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Original article

Earthworm communities along an elevation gradient in Northeastern Puerto Rico

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Abstract

In this study, we describe earthworm communities along an elevation gradient of eight forest types in Northeastern Puerto Rico, and determine whether their abundance, biomass and/or diversity is related to climatic, soil physical/chemical and/or biotic characteristics. We found that the density, biomass, and diversity of worms varied significantly among forest types. The density of earthworms was highest in the *Pterocarpus* forest. In terms of biomass, both elfin and the *Pterocarpus* forests had the highest values. The number of earthworm species significantly increased as elevation and annual rainfall increased and air temperature decreased. We conclude that differences in earthworm species richness along this elevation gradient may be due to a combination of biotic and soil physical and chemical factors. Soil pH and root length density are important predictors of number of worm species along this elevation gradient.

Keywords: Earthworms; Tropics; Mature forests; Natives; Puerto Rico

1. Introduction

Earthworms are the best known and often the most important animals influencing the functioning of soil ecosystems [11]. When present, they habitually dominate the soil food web [16,18,23] and their activities can greatly impact many ecosystem processes and services. In Puerto Rico, most of the earthworm ecological research has been done in the Luquillo Experimental Forest (LEF), particularly in the tabonuco forest (a subtropical wet forest). Early descriptive work on earthworms in this forest type indicated that on a weight basis, they are the most important animal fraction [23], and that their density and community structure are affected by land use changes [9,30]. Most recently, González and Seastedt [8] discovered that 66% of the litter decay in the tabonuco forest is due to faunal effects alone; mainly due to earthworms.

To our knowledge no study has described earthworm communities along climatic and elevation gradients within the tropical region. Little earthworm data have been gathered from tropical wet forests [7] and much less from tropical cloud (elfin), flooded or seasonal semi-deciduous forests. Given that (1) the processes that shape community (assemblage) attributes involve complex biotic and abiotic components [14], (2) that only 2.7% of the forest cover in Puerto Rico is

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dominated by tabonuco forests [10], and (3) available data indicate earthworms are important drivers of complex ecological processes in the tropics, we aim to expand our ecological and taxonomic knowledge of earthworm communities to other forest types in the island. Thus, in this study, we (1) describe earthworm communities (in terms of fresh density, biomass, developmental stage and diversity) along an elevation gradient of eight forest types in Northeastern Puerto Rico, and (2) determine whether the abundance, biomass and/or diversity of the earthworm assemblage along the elevation gradient is related to climatic (rainfall and temperature), soil physical/chemical properties (soil bulk density, water content, pH and nutrients) and/or other biotic characteristics (e.g., biomass of ground litter, microbes and roots). Further, we evaluate whether earthworms along this elevation gradient follow the general conception that species richness declines with an increase in elevation [24]. The Luquillo Mountains represent an ideal setting for this type of gradient analysis as within a short distance inland (25 km), we can find an elevation gradient spanning about 1000 m and differences in temperature and precipitation of about 5 °C and 2600 mm as we go from the coast to the top of the mountain, respectively (Fig. 1).

2. Materials and methods

This study was developed in the Northeastern region of Puerto Rico and focused within eight mature forest types (>60 years old). As elevation increases from just above sea level to 1010 m, the eight forest types are representative of Lowland subtropical dry, Lowland subtropical moist, Subtropical wet, Subtropical rain, Lower montane wet, and Lower montane rain forest life zones [5]. Mean annual temperatures decreased with increasing elevation along the gradient from 27.5 to 19.5 °C and mean annual rainfall increased along the gradient (1262 mm to 3908 mm) during 2001–2004 [10]. Four of the upper forests types (380 m and above) are located in the LEF (18°18′ N, 65°50′ W) and include elfin woodland, sierra palm, palo colorado, and the tabonuco forest types [27,29]. Four additional forest types include lowland moist and dry forests, and flooded *Pterocarpus* and mangrove forests. The latter four are located on federal (military), state, and private managed and unmanaged lands. All sites are on non calcareous colluvial or alluvial material derived from volcanic bedrock (montane and lowland sites) or marine deposits (coastal mangrove and *Pterocarpus* sites). A detailed description of forest community characteristics, locations, and soil macro- and micronutrients can be found at Gould et al. [10].

