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ORDINAL ABUNDANCE AND RICHNESS OF MILLIPEDES (Arthropoda: Diplopoda) IN A SUBTROPICAL WET FOREST IN PUERTO RICO

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SUMMARY

Millipedes, among other soil fauna, are important components of ecosystems because of their role in nutrient cycling. In this study, we quantified the density, biomass, and richness (in terms of order) of millipedes along a toposequence (ridges, slopes, and valleys) and different ground layers (litter, humus, 0-5 cm soil depth, and 5-10 cm soil depth) in a subtropical wet forest in Puerto Rico. Millipedes were surveyed from twelve 50 x 50 cm plots (3 topographic positions x 4 replicates) by hand sorting. Four orders of millipedes were found in El Verde tabonuco forest: Stemmiulida (the most abundant), Glomeridesmida, Spirostreptida, and Polydesmida (the least abundant). The density of millipedes and the richness of Orders varied depending on the topographic position, with ridges having significantly less of both. The ground layer also significantly affected millipede richness but not density, with the humus being the richest layer. The biomass of millipedes did not significantly differ among the different topographic positions or layers. There was a significant positive correlation between the soil pH and millipede richness. The number of millipede orders was also significantly and positively correlated with the amount of wood and fruit found in the litter and humus layers. In conclusion, millipedes have higher density and richness in slope and valley topographic positions than in ridges, and in less acidic soils in this tabonuco forest.

INTRODUCTION

Decomposition is influenced by three main factors: the physico-chemical environment, the substrate quality, and the decomposer organisms (Swift *et al*. 1979). Arthropods, a major component of the soil fauna, contribute to the decomposition process by fragmenting organic matter and stimulating microbial activity (Coleman and Crossley 1996). These two processes are intricately related as the fragmentation of litter by soil fauna increases the surface area of the substrate, allowing microbes to become established, thereby increasing the nutrients released into the soil (Scheu and Wolters 1991). Some decomposer organisms can also digest organic matter through symbiotic interactions with gut microorganisms (Edwards and Fletcher 1988). The fragmentation of litter and litter passage through the gut of macroarthropods, such as diplopods and isopods, can help in the establishment of soil bacteria (Cárcamo *et al*. 2000). Millipedes in particular can be important determinants of litter decomposition by fragmenting litter (Tian *et al*. 1995) and enhancing microbial activities (Anderson and Bignell 1980). In El Verde tabonuco forest, Ruan *et al*. (2005) found that the rate of litter decomposition was significantly correlated with two factors: soil millipede density (explaining 40 percent of the variance in litter decomposition) and microbial biomass (explaining 19 percent of the variance). Millipedes can be very selective about their microhabitat and community organization (Voigtländer and Dūker 2001; Warren and Zou 2002) which in turn can affect patterns of decomposition (Heneghan and Bolger 1998).

In the tropical wet forests of Puerto Rico the connection between species distribution and environmental variables has been well established for aboveground organisms (Holdridge 1971; Gould *et al*. 2006). Additionally, strong relationships between the distribution of tree species and topographic positions in the tabonuco forest have been noted (Wadsworth 1951, 1953, 1970; Johnston 1992); where some tree species occur only on ridges, while others occur exclusively in valleys (Wadsworth 1957; Johnston 1992) and the density, biomass, and richness of trees decreases from ridges to slopes to valleys (Basnet 1992; Weaver 2000). Earthworm distribution has also been found to vary according to topography in the tabonuco forest, with higher density and biomass of earthworms on ridges (118 ind./m^2 and 43.4 g/m^2) than in valleys (68 ind./m^2 and 23.5 g/m^2) (González *et al*. 1999). One previous study of arthropods in the tabonuco forest did not find a significant difference in the abundance of litter arthropods between ridge and valley topographic positions (Ruan *et al.* 2005) although another litter invertebrate study in this forest demonstrated a high degree of patchiness in arthropod distribution (Richardson *et al*. 2005). In this study, we quantified the density, biomass, and richness of orders of millipedes along a toposequence (ridges, slopes, and valleys) to determine if millipede distribution also follows a topographic pattern. Additionally, we quantified whether millipede density, biomass, and richness varies among different layers of the forest floor (litter, humus, 0-5 cm soil depth, 5-10 cm soil depth) to determine any interactions between topographic position and ground layer preference. We expect millipede abundance, biomass, and richness of orders to be significantly related to an increase in ground litter biomass given the results of 1) Ruan *et al*. (2005) that found millipede relative abundance significantly declined after litter removal and 2) Barros *et al*. (2002) who established that millipedes preferred litter opposed to any soil depth in Amazon forests. In the study site, litter biomass should be higher on slopes and valleys (Lugo and Scatena 1995; Weaver 2000). To our knowledge, this is the first study to describe the abundance and distribution of millipede orders within these microhabitats in a tabonuco forest in Puerto Rico.

