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Grizelle González · Ruth E. Ley · Steven K. Schmidt
Xiaoming Zou · Timothy R. Seastedt

Soil ecological interactions: comparisons between tropical and subalpine forests

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Abstract Soil fauna can influence soil processes through interactions with the microbial community. Due to the complexity of the functional roles of fauna and their effects on microbes, little consensus has been reached on the extent to which soil fauna can regulate microbial activities. We quantified soil microbial biomass and maximum growth rates in control and fauna-excluded treatments in dry and wet tropical forests and north- and south-facing subalpine forests to test whether soil fauna effects on microbes are different in tropical and subalpine forests. Exclusion of fauna was established by physically removing the soil macrofauna and applying naphthalene. The effect of naphthalene application on the biomass of microbes that mineralize salicylate was quantified using the substrate induced growth response method. We found that: (1) the exclusion of soil fauna resulted in a higher total microbial biomass and lower maximum growth rate in the subalpine forests, (2) soil fauna exclusion did not affect the microbial biomass and growth rate in the tropical forests, and (3) the microbial biomass of salicylate mineralizers was significantly enhanced in the fauna-exclusion treatment in the tropical wet and the south-facing subalpine forests. We conclude that non-target effects of naphthalene on the microbial community alone cannot explain the large differences in total microbial biomass found between control and fauna-excluded treatments in the subalpine forests. Soil fauna have relatively larger effects on the microbial activities in the subalpine forests than in tropical dry and wet forests.

Keywords Soil fauna · Tropics · Subalpine · Naphthalene · Substrate induced growth response

G. González (✉) · T.R. Seastedt
Institute of Arctic and Alpine Research and Department of EPO Biology, University of Colorado at Boulder, 1560 30th St., Boulder, CO 80309–0450, USA

R.E. Ley · S.K. Schmidt
Department of EPO Biology, University of Colorado at Boulder, Campus Box 334, Boulder, CO 80309–0334, USA

X. Zou
Institute for Tropical Ecosystem Studies, University of Puerto Rico, P.O. Box 363682, San Juan, PR 00936, USA

Present address:
G. González, International Institute of Tropical Forestry, US Forest Service, PO Box 25000, San Juan, PR 00928–5000, USA, e-mail: ggonzalez@fs.fed.us

Introduction

Soil fauna can influence soil processes via two main pathways: directly, by physically modifying the litter and soil environments, and indirectly, through interactions with the microbial community (Fig. 1; e.g. Seastedt 1984; Brown 1995; Lavelle et al. 1997). Soil fauna and microbial interactions are diverse. First, microarthropods can modify the surface area of organic substrates and affect microbial colonization and use. Webb (1977) argued that microarthropod feces may reduce the surface to volume ratio of organic materials. However, a review of 19 experimental studies from temperate, arctic and semi-arid ecosystems showed that the presence of microarthropods accelerates plant litter disappearance an average of 23% (Seastedt 1984). González and Seastedt (2001) reported that faunal effects on litter breakdown can be up to 66% in a tropical wet forest. Therefore, indirect effects of soil fauna on microbial activities can be generally considered positive as soil fauna increase the surface area for microbial use. Second, soil fauna can feed on microbes altering the microbial biomass and turnover rates. For example, oribatid mites (Cryptostigmata) may stimulate fungal growth by grazing on senescent hyphae (Griffiths and Bargett 1997) but, depending on the foraging intensity, net microarthropod effects on microbial activity could also be negative. Hanlon and Anderson (1979) reported inhibition of soil microbial respiration as the number of grazing collembolans was increased beyond an optimal number. Microbivorous arthropods (e.g. collembolans) may selectively graze thereby influencing fungal species composition and decomposition rates (Newell 1984). Selective feeding by soil fauna causes a reduction in microbial biomass (e.g. Parkinson et al.

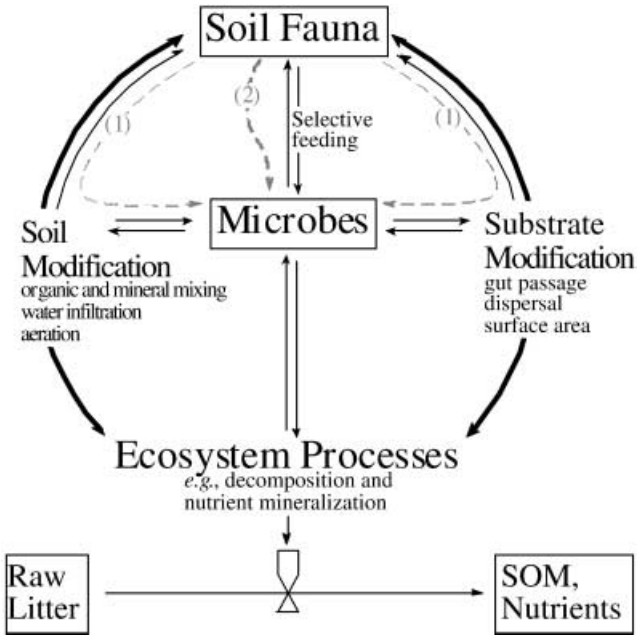

Fig. 1 Conceptual model indicating direct (—) and indirect (—) paths by which soil fauna affect ecosystem processes. Two hypotheses are illustrated: (1) soil fauna regulate microbial activities (*dashed lines 1,2*), and (2) the regulatory effect is maximized in the subalpine forests, where microarthropod densities are high (*dashed line 2*)

1979; Newell 1984). In addition, soil fauna can affect microbial community structure and activities through dispersal of spores on their integument, and by stimulation of microbial populations in their gut (Anderson 1987). Therefore, due to the functional complexity of soil organisms, and the complexity generated by their interactions, little consensus has been reached as to what extent soil fauna can regulate microbial activities (Moore and Walter 1988). Furthermore, no information is available about whether this regulation varies along latitudinal gradients.