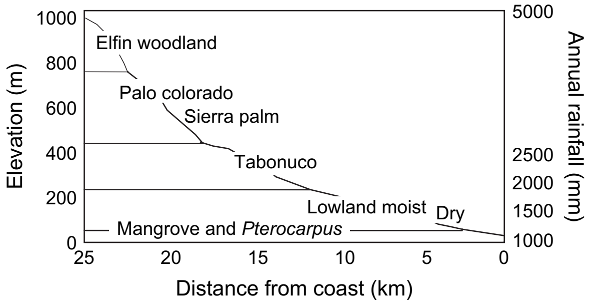

Fig. 1. Sequence of eight forest types along the gradient of elevation, rainfall, and distance from the coast in northeastern Puerto Rico.

Within this elevation gradient, we selected 24 geographically separated sampling areas in a number of forest patches throughout Northeastern Puerto Rico, three of each of the eight forest types. Within these general sampling areas, three 25 × 25 cm plots were randomly sampled for a total of 9 replicates per forest type (72 plots in total) during July and August, 2004. Earthworms were collected by hand-sorting the soils to a depth of 0–10 cm and 11–30 cm and fixed *in situ* in 10% formaldehyde. Ground litter (leaves and twigs <2 mm diameter) and roots (0–30 cm depth) were collected from each plot and stored in paper bags. Soil samples were taken from each plot for pH, water content and chemical analysis. The soil samples were air-dried and passed by a Wiley mill through a 0.85-mm (20-mesh) stainless steel sieve before chemical analyses. Soil total C, N, and S were determined with a LECO-2000 CNS analyzer following the procedure of Tabatabai and Bremmer [26]. Total nutrients (Al, Ca, Fe, K, Mg, Mn, Na, and P) were measured with a Beckman Spectra Span V (Fullerton, CA) plasma emission spectrometer following Luh Huang and Schulte [20] procedures. Soil pH will be measured using a paste of 1:1 ratio of fresh soil and deionized water.

In the laboratory, roots were sorted based on the following diameter classes: 0–2 mm (small), 2.1 - 4.9 mm (medium) and >5 mm (large). Ground litter biomass and root biomass were obtained after drying at 60 °C for at least 72 h. Root length was measured with a Delta-T scanner and software, based on the line-intercept method [3]. Root length density (RLD) was calculated as the root length (cm) over the soil volume at 30 cm depth (cm^3). Microbial biomass C was estimated by the substrate induced respiration (SIR) method [19] and calibrated for the study area (Zalamea and González, unpublished data), using an ER-10 Columbus Instruments respirometer. Conversion of CO_2 evolved to mg-C/g soil followed [1]. Earthworm biomass was recorded on the fresh weight basis after the worms were rinsed with water and dried with paper towels.

All statistical analysis were performed using the software SPSS (SPSS 11.5, Windows 2000). The significance level was set at $\alpha = 0.05$. Data were tested for homogeneity of variance by using Levene's test of equality of error variances, and skewness. A multivariate analysis of variance (MANOVA) was performed to look at the effects of forest type and soil depth (independent variables) on the density and biomass of total worms, and the number of earthworm species (dependent variables). When significant differences were found, Student–Newman–Keuls (SNK) tests were used to compare site means for the above mentioned dependent variables. A one-way ANOVA was employed to determine the effect of soil depth on the number of species of earthworms within a forest type using the general linear model (GLM) procedure. A simple linear correlation analysis was performed among the abundance, biomass and diversity of earthworms and climatic (rainfall and temperature), soil physical/chemical properties (bulk density, soil water content, pH, and nutrients) and biotic characteristics (ground litter biomass/depth, microbial biomass and root biomass/length). Stepwise linear regressions were performed for the number of earthworm species, and the total density and biomass of earthworms (dependent variables) using climatic, physical/chemical properties, and biotic characteristics as independent variables.

3. Results

There were significant differences in the mean total density and biomass of earthworms among forest types in the elevation gradient (Table 1). The *Pterocarpus* forest had the highest density of total earthworms (1024 worms/m^2), and the mangrove forest the lowest (2.7 worms/m^2). The rest of the forest types had intermediate levels of total earthworm density (ranging from 102 to 221 worms/m^2) when compared to the *Pterocarpus* and mangrove forests (Table 2). In terms of biomass, the elfin forest and the *Pterocarpus* forest had highest biomass (168.2 and 180.6 g/m^2, respectively), and the dry and the mangrove forests the lowest (<1.2 g/m^2) (Table 3). The palm, colorado, tabonuco and lowland moist forests had values of earthworm biomass ranging from 27.8 to 49.5 g/m^2.