MATERIALS AND METHODS

This study was conducted in a closed broad leaf subtropical wet forest located near El Verde Field Station (18º19' N, 65º45'W), in Río Grande, Puerto Rico. Vegetation at this elevation (420 m) is typical of a tabonuco forest, where *Dacryodes excelsa* is the dominant tree. The annual air temperature in the Luquillo Mountains is 22.3 °C (Brown *et al*. 1983), and mean annual precipitation is 3525 mm with rainfall distributed more or less evenly throughout the year (García-Martinó *et al*. 1996). The dominant soil orders in the Luquillo Experimental Forest are Ultisols and Inceptisols (Brown *et al*. 1983). Main soil series are further classified in the tabonuco forest as *Humatas* on ridges, *Zarzal* or *Cristal* on slopes, and *Coloso* in valleys (Johnston 1992; Soil Survey Staff 1995). Ridge sites often have lower pH, lower concentrations of cations, and higher carbon content while valley sites have higher pH, higher concentrations of cations, and lower carbon content (Scatena and Lugo 1995; Soil Survey Staff 1995).

Four replicates of each of the topographic positions (ridges, slopes and valleys) were chosen randomly, and sampled on June 19-23, 2006. Fifty by fifty centimeter plots were established at each site for a total of 12 plots sampled. Leaf litter, humus, 0-5 cm soil depth, and 5-10 cm soil depth were removed and placed into separate containers. Millipedes were immediately removed from each layer by hand sorting. In the lab, the millipedes were identified as to order and weighed (fresh). The density, biomass, and richness (in terms of orders) of millipedes were calculated. The litter and humus layers were collected from all 12 plots, sorted into categories (leaves, wood, fruit, and roots), dried, and weighed separately. Soil pH from each plot was measured by an Orion model 290A pH meter using a 1:1 water to soil ratio. Soil water content was also obtained from fresh soil samples from each of the 12 plots using a mix of 0-5 cm and 5-10 cm soil depth.

The general linear model procedure was used for multivariate analyses of variance (MANOVA) to test the effect of topographic positions and ground layers on the density, biomass, and orders of millipedes as well as on the characteristics of the ground litter (SPSS Inc., Statistical Package for the Social Sciences 2001, v. 11.0.1). Post hoc tests were performed to determine significant differences among topographic positions and ground layers for each of the dependent variables using Student-Newman- Keuls (SNK); alpha equaled 0.05 in all cases.

RESULTS

Millipedes

Millipedes belonging to four orders were found in this study: Stemmiulida (Family Stemmiulidae), Spirostreptida, Polydesmida and Glomeridesmida (Family Glomeridesmidae). Stemmiulida (n=67) and Spirostreptida (n=6) and Polydesmida (n=4) millipedes were the most and least abundant orders, respectively with Glomeridesmida (n=35) having an intermediate abundance. All orders of millipedes were significantly most abundant in the humus layer except Stemmiulida which was found in higher numbers in the 0-5 cm soil depth as compared to other layers (Fig. 1).

