



Altitudinal variation of diversity in landsnail communities from Maderas Volcano, Ometepe Island, Nicaragua

Variación altitudinal de la diversidad en comunidades de gasterópodos del Volcán Maderas, Isla de Ometepe, Nicaragua

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Recibido el 3-X-2003. Aceptado el 16-II-2004

ABSTRACT

In the present paper we investigated the altitudinal variation of diversity in the landsnail communities of the Maderas Volcano; it is located on the eastern side of Ometepe island, Rivas Department, Nicaragua, and has a height of 1350 m. Two transects were made: one on the north slope (Balgüe) and another on the south slope (San Ramón); along these transects seven altitudinal collecting stations were established, beginning at lake level, each one with a difference of 200 m in altitude, the following profile was obtained: I. 0-200 m asl, II. 200-400, III. 400-600, IV. 600-800, V. 800-1000, VI. 1000-1200, VII. 1200-1400. For analyzing altitudinal diversity we studied species composition in each altitudinal station and calculated Beta diversity by means of β_i , β_r , β_c and β_w indexes of Magurran.

Within the framework of this project we collected 26 species distributed between 14 families and 22 genera, on both transects; this value of species richness may be considered high and constitutes 46.4 % of the total number of species collected on Ometepe island, which is 56. Beta diversity indexes values were as follows: $\beta_c=7.5$, $\beta_r=1.5$, $\beta_i=1.05$ and $\beta_w=2.82$ for Balgüe, and $\beta_c=6$, $\beta_r=1.6$, $\beta_i=1.04$ and $\beta_w=3.75$ for San Ramón. Considering these results, the southern slope transect may be regarded as more beta diverse than the northern one. A significant negative relationship between vegetation cover and species richness with altitude was found, since when vegetation cover increases, species richness decreases ($R_s=-0.96$, $p<0.01$ for Balgüe; $R_s=-0.92$, $p<0.01$, for San Ramón). Regarding substratum, species preferred very significantly loose soil with litter over other substratum types ($X^2=17.7$, $p<0.01$ for Balgüe; $X^2=19.44$, $p<0.01$, for San Ramón). Analyzing the altitudinal distribution of each species separately we were able to identify two faunas, one from "lowlands", and another from "highlands", separated by a transition zone ranging from 400 to 600 m asl., with an inflection point around 500 m asl. Thus, we propose a sampling strategy for medium altitude mountains (up to 1500 m asl) which consists of making two collecting stations only: one below 400 m asl and the other above 600 m. This strategy may allow us to document the core species of both faunas, without high expenses.

RESUMEN

En el presente trabajo investigamos la variación altitudinal de la diversidad en las comunidades de moluscos gasterópodos del Volcán Maderas; este se encuentra ubicado en la zona occidental de la Isla de Ometepe, Departamento de Rivas, y tiene una altura de 1350 m. Para el estudio altitudinal se hicieron dos transectos: uno en la vertiente norte

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(Balgüe) y otro en la sur (San Ramón); a lo largo de ellos se establecieron siete estaciones de recolecta cada 200 metros: I. 0-200 m snm, II. 200-400, III. 400-600, IV. 600-800, V. 800-1000, VI. 1000-1200, VII. 1200-1400. Para el análisis de la diversidad altitudinal se estudió la variación de la composición de especies en cada estrato altitudinal y además se calculó la beta diversidad mediante los índices β_c , β_i , β_r , y β_w , propuestos por Magurran.

En el marco de este trabajo se recolectaron un total de 26 especies distribuidas en 14 familias y 22 géneros en ambos transectos realizados en las vertientes sur y norte del volcán. Estos valores de riqueza de especies pueden considerarse altos y constituyen un 46,4 % del total de especies recolectadas en la isla que es de 56 especies. Los índices de Beta diversidad arrojaron un resultado final de $\beta_c= 7,5$, $\beta_r= 1,5$, $\beta_i= 1,05$ y $\beta_w= 2,82$, para Balgüe, mientras que $\beta_c= 6$, $\beta_r= 1,6$, $\beta_i= 1,04$ y $\beta_w= 3,75$ para San Ramón, siendo el transecto sur más beta diverso. Se encontró una relación negativa muy significativa entre la cobertura vegetal y la variación de la riqueza de especies con la altitud, ya que cuando aumenta la primera disminuye la segunda ($R_s= -0,96$, $p < 0,01$ en Balgüe; $R_s= -0,92$, $p < 0,01$, en San Ramón). En el caso del sustrato, las especies prefieren muy significativamente el suelo de tierra suelta con hojarasca ($X^2=17,7$, $p < 0,01$ en Balgüe; $X^2= 19,44$, $p < 0,01$, en San Ramón). Analizando la distribución altitudinal de cada una de las especies separadamente identificamos dos comunidades, una de Tierras Bajas y otra de Tierras Altas separadas por una zona de transición, lo cual nos permite proponer una estrategia de muestreo en montañas de mediana altitud (hasta unos 1500 m snm) consistente en la realización de dos estaciones de muestreo: una por debajo de los 400 m snm y otra por encima de los 600 m snm, lo cual nos permitiría documentar los núcleos básicos de especies de ambas comunidades, sin incurrir en gastos elevados.

