest health. Tropical ecosystems are threatened by a plethora of phenomenon such as forest fragmentation, unintended effects of pesticides and fungicides, and global climate change. Baseline data in these poorly understood forests are needed in order to understand basic ecological patterns and requirements in order to make informed management decisions.

MATERIAL AND METHODS

The plots used in the current study were established in the Bladen Nature Reserve, Cockscomb Basin Wildlife Sanctuary, and the Belize Foundation for Research and Environmental Education (BFREE) in the Toledo District of southern Belize, Central America. Three ecological forest communities (1) early successional [S1], (2) intermediate [S2], and (3) undisturbed [S3] were defined in the lowland broadleaf evergreen rain forest based on the elapsed time since canopy disturbance. These locations were chosen by the structure and composition of the forest with assistance from a local forestry contact who was acquainted with the disturbance history of the area. Two sites representative of each community were characterized by the establishment of a 20 x 50 m plot (for a total of six plots). The two S1 plots (S1[a]: 16° 33′ 21″ N, 88° 42″ 02″ W; S1b: 16° 33″ 20″ N 88° 42″ 17″ W) were highly disturbed by a combination of logging and Hurricane Iris in 2001 and represented "jungle" habitat characterized by a species rich, almost impenetrable understory and a canopy dominated by cohune palm (*Attalea cohune*) and *Cecropia* sp. The S2 plots (S2[a]: 16° 34′ 17″ N, 88° 42″ 29″ W; S2b: 16° 34″ 20″ N 88° 42″ 13″ W) had gone without substantial canopy disturbance for approximately 50 to 100 years and were characterized by a fairly open understory dominated by give and take palm (*Chrysophila argentea*), bayleaf palm (*Sabal mauritiiformis*), and cohune palm; whereas, the overstory was dominated by substantial breadnut (Brosimum alicastrum), sapodilla (*Manikara zapota*), and bullhoff (*Drypetes brownii*) trees. The S3 plots (S3[a]: 16° 33′ 38″ N, 88° 42′ 44″ W; S3b: 16° 33′ 26″ N 88° 42′ 47″W) had escaped any significant canopy damage for approximately 150 years and were characterized by an understory consisting chiefly of cohune palm and an overstory dominated by large ironwood (*Dialium guianense*), breadnut, carbon tree (*Guarea grandifolia*), and jobillo (*Astronium graveolens*) trees.

A systematic grid of thirty points, each separated by five meters, was designated within each plot. Microsoft Excel was used to generate random numbers and the first ten non-repeating numbers between one and thirty represented the points within each plot from which samples were collected. Macro-snails (>5 mm) were identified and counted in the field. Micro-snails (<5 mm) were collected using 1 L cloth bags. Each bag was filled with 1 L of litter gathered from within a one meter radius surrounding each point (10 bags total). Four additional 1 L litterbags were filled opportunistically from areas within the plot that appeared most suitable for the occurrence of snails and a timed search (twenty person-minutes) was conducted for macro-snails. Snails were separated from the litter by soil sieves and hand-picked with the assistance of a magnifying head loop. The specimens were identified using the morphospecies concepts of Von Martens (1901), Dourson (2009), and Thompson (2011).

Percent canopy cover and aspect were recorded from the center and endpoints of each plot. The thickness of the leaf litter layer was measured and the Daubenmire cover class system (Daubenmire 1968) was used to quantify the cover attributed to leaf litter, bare ground, rock, coarse woody debris, bryophytes, shrubs, and herbs for each sample point.

Prior to analysis, the distribution and skewness of each parameter was evaluated with the JMP 6.0.2 statistical software package. A normal distribution curve was fit and the Shapiro-Wilk W test ($\alpha = 0.05$) was used to assess the goodness of fit to the normal distribution. Data that failed to approximate a normal distribution or that had an absolute skewness value greater than 1 was subjected to a monotonic transformation in order to decrease skewness and better approximate a normal distribution. Regression analysis was used to assess the response of species richness, number of collections, and Shannon-Wiener diversity to the environmental variables. A least-squares regression line and a 0.95 density ellipse was calculated for each regression. The degree of the correlations was assessed by examining the Pearson product-moment correlation coefficient (r).