The overall mean density of millipedes in this tabonuco forest was 37.3 (±11.6) individuals/m^2. The density of millipedes was significantly less on the ridge positions (0.75 ±0.54 individuals/m^2) than in the slope and valley positions (14.00 ±5.49 and 13.25 ±3.11 individuals/m^2, respectively), although the density did not vary significantly among ground layers (Fig. 1; Table 1). The density of Glomeridesmida millipedes was significantly affected by both the topographic position and the

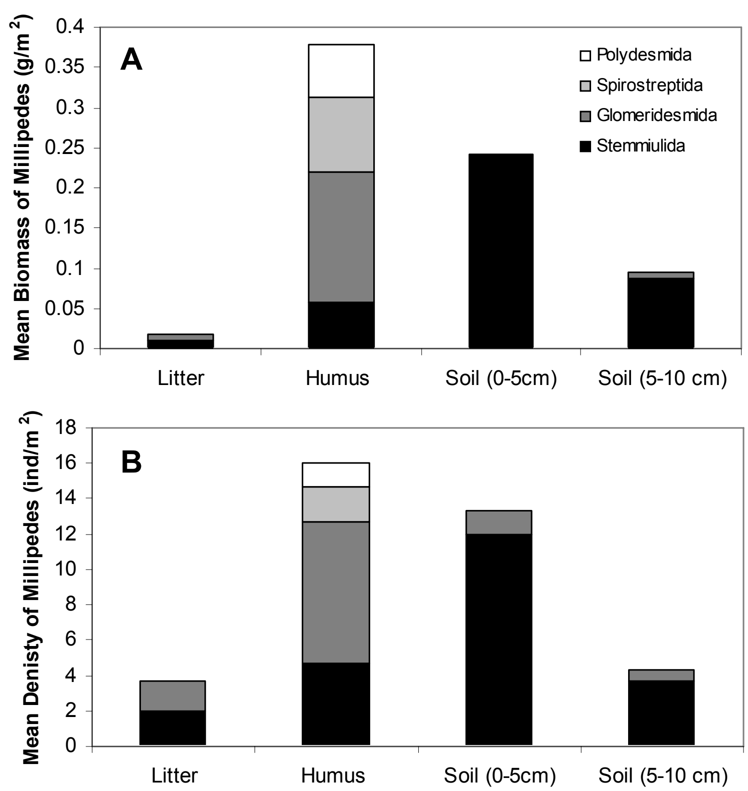

Figure 1. A) Mean biomass and B) density of millipedes among different ground layers in a subtropical wet forest in Puerto Rico.

ground layer and the interaction between them (Table 1). Glomeridesmida millipedes had a higher density in the valleys and the humus as compared to the other topographic positions and ground layers (Fig. 2). Polydesmida and Spirostreptida density was also significantly higher in the humus layer than in the other ground layers (Fig. 1). The biomass of millipedes did not significantly differ among topographic positions or ground layers (Table 1, Fig. 1). There was a significant effect of topographic position and ground layer on the richness of millipedes (Table 1). Ridges had significantly fewer orders than the slope and valley positions (Fig. 3). The humus layer had a significantly higher number of orders than the other three ground layers (Fig. 3).

Soil and Litter Characteristics

The topographic position had no significant effect on litter depth, total ground litter, leaves, wood, fruit, or root biomass (Table 2). There was significantly more biomass of wood and fruit in the humus layer than in the litter layer, while the depth, total ground biomass, leaves, and roots did not significantly differ between the two layers (Table 2). There was a significant and positive correlation between both ground wood and ground fruit biomass and the mean number of millipede orders (Table 3). In addition, there was a significant positive correlation between both ground wood and ground fruit biomass and total biomass of millipedes (Table 3). Ground fruit biomass was

Table 1. Effects of topographic position and ground layer on the density of millipedes as a whole and for each of the orders, the biomass of millipedes, and the richness of orders. Degrees of freedom (df), F and P values, and Power for MANOVA are presented. Bold numbers represent a significant effect of the source using SNK tests; α= 0.05.