KEY WORDS: Altitudinal diversity, gastropods, Ometepe, Nicaragua.

PALABRAS CLAVE: Diversidad altitudinal, gasterópodos, Ometepe, Nicaragua.

INTRODUCTION

There are few published studies concerning the assessment of diversity and its relation to altitude. In this sense the papers by KIKKAWA AND WILLIAMS (1971), on New Guinean birds, as well as TERBORGH' s (1977) on Andean birds, constitute very important contributions and are already classics. In Nicaragua, according to our data, the only previous reference we had is the paper by GILLESPIE AND PRIGGE (1997) on altitudinal zonation of vegetation, in Concepción Volcano, of Ometepe Island.

Other studies that deserve to be mentioned on biodiversity of Ometepe Island are the ones by GILLESPIE (1994, 1995), with an inventory of the flora and the vertebrate fauna, and the contribution by BONILLA AND ARANA (2001) on continental mollusks. Ometepe Island constitutes a very important spot since it is an island

within a continent, and might share characteristics of ocean islands (*vid.* MCARTHUR AND WILSON, 1967), as well as having some particular and distinctive ones of its own.

Regarding altitudinal diversity, BROWN AND GIBSON (1983) stated that the general pattern is that the number of species decreases when altitude increases, temperature being a limiting factor. Another interesting aspect of the relationship between temperature and altitude, was revealed by the results obtained by BURLA AND STAHEL (1983) who found significant differences in size among populations of *Arianta arbostorum* (Mollusca: Gastropoda) studied at different heights in the Swiss Alps; populations of lower altitudes were found to be smaller.

In the present paper we aimed at investigating the altitudinal distribution of gastropod communities in the Maderas

