Pedobiologia 44, 545–555 (2000)

http://www.urbanfischer.de/journals/pedo

Pedo
biologia

Comparison of the abundance and composition of litter fauna in tropical and subalpine forests

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Accepted: 24. March 2000

Summary

In this study, we quantify the abundance and composition of the litter fauna in dry and wet tropical forests and north- and south-facing subalpine forests. We used the same litter species contained in litterbags across study sites to standardize for substrate conditions, and a single method of fauna extraction from the litter (Tullgren method). Fauna densities were calculated per gram of dry litter. We found a higher density of total litter fauna and a higher taxonomic diversity in the tropical wet forest (80 individuals and 4 orders per g of dry litter and) as compared to the tropical dry (6 individuals and 1.5 orders per g of dry litter) and the subalpine forests (6–11 individuals and 2 orders per g of dry litter). Oribatid mites (Cryptostigmata) were the most abundant group of fauna across the study sites. The abundance of both micro- and macroinvertebrates was significantly higher in the tropical wet forest than all other sites. Taxonomic diversity (number of orders) was positively correlated with plant litter decomposition across all the sites. We conclude there is a significantly higher density of litter fauna and a greater taxonomic diversity per gram of litter in the tropical wet forest than in the tropical dry and the subalpine forests. Both of these factors can contribute to the differences in litter decomposition rates among the tropical and the subalpine sites.

Key words: tropical wet forest, tropical dry forest, subalpine forest, soil fauna, litter decomposition, diversity

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0031–4056/00/44/05–545 $ 12.00/0

Introduction

Decomposers are a species rich component of terrestrial ecosystems (Stanton 1979). These invertebrates differ in size, numbers, food sources, and interactions with food webs (Edwards & Bohlen 1995). Different ecosystems have different soil invertebrate communities that differentially facilitate the breakdown of organic matter (Heneghan et al. 1999; González & Seastedt, in press), contribute significantly to decomposition and nutrient cycling (Seastedt 1984; Moore et al. 1988), influence the functioning of the decomposer flora (Seastedt 1984; González & Seastedt, in press), and increase overall soil fertility (Edwards & Bohlen 1995).

The global pattern observed in the composition and abundance of the decomposer fauna suggests that the abundance and diversity of various soil fauna change with latitude (Swift et al. 1979). The soil microfauna (< 1 cm in length) are relatively more abundant in the temperate regions than they are in the tropics, whereas soil macrofauna (> 1 cm) are more common in the tropical regions than in the temperate zones. Seastedt (1984) summarized studies showing that the densities of microarthropods in the soil are typically higher in boreal forests than in the tropics. Densities of arthropods are approximately 300,000 or more per m^2 in boreal systems versus less than 50,000 per m^2 in the tropical forests. However, temperate forest ecosystems have low rates of mineralization in part due to slow biological activities (Deleporte & Tillier 1999). As a result, a greater standing crop of litter is present in the temperate systems as compared to the tropics. Tropical ecosystems have a high functional diversity of soil organisms in addition to milder climate. Therefore, the relative activity of the organisms is also presumably higher in the tropics (González & Seastedt, in press).

Few soil biologists have compared the composition of soil fauna across geographic areas, particularly temperate vs. tropical forests (Stanton 1979; Levings & Windsor 1985). Problems in doing such comparative work include varying type and amounts of litter across sites (Heatwole 1961; Stanton 1979), and inconsistency of extraction methods for the fauna (Peterson & Luxton 1982). In this study, we quantify the composition of litter fauna across a climatic gradient: in dry and wet tropical forests, and north- and south-facing subalpine forests. We extracted the fauna from litter using the Tullgren extraction method. Known amounts of two litter species contained in litterbags were employed to standardize for substrate conditions. An advantage of using this approach is that data of litter fauna within each site can then be correlated with litter decay rates, which are also obtained with this procedure. The relative density of the major groups of fauna was calculated in numbers per gram of dry litter. The objectives of this study are to: (1) quantify the abundance of the various groups of litter fauna in sites representing large differences in climate as measured by actual evapotranspiration rate (AET), and (2) determine how the relative density of these invertebrates changes along a climatic gradient.