Source	Dependent Variable	df	F	P	Power
Position	Overall Density	2	5.00	**0.01**	0.77
	Glomeridesmida Density	2	9.33	**<0.01**	0.97
	Polydesmida Density	2	1.50	0.24	0.30
	Spirostreptida Density	2	1.80	0.18	0.35
	Stemmiulida Density	2	2.98	0.06	0.54
	Biomass	2	1.95	0.16	0.38
	Orders	2	12.00	**<0.01**	0.99
Layer	Overall Density	3	2.60	0.07	0.59
	Glomeridesmida Density	3	6.33	**<0.01**	0.95
	Polydesmida Density	3	3.43	**0.03**	0.72
	Spirostreptida Density	3	5.40	**<0.01**	0.91
	Stemmiulida Density	3	1.50	0.23	0.36
	Biomass	3	1.75	0.17	0.42
	Orders	3	6.47	**<0.01**	0.95
Position x Layer	Overall Density	6	1.57	0.18	0.53
	Glomeridesmida Density	6	4.31	**<0.01**	0.96
	Polydesmida Density	6	1.50	0.21	0.51
	Spirostreptida Density	6	1.80	0.13	0.60
	Stemmiulida Density	6	1.05	0.41	0.36
	Biomass	6	0.78	0.59	0.27
	Orders	6	2.53	**0.04**	0.77

Figure 2. Density of Glomeridesmida millipedes in different topographic positions and ground layers from a Puerto Rican subtropical wet forest. Dissimilar letters indicate significant differences within the topographic position. (SNK, α= 0.05).

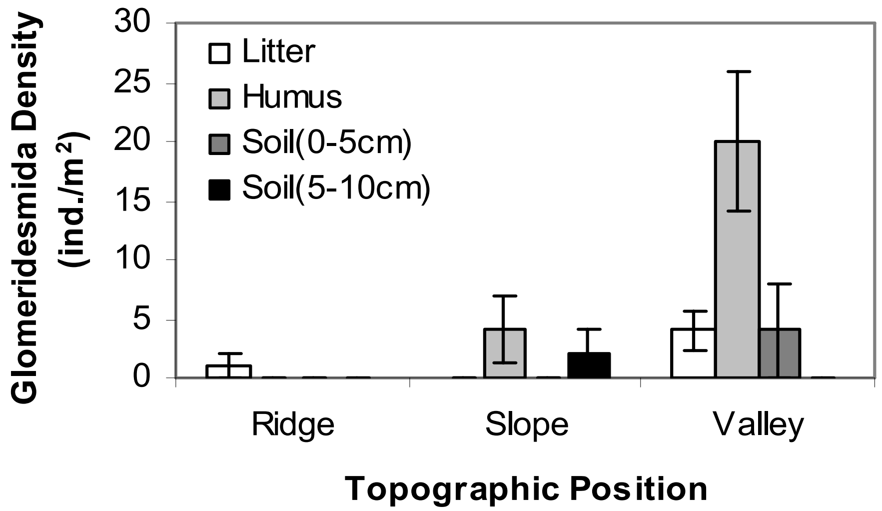

Table 2. The effect of position (Ridge, Slope, Valley) and layer (Litter and Humus) on different characteristics of the ground biomass. Degrees of freedom (df), F and P values, and Power for MANOVA are presented. Bold values represent significant effects (α= 0.05).

Source	Dependent Variable	df	F	P	Power
Position	Depth	2	1.59	0.23	0.29
	Total Ground Mass	2	0.03	0.97	0.05
	Leaves	2	0.20	0.82	0.08
	Wood	2	0.17	0.84	0.07
	Fruit	2	0.91	0.42	0.18
	Roots	2	0.58	0.57	0.13
Layer	Depth	1	2.39	0.14	0.31
	Total Ground Mass	1	3.41	0.08	0.42
	Leaves	1	1.83	0.19	0.25
	Wood	1	9.74	**<0.01**	0.84
	Fruit	1	8.73	**<0.01**	0.80
	Roots	1	2.15	0.16	0.28
Position x Layer	Depth	2	0.52	0.60	0.12
	Total Ground Mass	2	0.58	0.57	0.13
	Leaves	2	1.02	0.38	0.20
	Wood	2	0.49	0.62	0.12
	Fruit	2	0.92	0.42	0.18
	Roots	2	0.58	0.57	0.13