The relative abundance of various soil fauna changes with latitude. Soil macrofauna (>1 cm in length) are more abundant in the tropics than they are in temperate regions, whereas soil microfauna (<1 cm) are often more common in temperate regions than in the tropics (Swift et al. 1979). Macrofauna are important in the mixing of soil organic and mineral materials. Microfauna primarily ingest microorganisms and other microfauna (Wardle 1994; Lavelle et al. 1997). Macrofauna eat relatively large amounts of litter compared to microbes, although they also consume the microflora adhering to these substrates (Newell 1984). In contrast, due to more selective grazing patterns, the microfauna could have a stronger selective effect than macrofauna on microbial communities.

Superimposed on the abundance differences are the effects of climate on the activities of soil fauna. Climatic determinants are likely less important regulating factors of invertebrate activity in the tropics than in temperate ecosystems (Lavelle et al. 1993). Compared to temperate regions, climate is relatively constant the year round in the tropics. However, temperatures below 0°C in the temperate zones may greatly reduce the feeding activities of microarthropods due to lethal effects of ice formation (Leinaas 1981). Therefore, the control that soil fauna exert on microbes is potentially different in tropical and temperate ecosystems.

Most studies on soil fauna-microbial interactions have looked at the effects of particular species on microbial activities (e.g. Hanlon and Anderson 1979; Newell 1984; Teuben and Roelofsma 1990) and have been limited to microcosm experiments (Vedder et al. 1996). To our knowledge, no field experiment has measured the effects of soil fauna on microbes over a wide climatic gradient. In this study, we excluded the soil fauna in tropical and subalpine forests in order to: (1) quantify soil fauna effects on microbial biomass and maximum growth rates, and (2) test if the soil fauna exhibits different effects on microbial activities under diverse climatic conditions. We tested two hypotheses. First, we hypothesized that soil fauna can regulate microbial metabolism (e.g. biomass and maximum growth rate). Second, we hypothesized that this regulatory effect would be maximized in the subalpine forest, where microarthropod densities are high.

We used physical methods to exclude the soil macrofauna, and naphthalene to reduce the numbers of microarthropods. Some authors have pointed out the potential for increasing bacterial activity by using this biocide (e.g. Witkamp and Crossley 1966; Seastedt and Crossley 1981; Newell et al. 1987; Blair et al. 1989). However, Blair et al. (unpublished data) found no microbial changes in naphthalene-treated plots as compared to untreated plots in a field experiment. Therefore, we measured the effects of the fauna-exclusion treatment on the biomass and growth rate of the total microbial biomass and a specialized group of microbes, the salicylate mineralizers. Salicylate mineralizers are a functional group likely to be stimulated by the addition of naphthalene, as salicylate is not only a natural product of many plants but is also an intermediate in the most common naphthalene degradation pathway (Frantz and Chakrabarty 1986). Estimates of microbial biomass and maximum growth rates of functional groups were obtained with the recently developed substrate-induced growth response (SIGR) method (Schmidt 1992; Colores et al. 1996).

Materials and methods

Study sites

In the summer of 1997, four sites representing large differences in climate as measured by actual evapotranspiration rates (AET) were chosen for the study: two subtropical sites that include a wet and a dry forest, and two temperate sites that include north- and south-facing subalpine forests. 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) on the island of Puerto Rico. Mean

annual air temperature in LEF is 22.3°C (Brown et al. 1983) and annual precipitation is 3,524 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 moderately well drained Oxisols of 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 and 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–January 1999) in the LEF and Guánica forests were 1,342 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 3,400 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 coarse-textured (Johnson and Cline 1965). The AET value was 320 mm for the subalpine forests.

Experimental design

Within each of the four sites (tropical wet and dry, and north and south-facing subalpine forests), a randomized block design of four blocks with two plots within each block was established. Plots were 0.8×1.5 m in the tropics and 0.8×0.8 m in the subalpine forests. Two treatments (Fauna-excluded vs Control) were randomly assigned to the plots of each of the four blocks. Eight plots were established within each site (4 fauna-excluded and 4 controls). Fauna-excluded plots were created by (1) removing the litter, (2) sieving and removing the macroinvertebrates from the soil (0–10 cm), (3) placing a weed/gardening liner before replacing the litter and soil, to prevent immigration of soil fauna into the plot from the bottom and sides, (4) placing an aluminum fence (15 cm tall) around the plot, and (5) using naphthalene, an arthropod repellent, to prevent recolonization of the litter in the plot. The gardening liner permitted oxygen and water exchange between the soils on either side of the liner, so no difference in moisture condition was visible in the plots as compared to the surrounding soil. Naphthalene flakes were applied at a rate of 100 g m^{-2} every 2 weeks in the tropics. Naphthalene was applied at a rate of 100 g m^{-2} every 2 weeks during the growing season in the subalpine sites. Naphthalene application in the subalpine sites was stopped during the winter months as evaporation of naphthalene under the snow is negligible (G. González, personal observation). Naphthalene application for all sites started in July 1997. Control plots had (1) the litter removed, (2) the soil sieved, (3) the liner, and (4) the fence; but all macroinvertebrates were left within the plots and naphthalene was not applied. This procedure is a modification of previous plot experiments by Seastedt and Crossley (1981) and Heneghan et al. (1999).