Materials and Methods

Study sites

Two subtropical sites that include a wet and a dry forest, and two temperate sites that include north- and south-facing subalpine forests were chosen for the study. The subtropical wet forest is located in the Luquillo Experimental Forest (LEF) (18°20'N 65°49'W), and the subtropical dry forest is located in the Guánica Biosphere Reserve (17°57'N, 65°52'W), both in the island of Puerto Rico. Annual air temperature in LEF is 22.3 °C (Brown et al. 1983) and mean annual precipitation is 3524 mm (García-Martinó et al. 1996), with rainfall distributed more-or-less evenly throughout the year. *Dacryodes excelsa* Vahl. is the prevailing tree species at this elevation (420 m) (Zimmerman et al. 1995; Zou et al. 1995). The dominant soils are Oxisols classified as moderately well drained and have volcanic and sedimentary origin (Soil Survey Staff 1995). Annual air temperature in Guánica is 25.1 °C and average precipitation is 860 mm. Elevation is 160 m and the plant communities are typical of a semideciduous forest (Murphy & Lugo 1986). Soils have developed from a limestone bedrock and are categorized as stony, shallow and dry (Carter 1965). AET values for the study period (July 1997–Jan 1999) in the LEF and Guánica forests were 1342 and 891 mm, respectively.

The temperate north and south-facing subalpine forests are located near the Mountain Research Station (40°03'N, 105°36'W), 50 km west of Boulder, Colorado on the eastern slope of the Rocky Mountains. The subalpine sites are at an approximate elevation of 3400 m. Annual air temperature is 1.3 °C, and average precipitation is 692 mm (Greenland 1989). Vegetation is dominated by lodgepole pine (*Pinus contorta* var. *latifolia* Engel.) (Marr 1961), and soils are shallow Entisols and are coarse-textured (Johnson & Cline 1965). The AET value was 320 mm for the subalpine forests.

Experimental Design

Recently senesced leaves of *Quercus gambelii* Nuttall (scrub oak) and *Cecropia scheberiana* Miq. (yagrumo) were collected in the fall of 1996 at Roxborough Park in Colorado and at LEF in Puerto Rico, respectively. Measured amounts of approximately 3 g of scrub oak and 5 g of yagrumo air-dried leaves were placed separately in 16×16 cm fiberglass litterbags (1.8×1.6 mm mesh). This mesh size prevents the loss of litter fragments and does not inhibit the indirect effects of earthworm casts. In the summer of 1997, a total of 416 litterbags (272 litterbags in the tropical and 144 litterbags in the subalpine sites) were placed in four random plots in each of the four sites (34 bags per plot at the tropical wet and dry sites, and 18 bags per plot at the north and south-facing subalpine sites). Plots were 0.8 x 1.5 m in the tropics and 0.8×0.8 m in the subalpine forests. From July 1997 to January 1999, litterbags were collected randomly from each of the tropical and subalpine plots every two-three months and every 5–6 months, respectively (n = 2 bags/species/date/plot). A subset of four litterbags per site per collecting date per litter was placed in modified Tullgren extractors to remove all arthropods. Litter fauna were classified into broad taxonomic units. Mites were classified as: Cryptostigmata, Mesostigmata, Prostigmata, Astigmata (suborders, Acarina). Following the faunal extraction, the litter was oven-dried (60°C) and reweighted to determine remaining mass, and fauna densities were calculated per gram of dry litter.

Data Analysis

Data were tested for homogeneity of variance by using the Levene's test of equality of error variances and skewness (SPSS 9.0 Win). Log-transformations were employed when the data did not meet the assumptions of normality. The significant level was set at $\alpha = 0.05$. Annual decomposition rates (k) were calculated using a single negative exponential decay model (Olson 1963) by regressing the natural logarithm of the mean percent of mass remaining per plot vs. time.

Two 2 way-MANOVA (GLM) analyses were performed to look at the effect of site and litter species (independent variables) on: (1) the density of the various groups, and (2) the size and predator composition (dependent variables) of the litter fauna. One-way ANOVA was used to test for differences in the mean number of orders among sites. A simple linear regression analysis (GLM) was then performed between the number of orders and the annual decay rates.