also significantly and positively correlated with the total density of millipedes (Table 3). We found that ridges were more acidic than slope and valley sites (Table 4). The soil pH of ridges was significantly different from the valley soil pH (Table 4). Soil pH and the number of millipede orders were significantly and positively correlated (Fig. 4).

DISCUSSION

We add to previous studies of the tabonuco forest that not just tree species and earthworms but now an arthropod's distribution is affected by topographic position, though not following the same pattern (Weaver 2000; González *et al*. 1999). As expected, slopes and valleys had significantly higher density and richness of millipedes than ridges. The biomass of millipedes followed a similar pattern but it was not significant. We also add that some variability in millipede distribution and density is affected not only by the position (ridge, slope, or valley) but also by the ground layer. Of these layers, the humus layer was the most diverse layer and had the highest biomass and density of millipedes

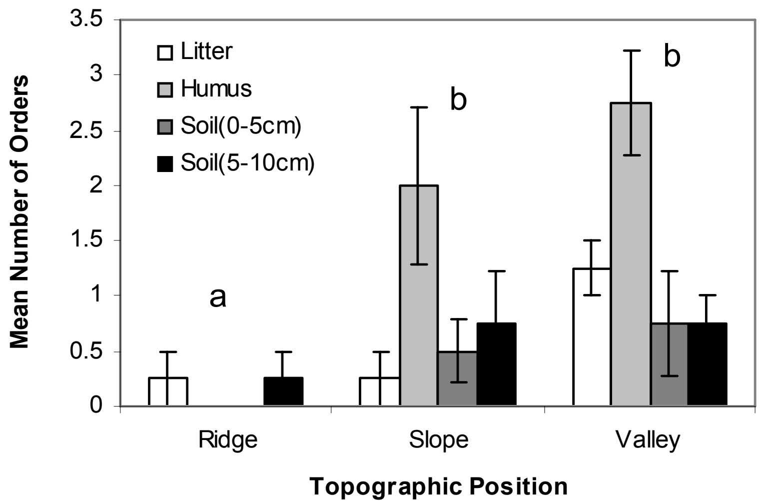

FIGURE 3. Mean number of orders along a toposequence for each of the ground layers in a subtropical wet forest in Puerto Rico. Error bars are + the standard error of the mean. Dissimilar letters indicate significant differences among the three topographic positions. (SNK, α= 0.05).

TABLE 3. Pearson correlation coefficients (r) between mean number of orders, the density, and biomass of millipedes and total biomass of ground litter, litter depth, and the biomass of individual parts of ground litter (leaves, wood, fruit, and roots). Bold numbers indicate P<0.05. Data were collected along a toposequence in the tabonuco forest in Puerto Rico.

Correlations	Mean number of orders	Total Density	Total Biomass
Leaves	0.27	0.14	0.31
Wood	**0.47**	0.28	**0.56**
Fruit	**0.64**	**0.41**	**0.79**
Roots	-0.07	-0.08	<0.01
Total Ground Litter	0.23	0.11	0.30
Litter Depth	0.24	0.06	0.12

Table 4. Mean soil pH and water content, and ground litter biomass (mean total litter, leaves, wood, fruit, and roots from the litter and humus layers per square meter) in different topographic positions in a subtropical wet forest (± standard error). Common letters within a column represent no significant difference (SNK, α= 0.05) among topographic positions.