Microbial assays

In the summer of 1998, three soil cores (10 cm deep, 5 cm diameter) were collected randomly from the eight treatment plots on each of the four sites. Soils were sealed in plastic bags and brought to the laboratory for analysis. Soil microbial biomass and maximum growth rates were quantified using the SIGR method (Schmidt 1992; Colores et al. 1996). Estimates of microbial functional groups were obtained by using glutamate and salicylate as two separate growth substrates. Glutamate is a readily decomposable substrate and a good general substrate for microbial growth (Alef and Kleiner 1986). Therefore, we estimated the total microbial biomass and growth using glutamate. On the other hand, salicylate is a natural plant product and an intermediate in the breakdown of lignin and naphthalene degradation. Therefore, by using salicylate as a substrate we obtained an estimate of the functional group that was likely to be stimulated by the addition of naphthalene in the fauna-exclusion treatment.

Measurements of soil microbial biomass and growth by the SIGR method were performed after the three replicate cores were homogenized for each plot, and the soil was sieved (2 mm) to remove rocks and large roots. A total of 32 samples (10–12 g dry mass equivalent), from the two treatments and the four study sites were each analyzed for glutamate and salicylate SIGR. Glutamate or salicylate along with a ^{14}C-tracer (Sigma Biochemical) were uniformly added to the soil in concentrations of 2 mg C g^{-1}, and 0.2 mg C g^{-1}, respectively. These amounts of substrate were previously determined to induce maximal respiration rates (Colores et al. 1996; Lipson et al. 1999). The final radioactivity per flask was 120,000 disintegration per minute (DPM) for glutamate and 240,000 DPM for salicylate. The respiration of each substrate was followed over time and measured as the CO_2 evolved during the trials. This CO_2 was captured in 1 ml of 0.5 M NaOH in the side arm of each biometer flask. To quantify $^{14}CO_2$ in each sample, 2.5 ml of ScintiVerse II scintillation cocktail (Fisher Scientific, Pittsburgh, Pa.) was added to the NaOH in 4 ml vials and the radioactivity was counted with a liquid scintillation counter (LKB Wallac, 1209 Rack Beta, Turku, Finland) (Colores et al. 1996). Estimates of the initial biomass level and the maximum specific growth rate of the biomass were obtained by fitting the following equation (Colores et al. 1996) to the data:

$$dP/dt=\mu_{max}[X_1 \exp(\mu_{max}t)]$$

where X_1 represents the biomass in terms of the product produced (in units of µg CO_2–C g^{-1}), P is the CO_2–C, and μ_{max} is the maximum specific growth rate. To convert the units of µg CO_2–C g^{-1} to biomass, the following formula from Colores et al. (1996) was used:

$$X_a=X_1 (Y_c/1-Y_c)$$

where X_a is the actual biomass with units of µg C-biomass g^{-1}, and Y_c is the empirically derived yield for salicylate (0.22 and 0.10 for the tropical and subalpine forests, respectively) and glutamate (0.50 and 0.39 for the tropical and subalpine forests, respectively).

Faunal assays

Densities of major groups of fauna were determined from a set of four litterbags per treatment and site. Each litterbag (1.8×1.6 mm mesh) contained a measured amount of ~3–5 g of freshly senesced leaves of *Quercus gambelii* Nutall or *Cecropia scheberiana* Miq. Litterbags collected from the tropical wet and dry forests (Puerto Rico) were shipped by overnight mail to Colorado. All faunal extractions were performed at the University of Colorado in Boulder using Tullgren funnels in an air-conditioned laboratory. The Tullgren technique consisted of placing the litterbags inside a funnel (20 mm in diameter at the widest end) that was connected to a collecting vial (containing 70% ethanol) at the tip, and that was placed underneath an electric bulb of 25 W 120 V. The litterbags were placed in the extractor within a day of collection from the field, and continued for 7 days. This technique extracts mites and collembolans, and also allows for a conservative estimate of other fauna (e.g., Protura, Psocoptera, Zoraptera, pseudoscorpions, etc.). Sample vials were rinsed in petri dishes, and microarthropods counted under a dissecting scope. Fauna were classified as: Cryptostigmata, Mesostigmata, Prostigmata (suborders, Acarina), Collembola (springtails) and other fauna. Faunal densities were expressed per gram of dry litter. Soils for the microbial assays and litterbags used for the faunal extraction were collected from the field at the same time.

Data analysis

All statistical analyses were performed using the software SPSS (SPSS 9.0, Win 1998). Data were tested for homogeneity of variance

Table 1 Soil microbial biomass and maximum growth rate (μm_{max}) as measured by the substrate induced growth response (SIGR) using glutamate and, salicylate as the growing substrates in response to site (tropical dry and wet, and north- and south-facing subalpine forests), treatment (control vs fauna-excluded) and the site × treatment interaction

Source	*df*[b]	Biomass[a]		μm_{max}	
		F	*P*	*F*	*P*
Glutamate					
Site (S)	3	10.6	<0.001	12.2	<0.001
Treatment (T)	1	5.0	0.035	1.3	0.013
S×T	3	6.0	0.004	5.0	0.008
R^2		0.69		0.71	
Salicylate					
Site (S)	3	5.0	0.009	19.7	<0.001
Treatment (T)	1	21.8	<0.001	1.2	0.280
S×T	3	2.3	0.100	7.2	0.002
R^2		0.64		0.78	

[a] Analysis of variance performed on log-transformed data
[b] Error *df*=24

by using the Levene's test of equality of error variances, and skewness. Log-transformations were employed when the data did not meet the assumptions of normality. The significance level was set at ∝=0.05.