There were significant differences in the mean total density and biomass of earthworms and the number of species between upper (0–10 cm) and lower (11–30 cm) soil depths; and a significant interaction between forest type and depth on the density of earthworms (Table 1). Consistently along the elevational gradient, the density, biomass and number of earthworms tended to be higher in the upper than in the lower soil layer, and this difference was significant for the density of total and immature worms in the elfin, colorado and lowland moist forests and for the biomass of total worms in the lowland moist forest (Fig. 2; data not shown for biomass). The number of worm species was higher in the upper than in the lower soil layers in the elfin forest (Fig. 3).

There were significant differences in the number of species found among the forest types along the elevation gradient (Table 1). On average, the elfin forest had the highest number of worm species (3 species/m^2) (Fig. 4). In the colorado forest, we found an average of 2 species/m^2; and that was not significantly different from the tabonuco and lowland moist forests. If earthworms were present, only one of three different species was found in the dry, *Pterocarpus* and mangrove forests (Fig. 4, Tables 2 and 3).

In total, we found a total of 14 species belonging to 6 families along the elevation gradient (Table 2). The elfin

Table 1
Effects of forest type and soil depth on the density and biomass of adult, immature and total worms and the number of earthworm species along an elevation gradient in Northeastern Puerto Rico

Source	Dependent variable	df	*F*	*P*	Power
FOREST	Total biomass	7	6.0	**<0.01**	0.99
	Total density	7	8.0	**<0.01**	1.00
	No. of species	7	11.6	**<0.01**	1.00
DEPTH	Total biomass	1	5.0	**0.03**	0.60
	Total density	1	32.6	**<0.01**	1.00
	No. of species	1	6.3	**0.01**	0.70
FOREST × DEPTH	Total biomass	7	0.6	0.72	0.26
	Total density	7	3.6	**<0.01**	0.97
	No. of species	7	1.2	0.30	0.49

Statistical analyses are based on tests of between-subjects effects of a two-way MANOVA.

Table 2
Earthworm density (number/m^2) and total number of species in eight forest types along an elevation gradient in Northeastern Puerto Rico

SPECIES	FOREST TYPE							
	Elfin	Palm	Colorado	Tabonuco	Lowland	Dry	*Pterocarpus*	Mangrove
EXOTICS								
Glossoscolecidae								
Pontoscolex corethrurus	14.22	128.00	94.22	176.00	107.56			
Ocnerodrilidae								
Ocnerodrilus occidentalis	16.00	3.56		5.33	19.55	117.33		
Moniligastridae								
Drawida barwelli					51.56			
NATIVES								
Glossoscolecidae								
Pontoscolex spiralis	3.56	16.00	44.44	30.22	30.22		1024.00	
Estherella sp.	19.56		1.78	8.00				
Estherella gatesi	1.78							
Onychochaeta borincana	0.89							
Octochaetidae								
Borgesia sp.	1.78		3.56					
Borgesia Montana	3.56							
Borgesia sedecimsetae	7.11	1.77	29.33					
Trigaster longissimus	10.67							
Trigaster yukiyu	14.22							
Exxidae								
Neotrigaster complutensis	3.56							
Neotrigaster rufa			8.89					
Unknown	5.33		3.56	1.78	5.33			2.67
Total density (±S.E.)	102.22 (18.75)b	151.11 (69.90)b	185.77 (28.76)b	221.33 (62.86)b	214.22 (65.04)b	117.33 (88.32)b	1024.00 (495.83)a	2.67 (2.67)c
Total no. of species	**12**	**4**	**6**	**3**	**4**	**1**	**1**	**1**

Different letters represent the significant effect of forest type on the total density of worms (MANOVA; SNK, $\alpha = 0.05$). Blank spaces represent zero values.