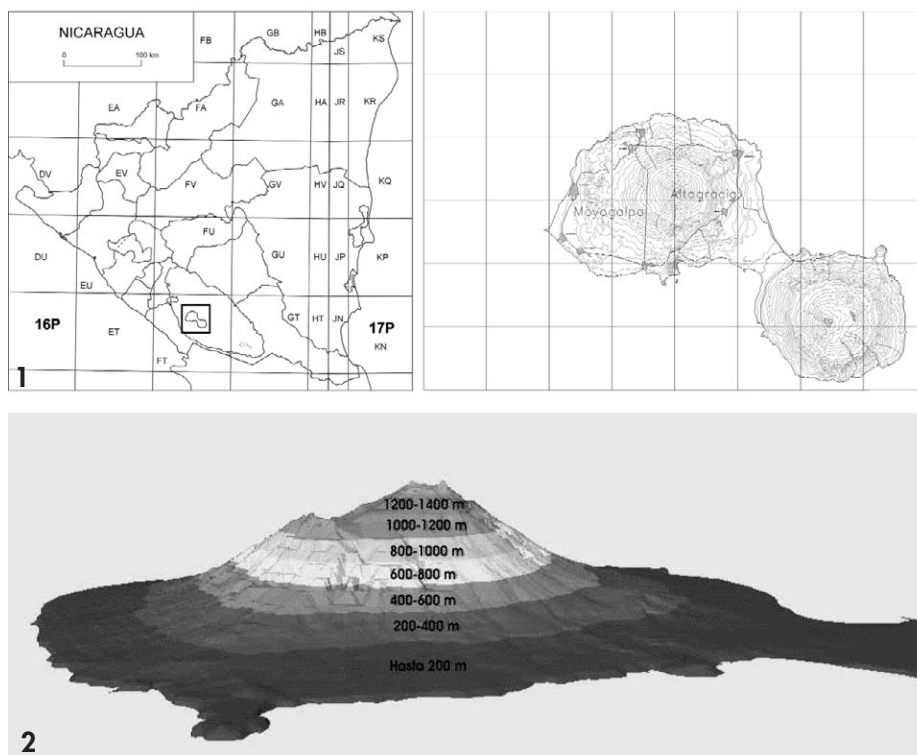


Figure 1. Ometepe Island, Rivas Department, Nicaragua (map at left). Maderas Volcano located on the eastern island (map at right). Figure 2. Digital diagram of Maderas Volcano by PUJOL AND POZO (2000) showing the volcano's profile with the altitudinal collecting stations.
 Figura 1. Isla de Ometepe, Departamento de Rivas, Nicaragua (mapa izquierdo). Volcán Maderas ubicado en la isla del este (mapa derecho). Figura 2. Diagrama digital del Volcán Maderas, elaborado por PUJOL Y POZO (2000), mostrando el perfil del volcán con las estaciones altitudinales de muestreo.

Volcano, so as to assess whether there is a pattern of altitudinal variation of diversity, and thus to design a strategy of sampling appropriate for high-lands that might be applied to other parts of the country as well as to the sampling of other biotic groups.

MATERIAL AND METHODS

Study site: In the Nicaraguan Pacific Slope only three volcanos still have vegetation cover from the base up to the summit: Chonco, Casitas and Maderas. Maderas Volcano is located on the eastern side of Ometepe Island, Rivas

Department, and has a height of 1,350 m (OVIEDO, 1993) (Fig. 1).

Samplings: Samplings were conducted in May 2001. Seven collecting stations were established, one every 200 m (Fig. 2): I. 0-200 m asl, II. 200-400, III. 400-600, IV. 600-800, V. 800-1000, VI. 1000-1200, VII. 1200-1400. At every collecting station there were four persons collecting for an hour. Two transects, were made, one on the northern (Balgüe) and another on the southern side (San Ramón) of the mountain, so in fact there were two collecting points at each station. Stations VI and VII were not considered in the analysis, since no species were found.

Table I. Species composition at each altitudinal station (every 200 m) on Maderas Volcano, Balgüe.

Tabla I. Composición de especies en cada estación altitudinal (cada 200 m) en el Volcán Maderas, Balgüe.

Especies	0-200	200-400	400-600	600-800	800-1000	Total
B. be	X	X	—	—	—	2
O. pr	X	X	X	—	—	3
E. cu	X	X	—	—	—	2
N. dy	X	X	X	X	—	4
D. di	X	X	—	—	—	2
L. mi	X	—	—	—	—	1
L. gr	X	—	—	—	—	1
L. la	X	X	X	X	—	4
B. co	X	X	X	—	—	3
G. gu	X	—	X	X	—	3
D. tr	X	—	—	X	—	2
D. sp	X	—	—	—	—	1
T. cr	X	—	—	—	—	1
C. con	—	X	X	X	X	4
L. li	—	X	—	X	—	2
H. tr	—	—	X	—	—	1
H. ch	—	—	X	—	—	1
H. mi	—	—	X	—	X	2
X. ta	—	—	—	X	—	1
D. att	—	—	—	X	—	1
P. ma	—	—	—	X	—	1
T. coac	—	X	—	X	—	2
TOTAL	13	10	9	10	2	44

Analysis of altitudinal diversity:

For analyzing altitudinal diversity on both sides of the volcano (Balgüe and San Ramón), we first studied species composition in each collecting station and afterwards calculated various indexes of Beta diversity: β_i , β_c , β_r and β_w , proposed by MAGURRAN (1987).

The objective of calculating these indexes is to identify quantitative measures of species turnover along the studied transects.

For analyzing variation of species composition with altitude we divided species into five categories:

- Plain (Lla): 0-400 m asl.
- Medium altitude (MedAL): 400-600 m asl.
- Plain to Medium altitude (LlaMAL): 0-600 m asl.

- High altitude (AL): 600-1000 m asl.

• Wide altitudinal range (AmDAL): Present in at least four collecting stations.