Analysis of variance was used to determine the significance of the two main factors (site and fauna-exclusion treatment) and their interaction on the biomass and maximum growth rates of glutamate and salicylate mineralizers, as well as the relationships between site or treatment and the densities of major groups of fauna. A one-way ANOVA was employed to determine differences in soil microbial biomass and maximum growth rates between the treatments within each site and growing substrate. Student-Newman-Keuls (SNK) tests were used to compare site means of soil microbial biomass and maximum growth rates within each treatment and growing substrate, and to compare site means of the densities of the major groups of fauna within each treatment. A simple linear correlation analysis was performed among the densities of major groups of fauna, and the soil microbial biomass and maximum growth rates (SIGR) of glutamate and salicylate mineralizers for the tropical and subalpine sites.

Results

Substrate induced growth response

There was a significant effect of site, treatment, and the interaction of site and treatment on the microbial biomass and the maximum growth rate of glutamate mineralizers (Table 1). Under control conditions, the microbial biomass of glutamate mineralizers was highest in the tropical wet forest (479 µg C g^{-1}), and did not differ between the tropical dry (71 µg C g^{-1}) and the subalpine forests (120–140 µg C g^{-1}) (Fig. 2A). There was no significant effect of tratment on the biomass and growth rate of glutamate mineralizers in the tropical forests (Fig. 2). However, in the subalpine forests, the microbial biomass of glutamate mineralizers was significantly higher in the fauna-exclusion than in the control treatment (Fig. 2A). The growth rate of glutamate mineralizers was

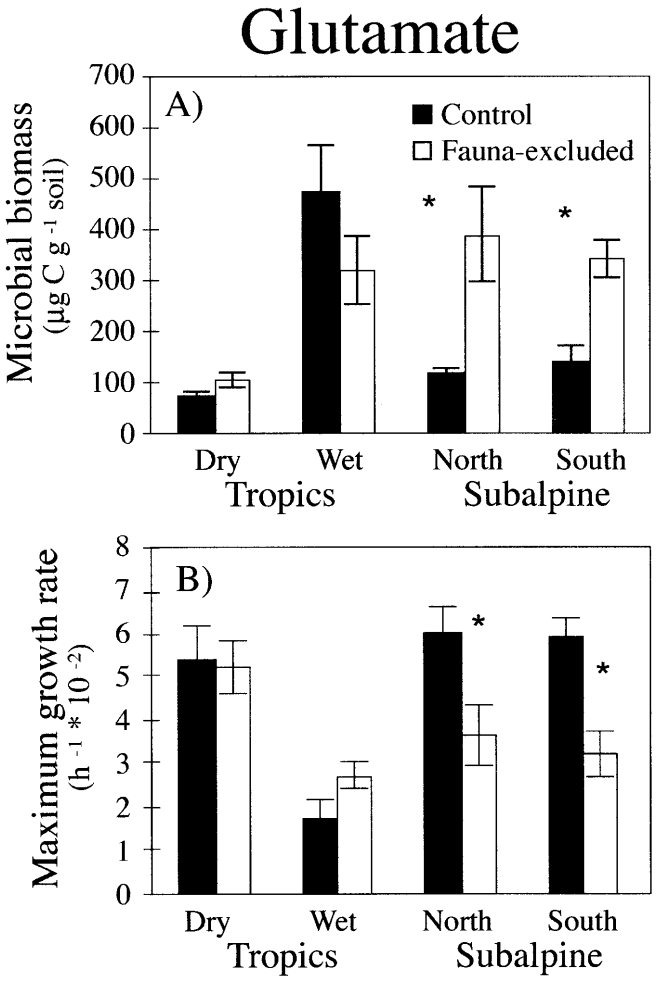

Fig. 2 A Microbial biomass and **B** maximum growth rate of glutamate mineralizers in control and fauna-excluded treatments in tropical wet and dry forests, and north- and south-facing subalpine forests. *Significant treatment effect within a site (one-way ANOVA, *P*=0.05)

significantly higher in the control than in the fauna-excluded treatment in the subalpine forests. The maximum growth rate of glutamate mineralizers was lower in the tropical wet forest (Fig. 2B) than in all other sites.

There was a significant effect of site and treatment on the microbial biomass of salicylate mineralizers (Table 1). In the control treatment, the biomass of salicylate mineralizers was highest in the north-facing subalpine forest (3.1 µg C g^{-1}), and lowest in the tropical dry forest (1.2 µg C g^{-1}). The biomass of salicylate mineralizers in the south-facing subalpine forest was not significantly different from that of the tropical and north-facing subalpine forests. The biomass of salicylate mineralizers was significantly higher in the fauna-exclusion than in the control treatment of the tropical wet and the south-facing subalpine forests (Fig. 3A). There was a significant effect of site, and the interaction of site and treatment on the maximum growth rate of salicylate mineralizers (Table 1). In the control treatment, the growth rate of salicylate mineralizers was highest in the tropical wet

Table 2 Densities (numbers per gram of dry litter) of major groups of mites, collembolans, and other fauna in control and fauna-excluded treatments in tropical wet and dry forests, and north- and south-facing subalpine forests. Values are means (n=4) ±SE. Common letters within a column and treatment indicate no significant difference among sites (SNK, ∝=0.05)