Table 3
Earthworm biomass (g/m^2) in eight forest types along an elevation gradient in Northeastern Puerto Rico

SPECIES	FOREST TYPE							
	Elfin	Palm	Colorado	Tabonuco	Lowland	Dry	*Pterocarpus*	Mangrove
EXOTICS								
Glossoscolecidae								
Pontoscolex corethrurus	4.10	23.08	25.24	30.72	28.05			
Ocnerodrilidae								
Ocnerodrilus occidentalis	0.07	<0.01		<0.01	0.24	1.21		
Moniligastridae								
Drawida barwelli					1.92			
NATIVES								
Glossoscolecidae								
Pontoscolex spiralis	0.24	4.57	15.86	6.02	2.56		168.25	
Estherella sp.	97.73		0.72	11.69				
Estherella gatesi	5.35							
Onychochaeta borincana	0.21							
Octochaetidae								
Borgesia sp.	0.03		0.25					
Borgesia Montana	0.11							
Borgesia sedecimsetae	0.38	0.05	1.23					
Trigaster longissimus	70.26							
Trigaster yukiyu	1.63							
Exxidae								
Neotrigaster complutensis	0.44							
Neotrigaster rufa			3.45					
Unknown	0.77	0.03	0.15	1.04	0.84			
Total biomass (±S.E.)	180.62 (63.34)a	27.77 (13.77)b	46.90 (11.49)b	49.50 (12.77)b	33.62 (5.55)b	1.21 (0.96)c	168.25 (67.74)a	<0.01c

Different letters represent the significant effect of forest type on the total biomass of worms (MANOVA; SNK, $\alpha = 0.05$). Blank spaces represent zero values.

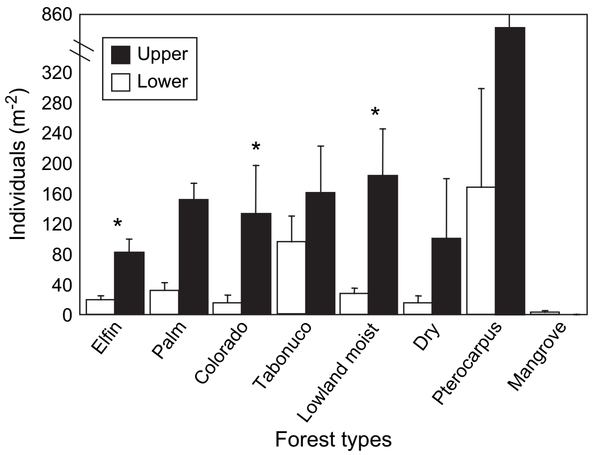

Fig. 2. Mean total density (per square meter ± S.E.; $n = 9$) of earthworms in upper (0–10 cm) and lower (11–30 cm) soil depths in eight forest types along an elevation gradient in Northeastern Puerto Rico. Asterisks indicate a significant effect of soil depth within a forest type (one-way ANOVA; $\alpha = 0.05$).

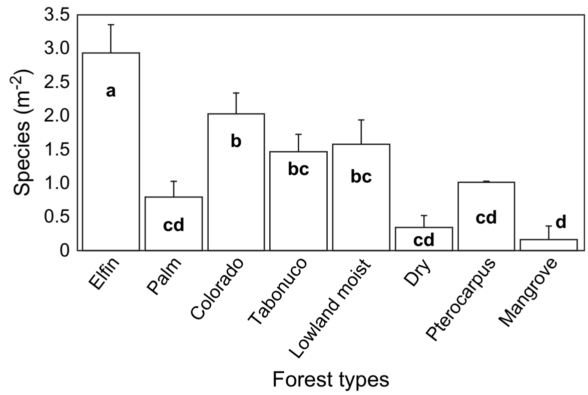

Fig. 4. Mean number of earthworm species at 0–30 cm soil depth in eight forest types along an elevation gradient in Northeastern Puerto Rico. Letters represent the effects of forest type where common letters indicate no significant difference among sites (MANOVA; SNK, $\alpha = 0.05$).

forest had the highest total number of earthworm species found at a given forest type (12 species); the second highest was the colorado forest with 6 earthworm species. These two forests also have the highest numbers of native earthworm species (10 and 5 species, respectively). *Pontoscolex corethrurus* was found in all but the dry, *Pterocarpus* and mangrove forests. *Ocnerodrilus occidentalis* was found in all but the colorado, *Pterocarpus* and mangrove forests. The lowland moist forest had the highest presence of exotic worms (Tables 2 and 3).