The Shannon-Wiener diversity index (Shannon and Weaver 1949) and the Simpson diversity index (Simpson 1949) expressed as 1-D were used to assess alpha diversity. The Sørensen coefficient of community (Sørensen 1948) and percentage similarity (Gauch 1982) were calculated to evaluate the degree of similarity among the assemblages recorded from the forest community types. The Chao1 estimator was used to assess the completeness of survey by utilizing the multinomial model for the prediction platform in the program SPADE (Chao & Shen 2003) to calculate the maximum number of expected species and then dividing the number of recovered species by the calculated expected number of species.

A nonmetric multidimensional scaling ordination (NMS) was conducted with the slow and thorough autopilot mode of PC-ORD utilizing squared Euclidean distance (250 runs with real data and 250 runs with randomized data) and the Monte Carlo test of significance. To reduce the "noise" associated with less common species, the ordination was run with only those species that accounted for more than 1% of the total individuals collected.

RESULTS

The sampling effort yielded 730 land snail specimens representing 36 species distributed among 35 genera (Table 1). Fourteen (39%) of the morphospecies could not be assigned to a known species and several likely represent species new to science. Collectively, *Cecilioides* sp. (106 collections), *Neocyclotus dysoni* (87 collections), and *Rectaxis* sp. (86 collections) were the most commonly recovered species accounting for 38% of the total collections. The remaining species each represented less than 10% of the total collections. The overall calculated Shannon-Wiener diversity (H') was 2.94. An examination of rank-abundance plots (Fig. 1), and both the Simpson and Shannon diversity indices indicated the highest diversity in the S1 communities and the lowest in the S3 (Table 2).

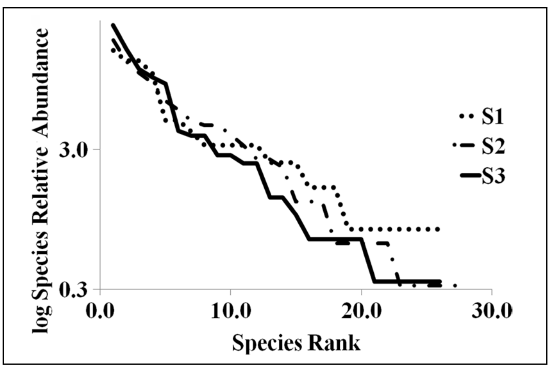

Figure 1. A rank/abundance "Whittaker Plot" for the land snail assemblages recovered among the three ecological forest community types. A greater slope angle indicates lower species diversity and evenness: S1 slope (-0.45), S2 slope (-0.50), S3 slope (-0.57).

Chao1 estimation of species richness indicated sufficient sampling of the S2 and S3 communities whereas, the S1 communities were estimated to be only 76% complete (Table 2). The number of land snails recovered from both the S2 and S3 communities was each more than twice the number recovered from the S1 communities. Calculations of percent similarity (PS) and Sørenson Coefficient of Community (CC) indicated the assemblages among the ecological forest community types were rather dissimilar (Table 3).

Only seven species were recorded from all six plots (Table 1). Four species, *Rectaxis* sp. (15%), *Cecilioides* sp. (13%), *Beckianum beckianum* (13%), and *Habroconus* sp. (11%) accounted for over half of the collections recovered from the highly disturbed S1 forest communities. *Cecilioides* sp. (18%), *Habroconus* sp. (13%), and *Xenodiscula taintori* (11%) were the dominant species recovered from the S2 forest communities, accounting for 42% of the collections. *Neocyclotus dysoni* (23%), Rectaxis sp. (16%), Cecilioides sp. (11%), and *Carychium* sp. (10%) were the dominant species, accounting for 60% of the collections, from the S3 forest communities.

The two S1 plots clustered close to one another in the NMS ordination as did the two S2 plots (Fig. 2). The S3 plots, however, were more variable and thus separated in ordination space. The ordination illustrates that there were characteristic assemblages of land snails associated with each of the ecological forest types. In addition, *Carychium* sp., *Chanonphalus pilsbryi, Miradiscops* sp., and *Neocyclotus dysoni* emerged as an ecological assemblage associated with increased shrub cover.

