

# Effects of soil productivity on invertebrate community structure in tropical forest ecosystems

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**Abstract:** Soil and leaf litter invertebrates play an important role in carbon turnover and nutrient cycling in tropical forests. We examined the relationships between invertebrate community structure and two surrogate measures of soil productivity, soil moisture and organic matter, in four Costa Rican tropical forests. We found that invertebrate richness and abundance in the leaf litter increased linearly with soil moisture and organic matter across these sites. Our results suggest that more productive soils can support a greater abundance and diversity of invertebrates.

**Key Words:** decomposition, diversity, carbon, nutrient cycling, productivity

## INTRODUCTION

Soils play an important role in carbon turnover and nutrient cycling in tropical forests. Storage and flux of materials in tropical soils are influenced by abiotic and biotic factors. Invertebrates in the leaf litter contribute to decomposition and nutrient recycling by consuming and shredding soil organic matter.

The energy available to detritus-based invertebrate communities (soil productivity) is one factor that may influence richness and abundance. In this study, we used two different indicators of potential productivity. First we used moisture as a surrogate measure of soil productivity because a) water availability influences leaf production, which ultimately provides resource inputs to the soil and b) moisture aids in decomposition and nutrient uptake within the litter layer by altering the microclimate. Second, we used soil organic matter as an indicator of productivity, because it may reflect past detrital inputs of leaf litter. Thus, both soil moisture and organic matter may indicate the microclimate and resources available to invertebrates.

Some studies in other ecosystems (i.e. grasslands and phytotelmata) have shown that species richness and abundance respond positively to increases in productivity, but then may decline at high productivity levels (Rosenzweig 1995; Dodson et al.

2000; Mittlebach et al. 2001). We predicted that as soil productivity increases and resources become less limiting, the ground layer will support a greater number of individuals and a larger variety of species. Specifically, we predicted that arthropod abundance and richness in the litter layer would be positively related to soil moisture and organic matter below the litter layer.

## METHODS

We examined soil arthropod communities at four locations in Costa Rica: Palo Verde National Park, Monteverde Biological Reserve, Corcovado National Park, and La Selva Biological Reserve. At each location, we chose four sample sites within 200 m of the main biological station. Site selection criteria included high canopy cover and sparse undergrowth.

Aboveground invertebrates were sampled by collecting leaf litter from a 1 x 1 m quadrat and placing it on a white sheet. Using an aspirator and plastic bottles, we collected all invertebrates in the leaves and from the top layer of soil in the quadrat. In addition, we collected a 3 L sample of leaf litter from an area adjacent to the quadrat, which we later rinsed and sifted for smaller invertebrates. All invertebrates were preserved in ethanol, sorted by morphotype, and identified to order. We did not match morphotypes among sites. For each quad-

rat, we calculated morphotype richness and abundance.

At each site we dug a soil pit to the O-horizon, which is the transition zone between soils comprised of primarily organic materials and those characterized by inorganic matter. Operationally, we identified this zone by changes in soil color and texture. We collected a 250 mL sample of homogenized organic soil and measured the proportions of soil particle sizes by sifting the soil sample through 3 mm and 1 mm sieves. We calculated soil moisture by drying each sample in an oven for one hour at 60° C and then recorded the difference between the wet and dry sample mass. We calculated organic matter by incinerating the dry sample in a muffle furnace for one hour at 500° C. Organic matter was recorded as the proportion of sample mass that was lost to combustion.

## RESULTS

Soil moisture and organic matter, invertebrate abundance and richness, and soil particle size distribution varied across the four sites (Table 1). Soil moisture content at Palo Verde was significantly lower than at other sites. Percent organic matter was significantly higher at La Selva than at the other three sites. Both invertebrate abundance and morphotype richness were highest at La Selva.