Ecological niche (Structural sub-niche): The terminology used regarding ecological niche follows SILVA AND BEROVIDES (1982); for these authors the resources studied are considered sub-niches of the ecological niche, e. g., structural (substratum, etc), temporal (activity, etc), climatic (illumination, temperature, etc.), etc. In this paper we considered substratum and vegetation cover as two dimensions of the structural subniche.

Spearman (Rs) correlation coefficient (SOKAL AND ROHLF, 1981), was calculated in order to determine if there is a relationship between vegetation cover and species richness.

Table II. Species composition at each altitudinal station (every 200 m). Maderas Volcano, San Ramón.

Tabla II. Composición de especies en cada estación altitudinal (Cada 200 m). Volcán Maderas, San Ramón.

Especies	0-200	200-400	400-600	600-800	800-1000	Total
B. be	X	—	—	—	—	1
L. li	X	X	X	—	X	4
P. gr	X	—	—	—	—	1
L. mi	X	—	—	—	—	1
L. gr	X	—	—	—	—	1
S. oct	X	—	—	—	—	1
B. co	X	—	—	—	—	1
L. la	X	X	X	—	—	3
H. mi	X	—	X	—	—	2
O. pu	X	—	—	—	—	1
C. co	X	X	—	—	—	2
E. cu	—	X	X	—	—	2
T. coac	—	X	—	—	—	1
N. dy	—	X	X	—	X	3
O. pr	—	X	X	—	—	2
D. dis	—	—	X	—	—	1
H. ten	—	—	X	—	—	1
S. sp	—	—	—	—	X	1
TOTAL	11	7	8	0	3	29

We calculated X^2 goodness of fit, by the same authors, in order to determine the preference of species for soil type in each collecting station. The soil sample were taken at a depth of two cm and classified in the field following the categories given by MARQUET (1985) (modified) (Anex 1).

RESULTS

Species composition: A total of 26 species distributed on 14 families and 22 genera (Anex 2) were collected in the two transects made on both, the south and north slopes of the volcano. This species richness value can be considered high and constitutes 46.4 % of the total number of species collected on the island, which is 56 (BONILLA AND ARANA, 2001).

Data on altitudinal distribution of species are given in Tables I, II and III,

which represent the presence or absence of species in each collecting altitudinal station. The cells with species present are shadowed in order to have a better understanding of distribution.

The analysis of altitudinal variation of species composition, gave the following results for each of the five categories considered:

- Plain (Lla) (0-400 m asl): 7 species.
- Medium altitude (MedAL) (400-600 m asl): 3 species.
- Plain to Medium altitude (LlaMAL) (0-600 m asl): 4 species.
- High altitude (AL) (600-1000 m asl): 7 species.
- Wide altitudinal range (AmDAL) (present in at least four collecting stations): 5 species.

Diversity: Beta diversity indexes give a quantitative measure of diversity turnover along a gradient, so they take sense in its comparison with other values calculated in similar conditions.

Table III. Synthesis of species composition at each collecting station (every 200 m) on both sampled slopes of Maderas Volcano. Abbreviations, see Anex 2.

Tabla III. Síntesis de los datos de composición de especies en cada estación de recolecta (Cada 200 m) en ambas vertientes del Volcán Maderas. Abreviaturas, ver Anexo 2.

Especies	0-200	200-400	400-600	600-800	800-1000	Total
H. ten	—	—	X	—	—	1
L. li	X	X	X	X	X	5
N. dy	X	X	X	X	X	5
S. sp	—	—	—	—	X	1
P. me	—	—	—	X	—	1
C. con	X	X	X	X	X	5
B. be	X	X	—	—	—	2
L. gr	X	—	—	—	—	1
L. mi	X	—	—	—	—	1
L. la	X	X	X	X	—	4
O. pu	X	—	—	—	—	1
S. oct	X	—	—	—	—	1
E. cu	X	X	X	—	—	3
G. gu	X	—	X	X	—	3
H. ch	—	—	X	—	—	1
H. tr	—	—	X	—	—	1
H. mi	X	—	X	—	X	3
T. coac	—	X	—	X	—	2
P. gr	X	—	—	—	—	1
T. cr	X	—	—	—	—	1
X. ta	—	—	—	X	—	1
B. co	X	X	X	—	—	3
D. di	X	X	X	—	—	3
D. tr	X	—	—	X	—	2
D. att	—	—	—	X	—	1
D. sp	X	—	—	—	—	1
O. pr	X	X	X	—	—	3
TOTAL	19	10	13	10	5	57

Thus, indexes obtained show somewhat contradictory results. Index β_c (7.5 for Balgüe and 6 for San Ramón) pointed towards a higher beta diversity in Balgüe transect, whereas index β_i (1.05 in Balgüe and 1.04 in San Ramón) were mathematically almost the same.