Treatment and site	Cryptostigmata	Mesostigmata[a]	Prostigmata	Collembola	Total Acari[ab]	Other[ac]	Total[a]
Control							
Tropical, Dry	0.08[a]±0.04	0[a]	0[a]	0[a]	0.08[a]±0.04	0[a]	0.08[a]±0.04
Tropical, Wet	54.92[b*]±17.47	17.31[b*]±6.11	0.31[a]±0.24	1.12[a]±0.43	81.38[c*]±27.40	25.41[b*]±15.01	107.91[c*]±± 41.68
Subalpine, North	0.36[a*]±0.05	2.29[a]±1.59	1.36[a]±0.82	1.30[a]±0.66	4.05[ab*]±2.42	0.16[a]±0.06	5.51[ab*]±± 2.89
Subalpine, South	1.96[a]±1.12	4.14[ab*]±1.56	1.17[a]±0.65	1.11[a*]±0.36	7.60[b*]±3.15	0.03[a]±0.03	8.74[b*]±2.92
Fauna-excluded							
Tropical, Dry	0[a]	0[a]	0[a]	0[a]	0[a]	0[a]	0[a]
Tropical, Wet	1.43[b]±0.44	2.46[b]±0.88	0.65[b]±0.25	2.40[a]±1.92	11.26[b]±3.79	1.52[b]±0.59	15.18[b]±5.53
Subalpine, North	0[a]	0[a]	0[a]	0[a]	0[a]	0[a]	0[a]
Subalpine, South	0[a]	0[a]	0[a]	0.03[a]±0.03	0[a]	0.05[a]±0.05	0.08[a]±0.05

[a] Statistics were performed on log-transformed data
[b] Includes unknown immatures
[c] Other fauna excluding mites and collembolans
* Significant treatment effect within a site (one-way ANOVA, P=0.05)

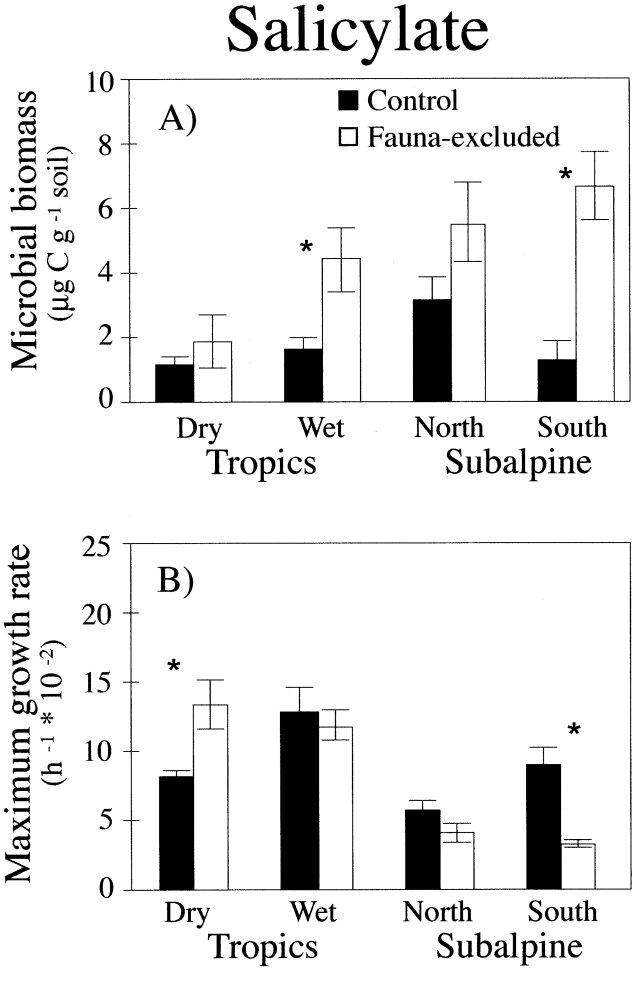

Fig. 3 **A** Microbial biomass and **B** maximum growth rate of salicylate mineralizers in control and fauna-excluded treatments in tropical wet and dry forests, and north- and south-facing subalpine forests. *Significant treatment effect within a site (one-way ANOVA, P=0.05)

forest, but it was not significantly different from that of the south-facing subalpine forest (Fig. 3B). When the fauna was excluded, the biomass of salicylate mineralizers did not differ among the forests, but the maximum growth rate was higher in the tropics (11.8–13.4 $h^{-1}\times10^{-2}$) than in the subalpine forests (3.2–4 $h^{-1}\times10^{-2}$) (Fig. 3B).

Fauna

The density of total fauna was higher in the tropical wet forest (108 individuals per gram of dry litter) than in all other sites (Table 2). The abundance of total fauna in the south-facing subalpine forest (9 per gram of dry litter) was lower than that of the tropical wet forest, but higher than those from the tropical dry (<1 per gram of dry litter) and the north-facing subalpine (5 per gram of dry litter) forests. The tropical dry and the north-facing subalpine forests did not differ in their abundance of total fauna. The density of oribatid mites (Crystostigmata) was highest in the tropical wet forest (55 per gram of dry litter), and lowest in the tropical dry forest (<1 per gram of dry litter) (Table 2). The subalpine forests did not differ in their abundance of oribatid mites when compared to the tropical dry forest. Mesostigmatid mites were abundant in the tropical wet forest, but were absent in the tropical dry forest (Table 2). There was no significant effect of site on the density of prostigmatid mites and collembolans. The total density of mites (Acari) and fauna was higher in the tropical wet forest than in the tropical dry and the subalpine forests. The total density of mites (Acari) and fauna was lowest in the tropical dry forest, but it was not significantly different from that in the control treatments of the north-facing subalpine forest (Table 2). The abundance of total mites and fauna was not significantly different between the subalpine forests. The exclusion treatment significantly reduced the density of the total fauna in all the sites except the tropical dry forest where total density of fauna was already low under control conditions.