Table 4 provides the environmental variables measured for each of the forest community types. Species richness was found to be positively correlated with canopy cover (r=0.86, P=0.0265) (Fig. 3a). Whereas the number of individuals per plot were found to be positively correlated with canopy cover (r=0.94, P=0.0052) and elevation (approaching significance, r=0.79, P=0.0614) (Fig. 3b). The cover of coarse woody debris (r=-0.84, P=0.0358) and shrubs (r=-0.92, P=0.0095) were found to be negatively correlated with species diversity (Fig. 3c). Three species displayed notable differential patterns of dominance across the sampled disturbance continuum and may represent indicator species for each of these forest community types with Beckianum beckianum indicative of recent disturbance, *Neocyclotus dysoni* of intermediate time since disturbance and Xenodiscula taintori of a relatively undisturbed community (Fig. 4).

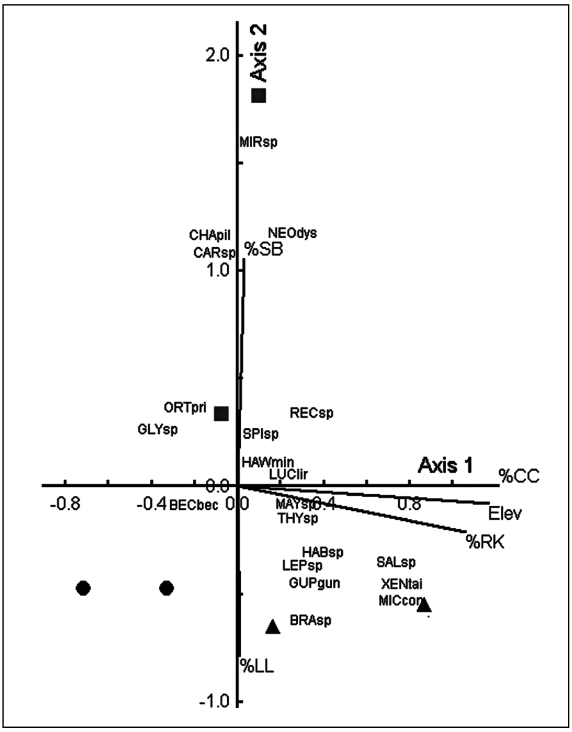

Figure 2. A NMS ordination of the twenty most abundant land snail species with a biplot indicating the degree and direction of the most substantial environmental variables. Note: Circles = S1 forest community plots, Triangles = S2 forest community plots, and Squares = S3 forest community plots. The full species name associated with the abbreviated name can be found in Table 1.

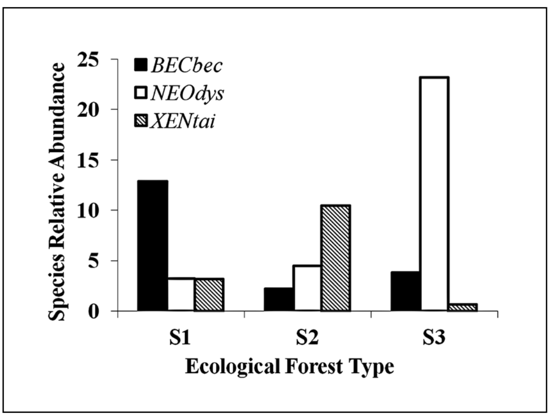

Figure 4. The relative abundance shifts for three "indicator" land snail species among the ecological forest communities.