Results

There was a significant effect of site and a non significant effect of litter species on the density of the various groups of litter fauna (Table 1). The densities of Acari (mites), crustaceans (isopods), diplopods (millipedes), collembolans (springtails), hymenopterans (ants), and homopterans (mostly coccids) were different among the forest sites (Table 2). Mites were most abundant in the tropical wet forest (70 individuals per gram of dry litter), and least abundant in the tropical dry forest (2 per gram of dry litter). Intermediate abundance of mites (5–10 per gram of dry litter) was found in the subalpine forests as compared to the tropical forests. Crustaceans, millipedes, and coccids were exclusively found in the tropical wet forest (Table 2). The density of collembolans was the lowest in the tropical dry forest as compared to all sites. However, it was not significantly different between the tropical wet and the subalpine forests. Ants were absent in the subalpine forests. An average of 4 ants per gram of dry litter was found in the tropical wet forest as compared to less than 1 in the tropical dry forest. The total density of fauna was the highest in the tropical wet forest (80 individuals per gram of dry litter), and the lowest in the tropical dry forest (2 per gram of dry litter). An intermediate total density of fauna was found in the subalpine forest (6–11 per gram of dry litter) when compared to the tropical sites (Table 2).

Table 1. Effects of site and litter species on the density of fauna groups in *Quercus gambelii* and *Cecropia scheberiana* litterbags. Degrees of freedom (df), F and P values, and Power for a two-way MANOVA are presented ($n = 160$)

Source	df	F	P	Power
Site	3	2.65	0.000	1.00
Litter	1	0.66	0.859	0.48
Site × Litter	3	0.58	0.995	0.78

Mites dominated the density of litter fauna in all sites (82–92 %) (Table 2). In the tropical dry and the subalpine forests, collembolans were the second most abundant group of fauna. In the tropical wet forest, ants are the second most abundant group of fauna, and collembolans the third. Ants, spiders, thysanurans (bristletails), and pseudoscorpions were present in the tropical dry forest. A higher number of faunal groups was present in the tropical wet forest as compared to all sites, although the relative density of most of those groups was less than 1 % (Table 2). On average, there is a significantly higher number of orders in the tropical wet forest than the tropical dry and the subalpine forests (Fig. 1). There was a significant linear relationship between the number of orders and the annual decay rates of *Q. gambelii* and *C. scheberiana* ($R^2 = 0.58$, $P = 0.03$) (Fig. 2). In the tropical wet forest, decay rates of *Q. gambelii* and *C. scheberiana* were 1.98 and 1.46 y^{-1}, respectively. In the subalpine forests, average decay rates of *Q. gambelii* and *C. scheberiana* were about 0.20 and 0.02 y^{-1}, respectively (Fig. 2).

Oribatid mites (Cryptostigmata) dominated the total density of mites in the tropics and the south-facing subalpine forests (Table 3). In the north-facing subalpine forest,

Table 2. Mean (± standard error) and relative density (numbers per g of dry litter) of fauna in tropical wet and dry, and north- and south-facing subalpine forests in *Quercus gambelii* and *Cecropia scheberiana* litterbags. Common letters within a faunal group represent no significant difference of density among the sites (MANOVA: SNK, $\alpha = 0.05$). ($n = 28$ for the tropics, and 14 for the subalpine forests)

	Tropics				Subalpine			
Taxonomic unit	Dry		Wet		North		South	
	Density	%	Density	%	Density	%	Density	%
Araneida	0.06±0.02a	2.51	0.42±0.17 a	0.52	0.03±0.02 a	0.50	0.01±0.01 a	0.09
Pseudoscorpionida	0.03±0.02a	1.25	0.02±0.02 a	0.02	0 a	0	0 a	0
Acari	1.99±1.05a	83.26	69.87±15.65c	86.83	4.94±1.36 b	82.47	10.31±3.80b	92.14
Crustacea	0 a	0	1.30±0.43 b	1.61	0 a	0	0 a	0
Diplopoda	0 a	0	0.70±0.32 b	0.87	0 a	0	0 a	0
Chilopoda	0 a	0	0.09±0.06 a	0.11	0 a	0	0 a	0
Collembola	0.13±0.13a	5.44	1.48±0.54 b	1.84	0.92±0.39 b	15.36	0.82±0.19 b	7.33
Thysanura	0.05±0.03a	2.09	0.05±0.03 a	0.06	0 a	0	0 a	0
Coleoptera	0.01±0.01a	0.29	0.10±0.06 a	0.12	0.03±0.02 a	0.50	0 a	0
Hymenoptera	0.07±0.04a	3.10	4.23±2.58 b	5.26	0 a	0	0 a	0
Homoptera	0 a	0	0.24±0.09 b	0.30	0 a	0	0 a	0
Diptera	0 a	0	0.07±0.06 a	0.09	0 a	0	0 a	0
Psocoptera	0 a	0	0.02±0.07 a	0.03	0 a	0	0 a	0
Thysanoptera	0.01±0.01a	0.54	0.05±0.04 a	0.06	0 a	0	0 a	0
Total †	2.39±1.10a		80.16±17.70c		5.92±1.65 b	11.19±3.74	b	