Soil moisture and organic matter

were not correlated ( $r^2 = 0.23$ ,  $df = 1$ ,  $P = 0.46$ ). We used multiple regression (backward elimination) to determine that together, soil moisture and organic matter were significant predictors of both aboveground invertebrate abundance ( $R^2 = 0.43$ ,  $df = 2$ ,  $P = 0.03$ ) and aboveground richness ( $R^2 = 0.54$ ,  $df = 2$ ,  $P = 0.02$ ). Invertebrate abundance was described by the equation: invertebrate abundance =  $131.6$  (% moisture) +  $56.3$  (% organic matter) -  $5.1$ . Invertebrate richness was described by the equation: invertebrate richness =  $22.0$  (% moisture) +  $9.4$  (% organic matter) +  $6.13$ . Partial correlation coefficients indicated that soil moisture contributed slightly more to the variance in invertebrate abundance ( $r = 0.37$ ) and richness ( $r = 0.67$ ) than soil organic matter (abundance  $r = 0.28$ , richness  $r = 0.63$ ).

## DISCUSSION

As we predicted, both morphotype richness and abundance increased with soil moisture and organic matter. Together, soil moisture and organic matter were strong predictors of both aboveground invertebrate richness and abundance. Soil moisture may increase decomposition, and therefore increase terrestrial biomass production. Alternatively, soil moisture may reduce invertebrate water stress and desiccation rates, which may permit higher growth rates and reduced mortality. The amount of

TABLE 1. Percent soil moisture and organic matter, morphotype richness, invertebrate abundance and % soil particle size (mean  $\pm$  SE) at four Costa Rican sites. Invertebrates were collected from leaf litter, identified to order and morphotyped. O-horizon soil samples were collected at each site, sifted by particle size, dried to measure moisture content, and ashed to measure organic matter. For each variable, sites were compared using a one-way ANOVA.

	Palo Verde	Monteverde	Corcovado	La Selva	P	F	n
Soil Moisture	0.04 $\pm$ 0.03	0.25 $\pm$ 0.03	0.26 $\pm$ 0.02	0.36 $\pm$ 0.07	< 0.01	10.38	16
% Organic Matter	0.36 $\pm$ 0.18	0.6 $\pm$ 0.07	0.01 $\pm$ 0.01	85.8 $\pm$ 15.4	0.02	4.94	16
Morphotype richness	12.3 $\pm$ 2.93	15.5 $\pm$ 3.07	11.75 $\pm$ 1.70	16.25 $\pm$ 1.93	0.50	0.84	16
Invertebrate abundance	16.0 $\pm$ 4.81	0.82 $\pm$ 0.11	28.75 $\pm$ 12.12	40.0 $\pm$ 9.95	0.01	6.41	16
% Coarse Soil	0.56 $\pm$ 0.13	0.50 $\pm$ 0.11	0.39 $\pm$ 0.166	0.65 $\pm$ 0.21	0.18	1.91	16
% Medium Soil	0.33 $\pm$ 0.03	0.46 $\pm$ 0.04	0.26 $\pm$ 0.03	0.33 $\pm$ 0.1	0.13	2.33	16
% Fine Soil	0.18 $\pm$ 0.03	0.02 $\pm$ 0.01	0.35 $\pm$ 0.09	0.01 $\pm$ 0.01	< 0.01	11.03	16

organic matter in the soil may be representative of leaf litter inputs to the aboveground invertebrate community. High levels of soil organic matter may be due to soil accumulation resulting from slow decomposition rates, which may indicate a less productive ecosystem. Alternatively, excess organic matter may represent high leaf litter input and a potentially productive ecosystem. In the latter scenario, high leaf litter inputs, coupled with high moisture levels, may increase resource availability to the detrital community.

If soil moisture and organic matter content indicate soil productivity, our results suggest that more productive soils can support a greater number of invertebrates across a wider range of morphotypes. Productivity, defined as the amount of energy available to a system, is essential to organismal growth and reproduction. High productivity may relax resource limitation and allow more individuals to coexist.

Our data suggest a positive linear relationship between diversity and productivity. To

determine the shape of the relationship between productivity and diversity of highly productive tropical soil communities, future studies should investigate the interactions between soil moisture, organic matter, soil productivity, and community structure.

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