A correlation analysis between the density of the major groups of fauna and the SIGR of glutamate and salicylate mineralizers showed no significant relationships within the tropical sites ($0.68<r<0.8$, $P>0.11$). In contrast, there was a significant negative correlation between the density of prostigmatid mites with the biomass of glutamate mineralizers in the subalpine forests ($r=–0.99$, $P>0.01$). Similarly, the density of collembolans was significantly and negatively correlated with the biomass of glutamate mineralizers in the subalpine forests ($r=–0.99$, $P>0.01$). A strong positive correlation was found between the growth rate of glutamate mineralizers and the density of the prostigmatid mites and collembolans in the subalpine forest ($r=0.99$, $P>0.01$ for both faunal groups).

Discussion

The goal of this study was to examine if the exclusion of soil fauna affects the soil microbial biomass and growth rates and whether this effect would be maximized in the subalpine forests. The SIGR method was used to quantify the overall effect of the fauna exclusion treatment on the microbial community. In addition, the biomass of salicylate mineralizers was also quantified in order to determine possible direct effects of the naphthalene applications on the microbial community in the fauna-exclusion treatment.

We expected to observe a higher microbial biomass in the absence of soil fauna than in their presence within each of the forest sites, as direct effects of soil fauna tend to reduce microbial abundance (Fig. 1). Further, naphthalene presence could stimulate the bacterial biomass (e.g. Blair et al. 1989). We found that the exclusion of soil fauna did not affect the total microbial biomass and maximum growth rates in the tropical forests. However, the fauna-exclusion treatment significantly affected the microbial biomass and maximum growth rates in the subalpine forests. Total microbial biomass was significantly higher in the fauna-exclusion treatment than in the control. Maximum growth rate of glutamate users was significantly lower in the absence of soil fauna than in their presence in the subalpine forests (Fig. 2). Therefore, we accept the hypotheses that soil fauna can regulate the microbial metabolism in the subalpine forests and, that soil fauna effects on microbes are greater in the subalpine than in the tropical forests. These findings suggest: (1) a different microbial-faunal interaction in tropical and subalpine forests, and (2) that soil fauna can affect ecosystem processes through interactions with the microorganisms.

Faunal effects on microbes can be considered in terms of relative body size and methods of feeding (Visser 1985; Anderson 1987). Anderson (1987) states that the "indirect physical effects of animals on microbial populations and activities increase with body size". Visser (1985) states that "it seems likely that smaller animals have a high chance of feeding on specific components of the microflora". Anderson (1987) and Visser (1985) support our argument on direct effects of the soil fauna on the microbial community in the subalpine forests. In this study, although we did not record the body size of the soil fauna, the proportion of other soil fauna (centipedes, millipedes, and coleopterans among others) was significantly greater in the tropical wet forest than in the tropical dry and the subalpine forests. In fact, the density of other soil fauna besides mites and collembolans was almost zero in the subalpine forests. Mites and collembolans can interact directly with microbes in the subalpine forests, and this direct interaction might be more important in the regulation of microbial activities compared to the indirect effects that soil fauna might have on the microbial activities in the tropical wet forest. The regulatory effect that soil fauna have on microbes via indirect mechanisms in the tropics might actually be small.

Given the small size of the subalpine invertebrates, soil fauna could affect ecosystem processes primarily through direct interactions with microorganisms in the subalpine forests we studied (Fig. 1). There was a negative correlation between the biomass of glutamate mineralizers and the density of prostigmatid mites and collembolans ($r=–0.99$, $P=0.01$ for both faunal groups), while there was a positive correlation between the maximum growth rate of glutamate mineralizers and the density of prostigmatid mites ($r=0.99$, $P=0.01$) and collembolans ($r=0.99$, $P=0.01$). Collembola and prostigmatid mites are abundant in most forested, grassland, and desert ecosystems (Seastedt 1984). Both groups of fauna have been reported to decrease fungal biomass (Newell 1984; Parker et al. 1984). Although, we do not pretend to establish a cause-effect relationship by means of a correlation, these data are consistent with the hypothesis that these two groups of fauna feed on glutamate mineralizers in the subalpine forests.

In the presence of soil fauna, the annual decay constant (k) of leaf litter of *Cecropia scheberiana* in the tropical wet forest is 1.46 $year^{-1}$ as compared to 0.02 $year^{-1}$ in the subalpine forests (González and Seastedt 2001). González and Seastedt (2001) reported an up to 45–66% increase in litter breakdown due to faunal effects in the tropical wet forest as compared to 12–50% in the subalpine forests, so direct effects of litter consumption and comminution are believed to be much larger in the wet tropics.