† includes unknowns and immatures

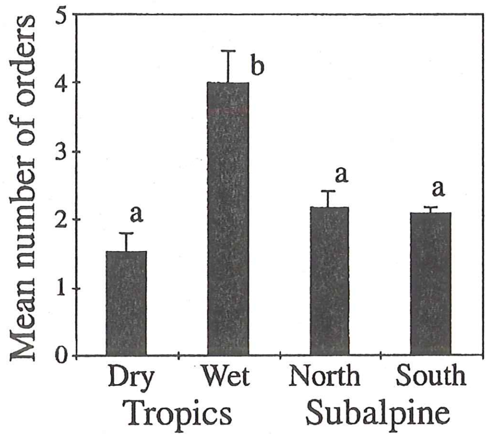

Fig. 1. Mean (± standard error bars) number of orders in tropical dry and wet forests, and north- and south-facing subalpine forests.

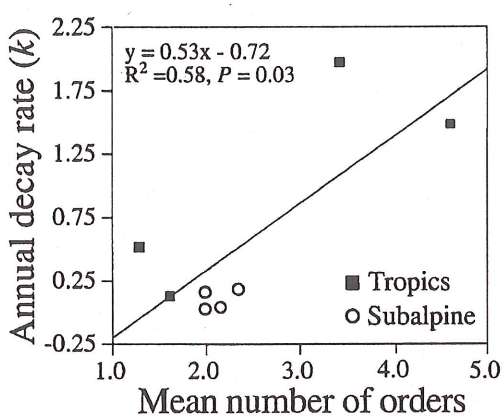

Fig. 2. Relationship of mean number of orders and the decomposition rates (k) of *Quercus gambelii* and *Cecropia scheberiana* in tropical dry and wet forests, and north- and south-facing subalpine forests

mesostigmatid mites constituted 46 % of the total density of mites, oribatids represented 29 %, and prostigmatid mites 22 %. Oribatid and astigmatid mites were significantly more abundant in the tropical wet forest as compared to the tropical dry and the subalpine forests. The densities of mesostigmatid and prostigmatid mites were the lowest in the tropical dry forest as compared to all sites, but did not differ among the tropical wet and the subalpine forests (Table 3).

There was a significant effect of site and a non-significant effect of litter species on the density of micro-, macroinvertebrates and predators (Table 4). Microinvertebrates were most abundant in the tropical wet forest, and least abundant in the tropical dry forest, with an intermediate abundance of microinvertebrates in the subalpine forests. Macroinvertebrates (> 3 mm) were more abundant in the tropical wet forest than the tropical dry and the subalpine forests. The density of macroinvertebrates did not differ among the tropical dry and the subalpine forests. The predator density was the lowest in the tropical dry forest as compared to all sites, and did not differ among the tropical wet and the subalpine forests (Table 5).