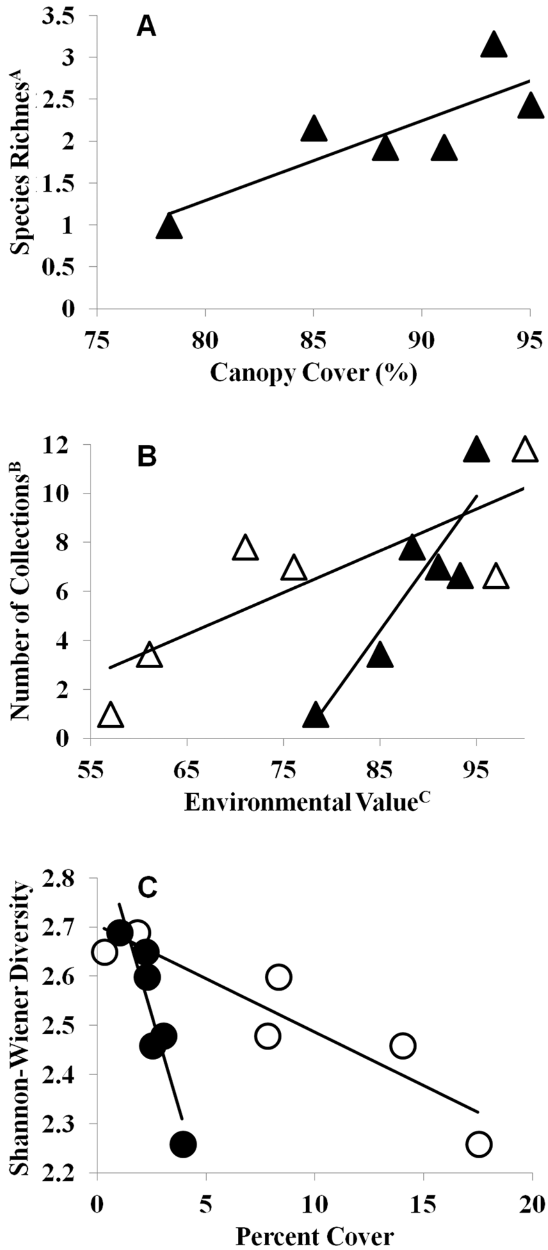

Figure 3. A comparison of the regression analyses of species richness, number of collections, and Shannon-Wiener diversity with respect to the statistically significant environmental variables. Filled triangles are canopy cover, open triangles are elevation, closed circles are course woody debris, and open circles are shrub cover. A species richness is reflected square root transformed, B number of collections is reflected square root transformed, C units for elevation is meters above sea level and percent cover for canopy cover.

DISCUSSION

The Shannon-Weiner species diversities (H' = 2.52-2.81) reported in the current study fall within the ranges reported from other studies in tropical areas. For example, Oroño *et al.* (2007) reported land snail diversities ranging from 1.08-3.13 in Argentina, Tattersfield *et al*. (2001) from 1.74-2.94 in Kenya, and Barker & Mayhill (1999) 1.55-4.77 from New Zealand. The greater degree of variation reported from other studies is likely a result of the wide range of elevations sampled in those studies. The current study examined only lowland rainforests with elevations ranging from 57-100 m. The overall structure of the land snail assemblages differed among the ecological forests settings (Fig. 1). The recently disturbed forest communities harbored a snail assemblage that approximated the "broken-stick" species abundance model. However, the community structure changed within the S2 and S3 forest communities more closely resembling the "log normal" species abundance model. The data suggested that as the forest community recovers following a disturbance event the snail assemblages become less even and less diverse. This pattern can be interpreted from figure 1, where species diversity and evenness decrease as the slope of the line increases.

It can be hypothesized that these changes could be associated with the structural changes and resulting environmental changes occurring in the forest community as it develops after a disturbance. The disturbance alters the forest structure and associated environmental parameters creating an opportunity for species which were originally excluded due to their ecological tolerances to attempt to establish a population. As a result, the greatest land snail diversity was observed with the colonization attempts for this open ecological space. However, as time passes species are competitively excluded and the assemblage becomes less diverse and evenness decreases (Fig. 1 & Table 2).

Three species *Beckianum beckianum, Xenodiscula taintori*, and *Neocyclotus dysoni* illustrate this pattern each showing a preference and reaching its greatest dominance within a different ecological forest setting (Fig. 4). *Beckianum beckianum* was characteristic of the recently disturbed forest communities and their associated environmental parameters. Whereas, X. *taintori* realized its greatest dominance in the intermediate disturbance setting and *N. dysoni* in the least disturbed communities.

Interpretation of the NMS ordination suggested a number of interesting trends (Fig. 2). The two recently disturbed S1 forest communities as well as the two S2 forest communities cluster together based on the assemblages of land snails suggesting that these ecological communities harbor characteristic land snail assemblages. This interpretation was further supported by the calculated CC and PS indices (Table 3). In contrast, the S3 forest communities did not form a close cluster suggesting the land snail assemblages associated with these older growth forests are more variable. Interestingly, the notable separation between the S3 forest communities can be attributed (in part) to the rather high coverage of shrubs in plot 6 ($S3^b$). This situation reinforces the probable importance of environmental parameters (associated with changes in forest structure) in organizing the land snail assemblage at a given location.