Position	pH	Soil water content (%)	Ground litter (g)	Leaves (g)	Wood (g)	Fruit (g)	Roots (g)
Ridge	4.2±0.1[a]	211.1±34.6[a]	588.8±284.2[a]	393.2±150.3[a]	76.7±22.1[a]	6.7±4.5[a]	224.3±222.5[a]
Slope	4.5±0.1[ab]	191.9±28.6[a]	529.7±140.5[a]	390.6±69.0[a]	94.4±47.7[a]	11.7±5.1[a]	44.1±28.3[a]
Valley	4.8±0.1[b]	238.2±36.0[a]	577.8±74.7[a]	470.6±65.2[a]	73.5±16.8[a]	18.7±10.6[a]	24.1±13.0[a]

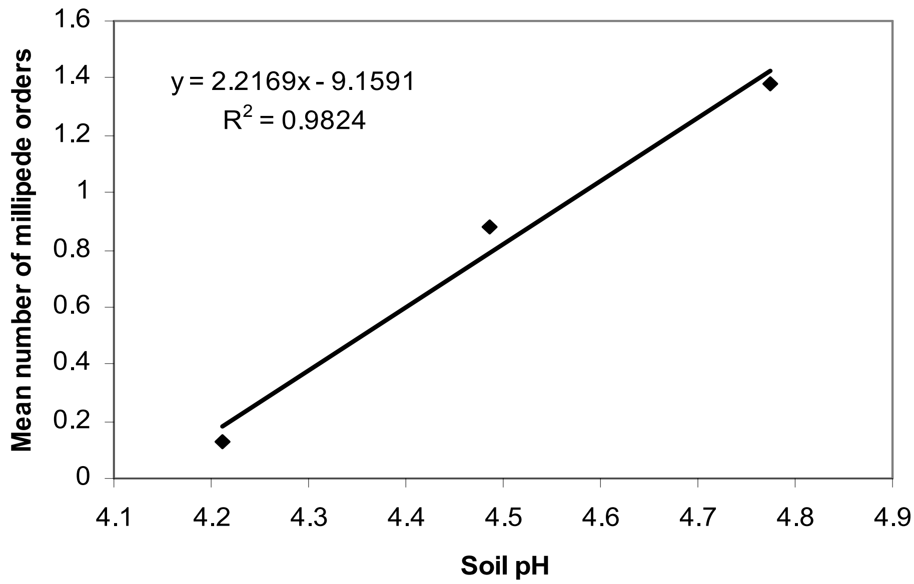

Figure 4. The relationship between the mean number of millipede orders and mean soil pH along the toposequence.

(although the latter two were not significant). This seems to be the best environment for most of the millipede orders (all of the millipede orders had the highest density in the humus except Stemmiulida) (Fig. 1). This layer retains more moisture than the litter layer and contains more wood and fruit, which could explain why millipedes prefer this microenvironment. Even though the diversity was the highest in the humus layer, the dominant group (Stemmiulida) had the highest density and biomass in the 0-5 cm of soil layer (Fig. 1), indicating the need not only to sample the litter and humus layers, which receive the most attention, but also the top soil layers when collecting and studying millipedes in this forest.

From this study, Stemmiulida seems to be the dominant order. The presence of this and other orders in the tabonuco forests in Puerto Rico was also found by Murphy and González in a pitfall trap/ soil core study but at much lower densities (unpublished data) (Table 5). Richardson *et al*. (2005) also found similar results of millipede density in their study of litter microarthropods in the same forest (Table 5). Comparison among studies is difficult because of differences in collection methods.

Hand sorting in the current study captured the larger millipedes (e.g. Stemmiulida) while hand sorting missed many of the more microscopic orders (Polyxenida and Polydesmida) that the other studies estimated at much higher densities. Also, Glomeridesmida are good at avoiding capture in pitfall traps because they can stick to the sides of containers and crawl out (C. Murphy, personal observation). Depending on the collection, method estimates of density vary, and we provide one more estimate to expand our understanding.