Table 3. Mean (± standard error) and relative density (numbers per g of dry litter) of suborders of Acari (mites) in tropical wet and dry, and north- and south-facing subalpine forests in *Quercus gamelii* and *Cecropia scheberiana* litterbags. Common letters within a mite group represent no significant difference of density among the sites (MANOVA: SNK $\alpha = 0.05$). ($n = 28$ for the tropics, and 14 for the subalpine forests)

	Tropics				Subalpine			
Taxonomic unit	Dry		Wet		North		South	
	Density	%	Density	%	Density	%	Density	%
Cryptostigmata	1.46±1.05a	73.4	43.17±7.54c	61.8	1.45±0.59a	29.3	4.97±2.58b	48.2
Mesostigmata	0.10±0.04a	4.9	8.90±2.30b	12.7	2.27±0.67b	45.9	3.07±0.79b	29.8
Prostigmata	0.19±0.13a	9.5	0.72±0.26ab	1.0	1.07±0.35b	21.7	0.85±0.30b	8.2
Astigmata	0.19±0.12a	9.5	15.83±8.02b	22.7	0.13±0.06a	2.6	1.18±0.80a	9.7
Total †	1.99±1.05a		69.87±15.65c		4.94±1.36b		10.31±3.80b	

† includes unknowns and immatures

Table 4. Effects of site and litter species on the density of microinvertebrates (< 3 mm), macroinvertebrates (> 3 mm) and predators in *Quercus gambelii* and *Cecropia scheberiana* litterbags. Degrees of freedom (df), F and *P* values, and Power for a two-way MANOVA (Pillai's Trace) are presented ($n = 160$)

Source	df	F	*P*	Power
Site	3	13.09	0.000	1.00
Litter	1	0.95	0.418	0.26
Site × Litter	3	0.35	0.958	0.18

Table 5. Density (numbers per g dry litter) of microinvertebrates (< 3 mm), macroinvertebrates (> 3 mm) and predators in tropical dry and wet, and north- and south-facing subalpine forests in *Quercus gambelii* and *Cecropia scheberiana* litterbags. Values are means ± standard error. Common letters within a column represent no significant difference of density of a trophic group among the sites (MANOVA: SNK, $\alpha = 0.05$)

Site		Microinvertebrates †	Macroinvertebrates	Predators
Tropical	Dry	1.84±1.01a	0.22±0.06a	0.19±0.05a
	Wet	61.52±14.24c	6.87±3.20b	9.34±2.48b
Subalpine	North	3.63±1.07b	0.03±0.02a	2.30±0.67b
	South	7.81±3.34b	0 a	3.08±0.79b

† Statistics performed on log +1 transformed data

Discussion

The main goal of this study was to quantify and compare the composition of litter fauna in tropical and subalpine forests. We used the same litter species across the study sites to standardize for substrate conditions, and a single method of fauna extraction from the soil (Tullgren method). We quantified the density of major groups of fauna in numbers per gram of litter, and found: (1) a higher density of the total litter fauna, and (2) a greater proportion of other fauna besides collembolans and mites in the tropical wet forest than the tropical dry and the subalpine forests.

In a review of 19 studies from temperate, arctic and semi-arid ecosystems, Seastedt (1984) reported that mites and collembolans account for about 95 % of the total microarthropod numbers in the soil. Oribatid mites (Cryptostigmata) are the most numerically abundant group in most forest ecosystems compromising about 50 % of the total microarthropod fauna. In this study, we found that mites and collembolans accounted for 89 to 99.5 % of the total litter fauna in both tropical forests and the south-facing subalpine forest, respectively (Table 2). Oribatid mites were the most dominant group of mites in the tropics and the south-facing subalpine forest, whereas in the north-facing subalpine forest, oribatid mites were the second most abundant group of mites after the mesostigmatids (Table 3). Therefore, this finding further supports the conclusion of oribatid mites being the most abundant group of fauna in forested ecosystems.

Mites and collembolans were abundant in the tropics, but the relative density of other fauna besides these two groups was higher in the tropics than in the subalpine forests (Table 2). The mean number of orders was significantly higher in the tropical wet forest than all other sites (Fig. 1). Furthermore, the density of macroinvertebrates was the highest in the tropical wet forest (Table 5). Swift et al. (1979) reviewed the patterns of latitudinal variation in the contribution of the macro-, meso- and microfauna to the total soil fauna. He concluded that soil macrofauna were more abundant in the tropics than they were in temperate regions, whereas soil microfauna were more common in temperate regions than in the tropics. In this study, we found that the density of both micro- and macroinvertebrates to be higher in the tropical wet forest than in the tropical dry and the subalpine forests. However, the relative abundance of soil microinvertebrates to macroinvertebrates was greater in the subalpine forests than in the tropics. In fact, macroinvertebrates were completely absent in the north-facing subalpine forests.