For example, *Carychium* sp., *Chanonphalus pilsbryi, Miradiscops* sp., and *Neocyclotus dysoni* emerge as an ecological group apparently associated with increased shrub cover (Fig. 2). Furthermore, the NMS ordination suggests that elevation and the amount of cover attributed to the canopy, leaf litter, and rocks may exert some influence in structuring terrestrial snail assemblages. *Brachypodella* sp., *Guppya gundlachi*, *Habroconus* sp., *Leptinaria* sp., appear to be associated with increased leaf litter coverage. Whereas, *Microceramus concisus*, *Salasiella* sp., and *Xenodiscula taintori* seem to prefer greater cover of canopy, rocks, and leaf litter. Beckianum beckianum appeared to show a preference for more highly disturbed communities (as mentioned above); in fact approximately half of the collections of this species were obtained from the S1 forest communities.

The negative correlation between shrub cover and snail diversity is somewhat puzzling and warrants further study. Pérez *et al*. (2004) reported a similar trend in Nicaragua where they found vegetation cover and species richness to be negatively correlated. However, in their study vegetation cover increased substantially with increasing elevation and they hypothesized that it was likely the cooler temperatures associated with the higher elevations and not the vegetation cover that depressed snail species richness at higher elevations. A temperature change with an increase in elevation is an unlikely factor in the current study where the elevational change was less than 50 m among the lowland sites.

Ceciliodes consobrinus, Neocyclotus dysoni, Leptinaria lamellata, and *Lucidella lirata* were the most commonly encountered species by Pérez et al. (2004) with the relative abundances of each species varying with respect to north versus south-facing slopes. Interestingly, *Cecilioides* sp., *Neocyclotus dysoni, Leptinaria* sp., and *Lucidella lirata* were among the most frequently recovered taxa (each occurring in at least five plots) in the current study. This may suggest that these taxa (and others *e.g., Habroconus* sp.) may represent members of a common faunal component of Neotropical forests. Furthermore, their absence in a survey could possibly be an indication of habitat degradation. *Xenodiscula taintori* has been commonly associated with well preserved habitats in highlands (Pérez *et al*. 2004), but was very common in the intermediately disturbed plots of the lowland forests sampled in the current study. This situation warrants further study.

The current study indicates that a rapid ecological assessment for land snails can be conducted to obtain useful baseline data. Such a survey can be used to assess ecological patterns occurring within and among different ecological settings or across the landscape. The data collected in such a survey can then be used as a starting point to determine which environmental parameters as well as the landscape units (*e.g.*, forest communities defined by disturbance, elevation gradients, underlying geology, annual precipitation etc.) warrant detailed examination. This type of preliminary data should be used to assist natural resource managers in making informed decisions with respect to implementing appropriate monitoring programs that maximize effectiveness and results while minimizing costs.

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Table 1. The thirty-six recovered land snail species ranked by total (all plots pooled) relative abundance. Abbreviations: Abb = species name abbreviation, RA = species relative abundance, T RA= total relative abundance and Np = the number of plots a particular species occurred.