Other factors that could affect the microbial activity include micro- and macroclimatic conditions. The effects of microclimatic conditions on soil microbial activities have been widely studied (e.g. McGill et al. 1986; Kieft et al. 1987; Wardle and Parkinson 1990). Wardle and Parkinson (1990) reported that the dynamics and turnover rates of the microbial biomass in an agricultural field were largely controlled by soil moisture. A decrease in microbial biomass and a shift in the microbial community structure have been reported due to reductions in water regimes (e.g. Bottner 1985; Schnürer et al. 1986). In this study, the biomass of glutamate mineralizers was not significantly different between the tropical wet forest and the subalpine forests when fauna were excluded (Fig. 2A). In the absence of fauna, the biomass of gluta-

mate mineralizers was lowest in the tropical dry forest. Meanwhile, the tropical wet forest has the highest AET rate, and the subalpine forests have the lowest AET value. These data indicate that macroclimatic conditions as measured by AET are not important in regulating microbial biomass dynamics across a wide climatic range.

The effects of naphthalene on salicylate mineralizers were also quantified in this study. The use of naphthalene as a method for exclusion of soil arthropods has received some attention (e.g. Witkamp and Crossley 1966; Newell et al. 1987; Blair et al. 1989) due to the potential non-target effects that it might have on soil microorganisms. Most of those studies indicate that naphthalene serves as a carbon source for some microbes and its presence can stimulate microbial biomass. Blair et al. (1989) reported that the number of bacteria was higher and the length of fungal hyphae lower in naphthalene-treated microcosms as compared to untreated ones. In this study, we found a significant effect of treatment on the biomass of salicylate mineralizers in the tropical wet, and the south-facing subalpine forests. The difference in increase in the biomass of salicylate mineralizers in the fauna-excluded treatment as compared to the control ranged from 0.6 µg C g^{-1} in the tropical dry forest to 5.2 µg C g^{-1} in the south-facing subalpine forest, whereas the difference in increase of total microbial biomass (glutamate mineralizers) in the fauna-excluded treatment as compared to the control ranged from 33.3 µg C g^{-1} in the tropical dry forest to over 200 µg C g^{-1} in the subalpine forests. Therefore, the effect of naphthalene application on the salicylate mineralizers in the fauna-excluded treatment does not account for the difference in total microbial biomass in the control and fauna-excluded plots.

To summarize, we found that: (1) the exclusion of soil fauna resulted in a higher total microbial biomass and lower maximum growth rate in the subalpine forests, (2) soil fauna exclusion did not affect the microbial biomass and growth rates in the tropical forests, and (3) the microbial biomass of salicylate mineralizers was significantly enhanced in the fauna-exclusion treatment as compared to the control in the tropical wet and the south-facing subalpine forests. We conclude that effects of naphthalene application on the microbial community alone cannot explain the large differences in total microbial biomass found between control and fauna-excluded treatments in the subalpine forests. A major implication of this study is the differential mechanism by which soil fauna might be affecting soil ecosystem processes in tropical and temperate systems. In the subalpine forest, soil fauna might play a more significant role on ecosystem processes through direct grazing of the microbial community. However, soil fauna in the wet tropics may influence ecosystem processes through indirect effects on microbes via comminution of organic matter and the modification of the soil and litter environment. To our knowledge, the evidence that soil fauna act on ecosystem processes through different mechanisms along a climatic gradient has not been reported before, but such inferences are supported by the present study.

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References

Alef K, Kleiner D (1986) Arginine ammonification, a simple method to estimate the microbial activity potentials in soils. Soil Biol Biochem 18:233–235

Anderson JM (1987) Interactions between invertebrates and microorganisms: noise or necessity for soil processes? In: Fletcher M, Gray TRG, Jones JG (eds) Ecology of microbial communities. Cambridge University Press, Cambridge, pp 125–145

Blair JM, Crossley DA Jr, Rider S (1989) Effects of naphthalene on microbial activity and nitrogen pools in soil-litter microcosms. Soil Biol Biochem 21:507–510

Bottner P (1985) Response of microbial biomass to alternate moist and dry conditions in a soil incubated with ^{14}C- and ^{15}N-labelled plant material. Soil Biol Biochem 17:329–337

Brown GG (1995) How do earthworms affect microfloral and faunal community diversity? Plant Soil 170:209–231

Brown S, Lugo AE, Silander S, Liegel L (1983) Research history and opportunities in the Luquillo Experimental Forest. USDA For Ser Gen Tech Rep SO-44. Southern Forest Experiment Station, New Orleans, La

Carter OR (1965) Soil Survey of the Lajas Valley Area, Puerto Rico. Soil Survey Series 1961 No. 23. USDA Soil Conservation Service

Colores GM, Schmidt SK, Fisk MC (1996) Estimating the biomass of microbial functional groups using rates of growth-related soil respiration. Soil Biol Biochem 28:1569–1577

Frantz B, Chakrabarty AM (1986) Degradative plasmids in *Pseudomonas.* In: Gunsalus IC, Stanier RY (eds) The bacteria, vol X. Academic Press, New York, pp 295–323

García-Martinó AR, Warner GS, Scatena FN, Civco DL (1996) Rainfall, runoff and elevation relationships in the Luquillo Mountains of Puerto Rico. Carib J Sci 32: 413–424

González G, Seastedt TR (2001) Soil fauna and plant litter decomposition in tropical and subalpine forests. Ecology 82: (in press)

Greenland D (1989) The climate of Niwot Ridge, Front Range, Colorado, USA. Arct Alp Res 21:380–391

Griffiths BS, Bargett RD (1997) Interactions between microbes-feeding invertebrates and soil microorganisms. In: Elsas JD vans, Trevors JT, Wellington EMH (eds) Modern soil microbiology. Dekker, New York, pp165–182

Hanlon RDG, Anderson JM (1979) The effects of collembola grazing on microbial activity in decomposing leaf litter. Oecologia 38:93–99