The implication of a more diverse assemblage of litter fauna is an acceleration of decomposition rates and nutrient mineralization processes in the tropical wet forest as compared to the tropical dry and the subalpine forests (e.g. Heneghan et al. 1999; González & Seastedt, in press). This contention is further supported by the significant and positive relationship between the mean number of orders and the annual decomposition rates of *Cecropia scheberiana* and *Quercus gambelii* (Fig. 2), where higher number of orders relate to a faster decomposition rate. A review of mostly temperate zone studies indicated that the presence of microarthropods accelerates plant litter disappearance by an average of 23 % (Seastedt 1984). (González & Seastedt, in press) showed that faunal effects on litter breakdown can account for up to 66 % in the tropical wet forest. However, this study and (González & Seastedt, in press) quantified the abundance of the fauna contained in litterbags as opposed to the entire soil profile. Therefore, these studies could underestimate diversity measures and faunal effects on decomposition.

Heneghan et al. (1998) studied the soil microarthropod community structure and litter decomposition dynamics in two tropical sites (LEF and Costa Rica) and a temperate forest (North Carolina). They found faster litter decomposition rates in the tropics than in the temperate forest, and suggested it was due to a higher diversity of soil fauna in the tropics in spite of higher soil fauna densities in the temperate forest (Heneghan et al. 1998). Seastedt (1984) reviewed data on soil arthropods per unit of area (i.e. numbers per m^2) and showed higher densities of soil fauna in boreal forests than in tropical forests. Data obtained from Seastedt (1984) and Heneghan et al. (1998) are consistent with the idea of higher soil fauna density in temperate forests than in tropical forests. This study is similar to Heneghan et al. (1998) in that it suggests: (1) a more diverse assemblage of litter fauna in the tropics than in the subalpine forests, and (2) that a diverse assemblage of litter fauna relates to faster decomposition rates (Fig. 2). However, when the density of fauna from the tropical wet and the subalpine forests is compared in terms of numbers per gram of dry litter, then the density of fauna is higher in the tropical wet forest than in the subalpine forests. Greater standing crop of litter in the temperate forests than in the tropics can explain the high density of fauna per unit of area. Therefore, not only the functional diversity of litter fauna is higher in the tropics than in the temperate forests but also the actual abundance of fauna per gram of litter is amplified in the tropical wet forests. Either one or both of these confounding effects may contribute to the differences in litter decomposition rates between the tropical wet and the subalpine forests. Given warmer annual temperatures, the relative activity of the fauna is also presumably higher in the tropics (González & Seastedt, in press).

González and Seastedt (in press) reported no significant differences in the decomposition rates of *C. scheberiana* and *Q. gambelii* between the tropical dry and the subalpine forests in the presence of fauna. The actual evapotranspiration (AET) was the highest in the tropical wet forest, and the lowest in the subalpine forests. The tropical dry forest had an intermediate value of AET when compared to the other sites. In this study, we report: (1) the lowest density of litter fauna in the tropical dry forest and, (2) no significant differences in the number of orders between the tropical dry forest and the subalpine forests. Therefore, the abundance and taxonomic diversity of litter fauna did not increase as a function of AET. The inconsistent relationship between the densities and taxonomic diversity of fauna and AET shows the difficulty of predicting decomposition rates by using climate as a single regulating factor.

We conclude there is a significantly higher density of litter fauna and a greater taxonomic diversity per g of litter in the tropical wet forest than in the tropical dry and the subalpine forests. These data are consistent with a hypothesis that the relative importance of fauna on decomposition processes is greater in the wet tropics than other areas, and that this effect may be generated by both greater densities of fauna per unit of litter and greater functional diversity of the fauna.

Acknowledgements

This research was supported by the Biosphere Atmosphere Research Training Program (BART) to the University of Colorado at Boulder, the Long Term Ecological Research (LTER) program, and a NASA (NAGW 4059) grant to the University of Puerto Rico. We thank William A. Gould, Nobuhiro Kaneko, Heather E. Reed, Xiaoming Zou and an anonymous reviewer for commenting on an earlier version of the manuscript.

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