In other studies millipede density, biomass, and richness showed considerable variation. In Mediterranean France, Bertrand and Lumaret (1992) found millipede densities ranging from nearly 0 to 214 individuals/m^2 and biomass from 0.02 to 5.7 g/m^2. Millipedes in the Brazilian Amazon varied according to land use with a density ranging from 0-16 ind./m^2 in forests, 32-138 ind./m^2 in fallow lands, 0-86 ind./m^2 in agroforestry plantations, 13-22 ind./m^2 in pastures, and 0-64 ind./m^2 in croplands (Barros *et al*. 2002). Millipede biomass followed a similar pattern, with the lowest values in the forest (0-0.94 g/m^2) and the highest in tree plantations (0.12-10.59 g/m^2) (Barros *et al*. 2002). In tree plantations of *Casuarina equisetifolia*, *Leucaena leucocephala*, and *Eucalyptus robusta* in Puerto Rico, millipede densities (individuals/m^2) were found to be 19, 56, and 15, respectively; while biomass (g/m^2) was 5.6, 15.6, and 6.4, respectively (Warren and Zou 2002). Millipede biomass was also significantly higher in the 0-10 cm depth soil than 10-20 cm depth in *C. equisetifolia* and *L. leucocephala* plantations; millipede biomass was also significantly correlated with N concentrations and C/N ratio of the incompletely decomposed litter layer (Warren and Zou 2002). Our values for millipede density and biomass fall in the middle ground of most of these studies.

Wood and fruit in the litter and humus layers were correlated with an increase in the biomass, richness, and density of millipedes (the latter was not significant for the wood). These may be important resources for millipedes both as food and shelter and may help explain the patchiness of arthropod distribution in this forest (millipedes were often found under the bark of sticks and in one instance a concentration of about 25 millipedes was found in a hollowed out fruit). Jabin *et al*. (2004) found that in the interior of an oak-beech forest in Germany there was a significantly higher density of millipedes near (within 10 cm) coarse woody debris than further from coarse woody debris (>500 cm). Topp *et al*. (2006) also confirmed that millipede density in Slovakia is much higher close to coarse woody debris than further from it (60-230 ind./m^2 and 15–75 ind./m^2 respectively) as well as significantly higher species richness near coarse woody debris than away from it. Additionally, soil pH was significantly more basic near coarse woody debris (Topp *et al*. 2006), which could also influence the presence of millipedes.

Table 5. Density of millipedes (individuals/m^2) in subtropical wet forests in Puerto Rico as found by other researchers. Data published with permission of authors.

Orders	Richardson *et al.*, 2005[1]	Murphy and González[2]	Murphy and González[3]	Current study[4]
Stemmiulida	7.67	0.45	0.00	22.33
Spirostreptida	5.00	0.00	0.00	2.00
Polyxenida	0.67	0.00	39.72	0.00
Polydesmida	17.33	0.45	52.96	1.33
Glomeridesmida	8.33	0.00	0.00	11.67

[1]Litter and humus, Tulgren funnel extraction; [2]Pitfall traps (ind./m^2/day); [3]Soil cores, high-gradient extraction; [4]Litter, Humus, and soil to 10 cm depth, hand sorted.

Finally, we found that on the ridges the soil was more acidic than in the slopes and valleys (where we found higher density and richness of millipedes). The mean number of millipede orders was highly and positively correlated (r^2=0.98) with soil pH (Fig. 4). The soil pH could have been one of the factors driving the higher order richness in the slopes and valleys, although this is based on only a small sample and pH range. Dlamini and Haynes (2004) pointed out that earthworm numbers are positively related to soil pH among 11 different land-use sites (from forests to sugarcane farms) in tropical South Africa. Abbott (1985) suggested that soil pH and soil silt and clay texture were useful predictor variables for earthworm communities among 12 soil characteristics. Soil pH could be affecting community structure for both these forest floor dwellers, although these relationships should be investigated further and along a more extended pH gradient.

We established some factors influencing the distribution of millipedes in the subtropical wet forests of Puerto Rico, such as topographic position, ground layer, wood and fruit in the ground litter, and soil pH. Future millipede studies could further investigate these relationships.

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