Results shown in Tables IV and V indicate species pairs overlapping along an altitudinal gradient, and it is the procedure to follow for calculating β_r ; $\beta_r=1.5$ in Balgüe, and $\beta_r=1.6$ in San Ramón showing a higher beta diversity in San Ramón transect.

For taking a final decision on this issue we calculated β_w index. This was 2.82 for Balgüe, and 3.75 for San Ramón. At this point we should recall MAGURRAN'S (1987) statement that " β_w is the first and most straightforward measure of beta diversity", which would mean that this index better quantifies species turnover in the transects studied.

Ecological niche (Structural sub-niche): Spearman's correlation coefficient was calculated in order to determine the relationship between vegeta-

Table IV. Species pairs common to each altitudinal collecting station (San Ramón).

Tabla IV. Pares de especies comunes para cada estación de recolecta altitudinal (San Ramón).

	B. be	O. pu	E. cu	N. dy	P. gr	L. mi	L. r	L. la	B. co	S. sp	Tr. co	C. co	L. li	H. mi	D. dis	O. pr	S. oc	H. tn
B. be	X																	
O. pu	1	X																
E. cu	0	0	X															
N. dy	0	0	2	X														
D. do	1	1	0	0	X													
L. mi	1	1	0	0	1	X												
L. gr	1	1	0	0	1	1	X											
L. la	1	1	1	1	1	1	1	X										
B. co	1	1	1	1	1	1	1	1	X									
S. sp	0	0	0	0	0	0	0	0	0	X								
Tr. co	0	1	1	1	0	0	0	1	0	0	X							
C. co	1	1	1	1	1	1	1	2	1	0	1	X						
L. li	1	1	2	2	1	1	1	2	2	1	1	2	X					
H. mi	1	0	1	1	1	1	1	1	2	0	0	1	2	X				
D. dis	0	0	1	1	0	0	0	0	1	0	0	0	1	1	X			
O. pr	0	0	2	2	0	0	0	1	1	0	1	1	2	1	1	X		
S. oc	1	1	0	0	1	1	1	1	1	0	0	1	1	1	0	0	X	
H. tn	0	0	1	1	0	0	0	0	1	0	0	0	1	1	1	1	0	X
TOTAL	10	9	10	9	8	7	6	7	7	1	3	4	5	4	2	1	0	93

tion cover and species richness at each collecting station (Tables VI and VII).

We obtained an R_s of -0.96, $p < 0.01$ in Balgüe while in San Ramón the calculated R_s was -0.92, $p < 0.01$, showing in both cases that there is a significant negative relationship between the studied variables (vegetation cover and species richness).

For the results given in Tables VIII and IX we calculated X^2 in order to determine the preference that species might have for soil type. We obtained a X^2 of 17.7, $p < 0.01$ in Balgüe and a X^2 of 19.44, $p < 0.01$, in San Ramón.

DISCUSSION

KIKKAWA AND WILLIAMS (1971), pointed out that species richness decreases with lower temperatures related to the increase of altitude. These data agree with our results since species richness at the volcano's base was 19 species and at the highest collecting

station it was five, both slopes taken together.

In this sense, is interesting to remark that in the study made by GILLESPIE AND PRIGGE (1997) on floristic composition along an altitudinal gradient (from 200 to 1500 m asl) at Concepción Volcano, also in Ometepe Island, vegetation cover increased with elevation as well as floristic diversity; this last reached its highest level between 500 and 1100 m. In our study of Maderas Volcano, we also observed a very important increase of vegetation cover (Tables VI, VII) which according to GILLESPIE (1994, 1995) would also imply an increase of floristic diversity.

Species richness at the volcano's northern slope is 22 species and on the southern slope it is 18 species. Analyzing these results by altitudinal collecting stations, we determined that species richness is high on both slopes and shows values that range between four and seven species per altitudinal stratum or station. On the north slope

Table V. Species pairs common to each altitudinal collecting station (Balgüe).
 Table V. Representación de los pares de especies comunes en cada estrato altitudinal (Balgüe).