Species	Abb	S1RA	S2 RA	S3 RA	T RA	Np
Cecilioides sp. (A. Ferussac 1814)	CECsp	12.9	18.2	11.3	14.5	6
Neocyclotus dysoni (Pfeiffer 1849)	NEOdys	4.0	4.5	23.2	11.9	5
Rectaxis sp. (Baker 1926)	RECsp	15.3	6.7	15.7	11.8	6
Lucidella lirata (Pfeiffer 1847)	LUClir	3.2	8.9	8.9	7.9	6
Habroconus sp. (Fischer & Crosse 1872)	HABsp	10.5	12.8	1.4	7.8	6
Xenodiscula taintori (Goodrich & Van der Schalie 1973)	XENtai	3.2	10.5	0.7	5.3	4
Beckianum beckianum (Pfeiffer 1846)	BECbec	12.9	2.2	3.8	4.7	6
Carychium sp. (O.F. Muller 1774)	CARsp	2.4	0.0	9.9	4.4	3
Guppya gundlachi (Pfeiffer 1846)	GUPgun	4.8	5.8	0.7	3.6	6
Thysanophora sp. (Strebel & Pfeffer 1880)	THYsp	1.6	4.8	2.4	3.3	5
Volutaxis sp. (Strebel & Pfeffer 1882)	VOLsp	1.6	2.6	2.7	2.5	5
Miradiscops sp.B (Baker 1925)	MIRspB	4.8	0.0	3.8	2.3	3
Orthalicus princeps (Broderip 1833)	ORTpri	1.6	0.6	4.1	2.2	5
Salasiella sp. (Strebel 1877)	SALsp	0.0	4.5	0.7	2.2	4
Leptinaria sp. (Beck 1839)	LEPsp	2.4	3.2	0.3	1.9	5
Hawaiia miniscula (A. Binney 1840)	HAWmin	3.2	1.3	1.4	1.6	6
Microceramus concisus (Morelet 1849)	MICcon	0.0	3.8		0.0	1.6
Chanomphalus pilsbryi (H.B. Baker 1927)	CHApil	2.4	0.0	2.4	1.4	2
Brachypodella speluncae (Morelet 1852)	BRAspe	0.0	2.9	0.0	1.2	2
Miradiscops sp.A (Baker 1925)	MIRsp	0.8	0.0	2.7	1.2	2
Helicina amoena (Pfeiffer 1849)	HELamo	3.2	0.0	0.7	0.8	3
Lamellaxis sp. (Strebel & Pfeffer 1882)	LAMsp	0.8	1.3	0.3	0.8	4
Streptostyla sp. (Shuttleworth 1852)	STRsp	4.0	0.0	0.3	0.8	3
Bulimulus unicolor (Sowerby 1833)	BULuni	0.8	0.0	1.0	0.5	2
Helicina arenicola (Morelet 1849)	HELare	0.0	1.3	0.0	0.5	2
Punctum sp. (Morse 1864)	PUNsp	0.8	0.6	0.3	0.5	3
Thysanophora plagioptycha (Shuttleworth 1854)	THYpla	0.8	0.6	0.3	0.5	3
Sterkia eyriesii (Drouet 1859)	STEeyr	0.0	1.0	0.0	0.4	2
Chondropoma rubicundum (Morelet 1849)	CHOrub	0.0	0.6	0.0	0.3	1

Continuation Table 1

Species	Abb	S1RA	S2 RA	S3 RA	T RA	Np
Euglandina ghiesbreghti (Pfeiffer 1846)	EUGghi	0.8	0.3	0.0	0.3	2
Gastrocopta pentodon (Say 1822)	GASpen	0.0	0.0	0.7	0.3	1
Drymaeus sulfureus (Pfeiffer 1856)	DRYsul	0.8	0.0	0.0	0.1	1
Helicina oweniana (Pfeiffer 1849)	HELowe	0.0	0.3	0.0	0.1	1
Pyrgodomus microdinus (Morelet 1851)	PYRmic	0.0	0.3	0.0	0.1	1
Trichodiscina coactiliata (Fèrussac 1838)	TRIcoa	0.0	0.0	0.3	0.1	1
Unknown sp.	UNK	0.0	0.3	0.0	0.1	1

Table 2. The diversity statistics for the land snail assemblages recovered from three different forest community types.

	S1	S2	S3	Total
Number of Collections	124	313	293	730
Species Richness	25	26	26	36
Predicted Richness	33	29	29	43
Survey Completeness (%)	76	90	90	84
Shannon Diversity	2.81	2.73	2.52	2.93
Shannon Evenness	0.86	0.84	0.77	0.81
Simpson Diversity	0.93	0.91	0.89	0.93

Table 3. Calculated measures of community similarity between the assemblages of land snails collected from three forest community types. Percent similarity is given in the upper right and Sørensen's coefficient of community in the lower left.

	S1	S2	S3
S1	***	56.8	58.3
S2	0.65	***	45.2
S3	0.88	0.65	***

Table 4. The average values obtained for environmental variables assessed for each forest community type. Note: COM = community type, CC = leaf litter, BG = bare ground, RK = rock, CWD = coarse woody debris, BP = bryophytes, SB = shrub, HB = herbaceous, LD = litter depth, and ELEV = elevation.

COM	CC (%)	LL (%)	BG (%)	RK (%)	CWD (%)	BP (%)	SB (%)	HB (%)	LD (cm)	ELEV (m)
S1	81.7	57.6	30.1	0.0	29.1	7.9	4.0	8.9	0.5	59
S2	94.2	78.4	12.0	10.1	23.4	6.0	5.0	5.6	1.7	98
S3	89.7	49.3	23.9	0.8	31.1	5.1	15.8	5.4	1.3	74