Heneghan L, Coleman DC, Zou X, Crossley DA Jr, Haines BL (1999) Soil microarthropod contributions to decomposition dynamics: tropical-temperate comparisons of a single substrate. Ecology 80: 1873–1882

Johnson DD, Cline AJ (1965) Colorado mountain soils. Adv Agron 17:233–281

Kieft TL, Soroker E, Firestone MK (1987) Microbial biomass response to a rapid increase in water potential when dry soil is rewetted. Soil Biol Biochem 19:119–126

Lavelle P, Blanchart E, Martin A, Martin S (1993) A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. Biotropica 25:130–150

Lavelle P, Bignell D, Lepage M, Wolters V, Roger P, Ineson P, Heal OW, Dhillion S (1997) Soil function in a changing world: the role of invertebrate ecosystem engineers. Eur J Soil Biol33: 159–193

Leinaas HP (1981) Activity of Arthropoda in snow within a coniferous forest, with special reference to Collembola. Holarct Ecol 4:127–138
Li Y (1998) Soil organic carbon dynamics in tropical wet forests in Puerto Rico. Dissertation, University of Puerto Rico, Rio Piedras
Lipson DA, Schmidt SK, Monson RK (1999) Links between microbial population dynamics and nitrogen availability in an alpine ecosystem. Ecology 80:1623–1631
Marr JW (1961) Ecosystems of the east slope of the Front Range in Colorado. University of Colorado Studies. Series in Biology No. 8. University of Colorado Press, Boulder
McGill WB, Cannon KR, Robertson JA, Cook FD (1986) Dynamics of soil microbial biomass and water-soluble organic carbon in Breton after 50 years of cropping to two rotations. Can J Soil Sci 66:1–19
Moore JC, Walter DE (1988) Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. Annu Rev Entomol 33:419–439
Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. Annu Rev Ecol Syst 17:67–88
Newell K (1984) Interactions between two decomposer Basidiomycetes and a collembolan under Sitka spruce: distribution, abundance and selective grazing. Soil Biol Biochem 16: 235–239
Newell K, Franklin JC, Whittaker JB (1987) Effects on microflora of using naphthalene or X-rays to reduce arthropod populations in the field. Biol Fertil Soils 3:11–13
Parker LW, Santos PF, Phillips J, Whitford WG (1984) Carbon and nitrogen dynamics during the decomposition of litter and roots of a Chihuahuan desert annual. Ecol Monogr 54:339–360
Parkinson D, Visser S, Whittaker JB (1979) Effects of collembolan grazing on fungal colonization of leaf litter. Soil Biol Biochem 11:529–535
Schmidt SK (1992) A substrate-induced growth-respiration method for estimating the biomass of microbial functional groups in soil and aquatic systems. FEMS Microbiol Ecol 101:197–206
Schnürer J, Clarholm M, Bostrom S, Rosswall T (1986) Effects of soil moisture on soil microorganisms and nematodes: a field experiment. Microb Ecol 12:217–230
Seastedt TR (1984) The role of microarthropods in decomposition and mineralization processes. Annu Rev Entomol 29:25–46
Seastedt TR, Crossley DA Jr (1981) Nutrients in forest litter treated with naphthalene and simulated throughfall: a field microcosm study. Soil Biol Biochem 15:159–165
Soil Survey Staff (1995) Order 1 Soil survey of the Luquillo Long-Term Ecological Research Grid, Puerto Rico, USDA, NRCS, Lincoln, Neb
SPSS 9.0 for Windows (1998) SPSS, Chicago, Ill
Swift MJ, Heal OW, Anderson JM (1979) Decomposition in terrestrial ecosystems. Blackwell, London
Teuben A, Roelofsma TAPJ (1990) Dynamic interactions between functional groups of soil arthropods and microorganisms during decomposition of coniferous litter in microcosm experiments. Biol Fertil Soils 9:145–151
Vedder B, Kampichler C, Bachmann G, Bruckner A, Kandeler E (1996) Impact of faunal complexity on microbial biomass and N turnover in field mesocosms from a spruce forest soil. Biol Fertil Soils 22:22–30
Visser S (1985) Role of the soil invertebrates in determining the composition of soil microbial communities. In: Fitter AH, Atkinson D, Read DJ, Usher MB (eds) Ecological interactions in soil: plants, microbes and animals. Blackwell, Palo Alto, pp 297–317
Wardle DA (1994) Impacts of disturbance on detritus food webs in agro-ecosystems of contrasting tillage and weed management practices. Adv Ecol Res 26:105–185
Wardle DA, Parkinson D (1990) Interactions between microclimatic variables and the soil microbial biomass. Biol Fertil Soils 9: 273–280
Webb DP (1977) Regulation of deciduous forest litter decomposition by soil arthropod feces. In: Matson WJ (ed) The role arthropods in forest ecosystems. Springer, Berlin Heidelberg New York, pp 57–69
Witkamp M, Crossley DA Jr. 1966. The role of arthropods and microflora in breakdown of white oak litter. Pedobiologia 6:293–303
Zimmerman JK, Pulliam WM, Lodge DJ, Quiñones-Orfila V, Fetcher N, Guzmán-Grajales S, Parrota JA, Asbury CE, Walker LR, Waide RB (1995) Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forest from hurricane damage. Oikos 72:314–322
Zou X, Zucca C, Waide R, McDowell W (1995) Long-term influence of deforestation on tree species composition and litter dynamics of a tropical rain forest in Puerto Rico. For Ecol Manage 78:147–157