	B.be	D.dis	E.cu	N.dy	O.pr	L.mi	L.gr	L.la	B.co	G.gu	D.tr	D.sp	T.cr	Tr.co	C.co	L.li	H.mi	H.ch	H.tr	P.me	X.ta	D.att
B. be	X																					
D. dis	2	X																				
E. cu	2	2	X																			
N. dy	2	2	2	X																		
O. pr	2	2	2	3	X																	
L. mi	2	1	1	1	1	X																
L. gr	1	1	1	1	1	1	X															
L. la	1	2	2	4	3	1	1	X														
B. co	2	2	2	3	3	1	1	3	X													
G. gu	2	1	1	3	2	1	1	3	2	X												
D. tr	1	1	1	2	1	1	1	2	1	2	X											
D. sp	1	1	1	1	1	1	1	1	1	1	1	X										
T. cr	1	1	1	1	1	1	1	1	1	1	1	1	X									
Tr. co	1	0	1	1	1	0	0	1	1	0	0	0	0	X								
C. co	1	1	1	3	2	0	0	3	2	2	1	0	0	1	X							
L. li	1	1	1	1	1	0	0	1	1	0	0	0	0	1	1	X						
H. mi	1	0	0	2	1	0	0	2	1	2	1	0	0	0	3	0	X					
H. ch	0	0	0	1	1	0	0	1	1	1	0	0	0	0	1	0	1	X				
H. tr	0	0	0	1	1	0	0	1	1	1	0	0	0	0	1	0	1	1	X			
P. me	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0	X		
X. ta	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0	1	X	
D. att	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0	1	1	X
TOTAL	15	13	13	18	19	7	6	14	10	10	7	1	0	2	7	0	5	1	0	2	1	151

(Balgüe) three species are present at most of the collecting stations: *Caeciliodes consobrinus*, *Neocyclotus dysoni nicaraguense* and *Leptinaria lamellata*. On the south slope (San Ramón) only *Lucidella lirata* was found at four out of the five collecting stations.

The presence of *Drymaeus attenuatus* and *Xenodiscula taintori* at 670 (600-800 m asl) m of height on the north slope is worth mentioning, since previously they had been only collected in the Central-Northern region of the country. These are species associated with moist habitats on highlands, and besides are restricted to well preserved ecosystems. *Drymaeus translucens* is also important because in the project conducted by PÉREZ (1999) comprising the continental snail fauna of the whole Nicaraguan Pacific region, it was only found at Mom-bacho Volcano, Department of Granada.

At Maderas Volcano it was found in Balgüe, at 670 m asl (600-800 m asl).

A very important aspect to point out is that, according to the range categories of species altitudinal distribution, the results obtained allow us to identify the existence of two communities: one of lowlands comprising plain species (7) and medium altitude-plain species (5) for a total of 12 species, and another community of highlands comprising species of high altitude (4) and medium altitude (3) for a total of seven species. In this analysis we excluded wide altitudinal range species.

This is a very important analysis, since one of the goals of the present project was to try to establish a sampling strategy intended to study biodiversity on medium altitude mountains (1000-1500 m), which are the majority of highlands in Nicaragua. Summarizing the

Table VI. Vegetation cover and species richness at each collecting station, Maderas Volcano, Balgüe.

Tabla VI. Cobertura de vegetación y riqueza de especies en cada estación de recolecta, Volcán Maderas, Balgüe.

Collecting station	Vegetation cover (%)	Species richness
0 - 200 m	27	13
200 - 400 m	32.3	10
400 - 600 m	46.5	9
600 - 800 m	76	9
800 - 1000 m	95.5	2

Table VII. Vegetation cover and species richness at each collecting station, Maderas Volcano, San Ramón.

Tabla VII. Cobertura de vegetación y riqueza de especies en cada estación de recolecta altitudinal, San Ramón.

Collecting station	Vegetation cover (%)	Species richness
0 - 200 m	32.4	11
200 - 400 m	35	8
400 - 600 m	48	8
600 - 800 m	78	3
800 - 1000 m	97.3	2

previous results, it can be said that there is a community of lowlands and a community of highlands, with a transition zone between 400 m and 600 m asl; this transition zone defines an inflexion point located approximately at 500 m asl.

Consulting other national specialists we have been able to prove that the same phenomenon takes place in other animal groups, such as insects (J. M. Maes, pers. comm.) and birds (J. McCrary, pers. comm.), as well as in plants (A. Grijalva, pers. comm., R. Rueda, pers. comm.)