A correlation analysis demonstrated significant positive relationships between elevation and rainfall, and the biomass of total worms, and the number of species of earthworms (Table 4). Temperature was significantly negative related to these variables. The density of worms was negatively related to soil S. The number of species negatively correlated with microbial biomass and was also related to many of the other biotic and soil property variables measured in the study. Soil bulk density was significantly correlated to the total biomass and the number of species of earthworms (Table 4). Stepwise linear regressions showed (1) soil pH and the length density of large roots to be good predictors of the number of worm species ($r = 0.68$, $F = 22.61$, $P < 0.001$ for both factors combined), (2) soil C and pH to be good predictors of the total biomass of earthworms ($r = 0.56$, $F = 12.29$, $P < 0.001$ for both factors combined), and (3) soil S and pH to be good predictors of the total density of earthworms ($r = 0.47$, $F = 7.52$, $P = 0.001$ for both factors combined).

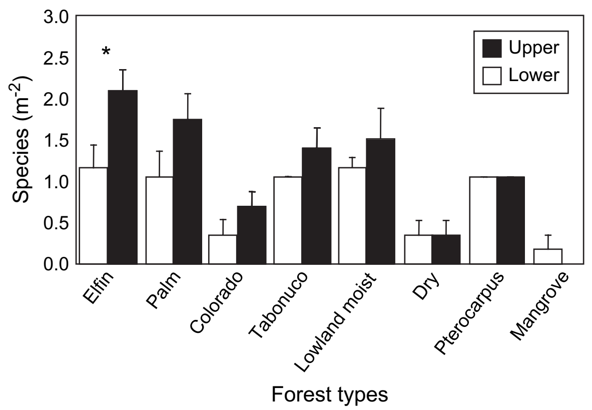

Fig. 3. Mean number of earthworm species in upper (0–10 cm) and lower (11–30 cm) soil depths in eight forest types along an elevation gradient in Northeastern Puerto Rico. Asterisks indicate a significant effect of soil depth within a forest type (one-way ANOVA; $\alpha = 0.05$).

4. Discussion

Previous earthworm research in the Luquillo Mountains centered in the tabonuco forest. In this study, we expand that research to include other forest types: three within the LEF, and four at lower elevations in Northeastern Puerto Rico. We found that the density, biomass and diversity of earthworms varied significantly among forest types. The density of earthworms was highest in the *Pterocarpus* forest. In terms of biomass, both elfin and the *Pterocarpus* forests had the highest values. Zou and González [30] studied changes in earthworm density and community structure during secondary succession in abandoned tropical pastures. They found

Table 4
Pearson correlation coefficients (*r*) for the density and, biomass of total worms, and the number of species of earthworms and climate (rainfall and temperature), biotic (roots, microbial biomass and ground litter biomass/depth) and soil properties (bulk density, soil water content, pH, and nutrients)

Variables	Total density	Total biomass	No. of species
Elevation	−0.18	**0.31**	**0.47**
Rainfall	−0.06	**0.34**	**0.44**
Temperature	0.09	**−0.29**	**−0.53**
Roots			
Small			
DW	−0.91	0.21	**0.32**
RLD	−0.08	0.20	**0.30**
Medium			
DW	−0.13	0.21	**0.31**
RLD	−0.09	0.07	0.21
Large			
DW	−0.12	−0.05	0.11
RLD	0.08	0.04	**0.35**
Total			
DW	−0.14	0.05	0.23
RLD	−0.19	0.18	**0.40**
Microbial biomass	0.01	−0.15	**−0.27**
Ground litter			
Biomass	−0.05	0.05	0.07
Depth	−0.02	0.25	**0.41**
Soil properties			
Bulk density	0.18	**0.34**	**0.32**
Water content	0.09	**0.40**	**0.35**
pH	−0.15	**−0.33**	**−0.63**
C	−0.13	**0.34**	**0.44**
N	−0.13	0.19	0.22
P	0.08	0.04	**−0.40**
Ca	−0.15	**−0.29**	**−0.54**
S	**−0.30**	0.08	0.01

DW, dry weight; RLD, root length density. Numbers in bold font represent correlation coefficients with a significant two-tailed probability value <0.05.

the highest density (831 worms/m^2) and biomass (175 g/m^2) in active pastures where tabonuco vegetation had been cleared. In this study, we report a similar earthworm biomass but higher density of earthworms; which is the highest recorded for the island and for other tropical forests. Fragoso and Lavelle [7] reported an average earthworm abundance and biomass of 68 worms/m^2 and 12.9 g/m^2, respectively from a comparative study of 12 tropical rain forests. In comparison to that study, we found a much higher density of earthworms in all but the mangrove sites along this elevational gradient and a higher biomass except for the dry and mangrove forests.