When comparing the results of species richness on both slopes of the volcano, we observed it is higher in Balgüe transect (North), at all altitudinal collecting stations, which might be due to the existence of a greater microhabitat availability on this slope, as well as to more appropriate soils for gastropod communities, such as loose soils with different degrees of litter.

An interesting fact is that *Lamellaxis micra* and *Lamellaxis gracilis* are present only as high as 200 m asl. The interest of this fact lies in the wide geographical and ecological distribution that these species seem to have, according to the study by PÉREZ (1999), which we have explained as a remarkable case of wide ecological tolerance. However, in spite of previous mentions their distribution on Maderas volcano does not reach heights above 200 m asl, probably because these species are associated with plains, as is the case of most ecosystems on the Nicaraguan Pacific region.

Through the results of beta diversity indexes of MAGURRAN (1987) we can affirm that beta diversity, or, in other words, spatial heterogeneity, is higher on the southern slope than in the northern one. However, as happens with alpha diversity indexes, it cannot be stated in absolute terms whether

Table VIII. Soil type and species richness at each collecting station, Maderas Volcano, Balgüe.
Tabla VIII. Tipo de suelo y riqueza de especies en cada estación de recolecta, Volcán Maderas, Balgüe.

Collecting station	Soil type	Species richness
0 - 200 m	Sandy land	13
200 - 400 m	Litter	10
400 - 600 m	Litter	9
600 - 800 m	Moderately clayey	9
800 - 1000 m	Clay	2

Table IX. Soil type and species richness at each collecting station, Maderas Volcano, San Ramón.
Tabla IX. Tipo de suelo y riqueza de especies en cada estación de recolecta, Volcán Maderas, San Ramón.

Collecting station	Soil type	Species richness
0-200 m	Litter	11
200-400 m	Sandy land	8
400-600 m	Moderately clayey	8
600-800 m	Clay	3
800-1000 m	Clay	2

these figures are high or low, since these indexes make sense in comparison with other values of indexes calculated at the same time in different places, or at the same place at different moments, always with the same sampling effort. Up to the present few reference values exist for comparison, and in this sense it is worth mentioning the works by MAGURRAN (1987) and MORENO (2000), which among other things provide values of alpha and beta indexes that are very useful for this purpose.

Analyzing species richness and its relation to vegetation cover (Tables VIII and IX), it can be observed that the former decreases significantly with the increase of the latter ($R_s = -0.92$, $p < 0.01$ for Balgüe; and $R_s = -0.96$, $p < 0.01$ for San Ramón). However, in our opinion it is more likely to be explained by the nature of the soil than by the increase of vegetation cover. Soil type varies in both volcano slopes from soil with litter to clayey soil, having a significant relationship with the reduction of species richness ($X^2 = 17.7$, $p < 0.01$ for Balgüe; and $X^2 = 19.44$, $p < 0.01$ for San Ramón). This

issue was also addressed by PÉREZ, SOTELO AND ARANA (in press) for the whole Pacific region, concluding that clayey soils are not appropriate for the development of gastropod communities and loose soils with litter are very likely to hold a very diverse community of these animals.

CONCLUSIONS

1. Our results agree with other authors who state that diversity decreases with an increase of altitude above sea level. This phenomenon could be related to the reduction of temperature, but in the particular case of gastropod mollusks, it might also be related to the soil type.

2. The identification of two communities, one of lowlands and another of highlands, separated by a transition zone, allow us to propose a sampling strategy on mountains of medium altitude (up to 1500 m), which consists of making two collecting stations: one below 400 m and the other above 600 m asl. This strategy might allow us to

collect the core species of both communities, without incurring high expenses.

ACKNOWLEDGEMENTS

We would like to acknowledge M. Sc. Alfredo Grijalva (Universidad Centroamericana), and Drs. Jean-Michel Maes (Museo Entomológico Autónomo de León), Jeffrey McCrary (Universidad Centroamericana) and Ricardo Rueda (Universidad Nacional Autónoma de Nicaragua-León); the commentaries

made by these colleagues on data related to altitudinal diversity were very important to us.

We would like to thank also M. Sc. Byron Walsh, for the favorable comments he made regarding the results of this project. We have had at all times the support and encouragement of Dr. Al López, SJ, former director of the Centre of Malacology / Animal Diversity.