The distribution of earthworms within the soil can be related to abiotic and behavioral factors [22]. For the tropics, it has been argued that the vertical distribution of earthworm results from low overlap and the utilization of the whole spectrum of food along the soil profile [6]. Yet, Fragoso and Lavelle [7] found that earthworms were mostly concentrated in the first 0–10 cm of soil depth. Similarly, in this study, earthworm biomass, density and species numbers were consistently higher in the upper (0–10 cm) than in the lower horizons (11–30 cm). The total density of earthworms was significantly higher in the upper than in the lower horizons in the elfin forest, colorado and lowland moist forests. Borges and Alfaro [2] studied the earthworms of Baño de Oro in the Luquillo Mountains and found that in terms of density, 57% of the earthworms were concentrated in the upper 10 cm soil layer where the organic matter content was higher. They also found that in colorado and palm stands, the biomass of the second soil layer (10–20 cm) was higher due to the presence of the giant worm T. *longissimus*. Jiménez and Decaëns [12] reasoned that differences in the vertical distribution of earthworms might be an adaptive strategy of large topsoil species to avoid higher densities of individuals in the upper layers of soil during the reproductive period. Thus, we deduce as likely that a combination of abiotic, food resources and behavioral characteristics are determining the vertical stratifications of earthworms in the soil profiles along this gradient.

There is a general perception that species richness declines with elevation yet, there are numerous examples of species richness peaking at intermediate elevations [25]. At LEF, the number of tree species declines with increasing elevation [28] though, the percentage of total tree endemics increases with elevation [10]. While, litter invertebrate communities decline with increasing elevation mainly due to the chemical and physical nature of litter rather than direct effects of temperature and rainfall [25]. In this study, the number of earthworm species significantly increased as elevation and annual rainfall increased and air temperature decreased. Although it is difficult to make cause and effects relationships by means of a correlation, our results suggest that differences in earthworm species richness along this elevational gradient may be due to a combination of biotic and soil physical and chemical factors; as the number of species of earthworms is well predicted by soil pH and the root length density of large roots. Thus, climatic factors (rainfall and temperature) are proxy variables for other important drivers of earthworm diversity along this elevation gradient (Table 3). In 1969, Lyford [21] studied the ecology of the elfin forest in the Luquillo Mountains and discussed that the climate and vegetation of this area was ‘‘much the same now as it has been for centuries because of its particular location in respect to the ocean". In Puerto Rico, deforestation occurred extensively during the late 1800s and early 1900s. Much of the deforested area on montane slopes was converted to cattle pasture all the way up the tabonuco forest but not reaching its mountain tops. The coastal *Ptercarpus* forests are remnants of formerly extensive freshwater swamp forests. While these forests are also likely much the same (although smaller in extent) as they have been for centuries, the soil moisture conditions are much more seasonally variable (flooded) than the elfin forest. Thus, here we argue that a greater diversity of earthworm species at higher elevations than in lower elevations along this gradient might be also due to a number of factors that include: (1) biotic characteristics inherent to different earthworm species, (2) a response to a gradient in disturbance in areas surrounding these mature forests, (3) greater isolation, and (4) stability of edaphic conditions than can be more conducive for earthworm reproduction, growth, and maturation.

Working at the regional scale in northeast Germany, Joschko [13] identified soil pH and total nitrogen important for estimating earthworm biodiversity; a result consistent to previous studies and for variety of soils and ecosystems [4,18]. Lavelle [15] found that at a latitude level, the structure and diversity of worms was mainly determined by temperature. Further, it was argued that the increase of biodiversity associated with high temperature may have originated from an improved access to soil nutrients and organic resources [17]. Results from our study support the above contentions yet, we also found significant positive relationships between the biomass and species number of worms and root parameters. Therefore, our data suggest that the biomass of different diameter classes of roots and their length density are important to determine worm population and community characteristics along this elevation gradient.

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