This project was funded by PANIF-MARENA and consequently we would like to thank Dr. José Villa and M. Sc. Byron Walsh for their support.

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Anex 1. Field form for soil sampling.

Anexo 2. Formulario de campo para la clasificación de suelos.

I. Human settlements.

- Constructions.
- On walls of ruins.
- Gardens and parks.
- Ploughed land.
- Plantation.
- Piled land.
- Grassland.
- Quarry.
- Burnt land.
- Road sides.

II. Vegetation.

Forests.

- Low to medium deciduous forest.
- Low to medium semideciduous forest.
- Medium to tall perennial forest.
- Medium to tall subperennial forest.
- Low estuary forest.

Other wooded formations.

- Riparian forest.
- Low savanah forest.
- Arboretum.

Not wooded formations.

- Spiny bushes.
- Savanah.
- Savanah of jícaros and/or genízaros.

No vegetation.

III. Soil type.

- Debris.
- Sand.
- Limestone.
- Chalk.
- Bricks and others.
- Clay.
- Granite gravel.
- Volcanic gravel.
- Land with litter.
- Land without litter.

IV. Soil humidity.

- Saturated.
- Wet and loose.
- Wet and compact.
- Dry and loose.
- Dry and compact.

V. Illumination.

- Shadow.
- Penumbra.
- Filtered sun.
- Sun patches.
- Open sun.

VI. Altitude (asl).

Anex 2. Systematic species list.

Anexo 2. Lista de especies.

Family Helicinidae Lamarck, 1899	
<i>Lucidella lirata</i> (Pfeiffer, 1847)	L. li
<i>Helicina tenuis</i> (Pfeiffer, 1848)	H. ten
Family Poteriidae Gray, 1850	
<i>Neocyclotus dysoni nicaraguense</i> (Bartsh and Morrison, 1942)	N. dy
Family Vertiginidae Fitzinger, 1833	
<i>Pupisoma medioamericana</i> Pilsbry, 1920	P. me
Family Ferussacidae Bourguignat, 1883	
<i>Caeciliodes consobrinus</i> (Orbigny, 1849)	C. con
Family Subulinidae Crose and Fischer, 1877	
<i>Beckianum beckianum</i> (Pfeiffer, 1846)	B. be
<i>Lamellaxis gracilis</i> (Hutton, 1834)	L. gr
<i>Lamellaxis micra</i> (Orbigny, 1835)	L. mi
<i>Leptinaria lamellata</i> (Potiez and Michaud, 1838)	L. la
<i>Opeas pumillum</i> (Pfeiffer, 1840)	O. pu
<i>Subulina octona</i> (Bruguiere, 1792)	S. oct
Family Spiraxidae Baker, 1955	
<i>Euglandina cumingii</i> (Beck, 1837)	E. cu
<i>Spiraxis</i> sp.	S. sp.
Family Helicarionidae Bourguignat, 1888	
<i>Guppya gundlachi</i> (Pfeiffer, 1880)	G. gu
<i>Habroconus trochulinus</i> (Morelet, 1851)	H. tr
<i>Habroconus championi</i> (Martens, 1892)	H. ch
Family Zonitidae Morch, 1864	
<i>Hawaiiia minuscula</i> (Binney, 1840)	H. mi
Family Helminthoglyptidae Pilsbry, 1939	
<i>Trichodiscina coactiliata</i> (Deshayes, 1838)	H. mi
Family Polygyridae Pilsbry, 1895	
<i>Praticollela griseola</i> (Pfeiffer, 1841)	P. gr
Family Thysanophoridae Pilsbry, 1926	
<i>Thysanophora crinita</i> (Fulton, 1917)	T. cr
Family Sagdidae Pilsbry, 1895	
<i>Xenodiscula taintori</i> (Goodrich and Schalie, 1937)	X. ta
Family Bulimulidae Tryon, 1867	
<i>Bulimulus corneus</i> (Sowerby, 1833)	B. co
<i>Drymaeus discrepans</i> (Sowerby, 1833)	D. di
<i>Drymaeus attenuatus</i> (Pfeiffer, 1851)	D. att
<i>Drymaeus</i> sp.	D. sp.
Family Orthalicidae Pilsbry, 1899	
<i>Orthalicus princeps</i> (Broderip, 1833)	O. pr