

Phosphorus Limits Tropical Rain Forest Litter Fauna

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ABSTRACT

The stoichiometry of resources may explain bottom-up regulation of higher trophic levels. We tested the effects of soil and litter nutrient stoichiometry on the invertebrate litter fauna of a Costa Rican tropical rain forest. Animal densities were estimated from 15 sites across a phosphorus gradient. The density of the invertebrate litter fauna varied considerably, and was strongly tied to soil and litter phosphorus concentrations. An increase in phosphorus concentrations corresponded with an equally proportionate increase in animal densities. Natural variation in nutrient levels can thus serve as a predictor of density in a highly diverse tropical animal community.

Key words: bottom-up; Costa Rica; detritus; nutrient limitation; phosphorus; stoichiometry; terrestrial food web; trophic cascade; tropical forest.

RESEARCH IN TROPICAL FORESTS HAS SUGGESTED THAT TOP-DOWN FORCES such as predation and parasitism affect the structure of invertebrate communities (Hairston *et al.* 1960, Morris *et al.* 2004). Bottom-up effects on tropical forest animal communities, however, can be more substantial (Dyer & Letourneau 1999, Terborgh *et al.* 2001). Classic ideas about nutrient limitation (*e.g.*, Andrewartha & Birch 1954) have been energized by a recent emphasis on stoichiometry (Sterner & Elser 2002, Schade *et al.* 2003). Because resource stoichiometry can drive the individual growth rate and abundance of organisms at the population level (Rosemond *et al.* 2001, Fagan *et al.* 2002, Schade *et al.* 2003), within-landscape variation in resource stoichiometry may lead to spatial heterogeneity in tropical rain forest animal densities at the community level.

In old-growth lowland tropical rain forest in Costa Rica, we investigated the relations between the substantial within-landscape variation in soil carbon (C) and phosphorus (P), and the abundance and composition of the invertebrate litter fauna. In this forest, like most other tropical forests, P is limiting (Sanchez 1976, Vitousek & Sanford 1986, Cleveland *et al.* 2002, McGroddy *et al.* 2004). Across a 600 ha forest landscape, we explicitly tested whether the natural variation in soil and litter C:P ratios explains variation in the abundance of leaf-litter invertebrates. In several temperate-zone studies animal densities have been shown to loosely track nutrient concentrations (such as Hasegawa & Takeda 1996, Ritchie 2000), but the relationship between environmental nutrient concentrations

and the hyperdiverse invertebrate litter fauna of tropical forests has never been considered.

METHODS

Our study site was in lowland tropical wet forest at the La Selva Biological Station, Costa Rica (10°26' N, 84°00' W; elevation 37–150 m, mean annual rainfall 4 m; McDade *et al.* 1994). We sampled 15 0.5 ha old-growth forest plots (CARBONO plots; Clark & Clark 2000) set out in a stratified-block design across the major edaphic gradients (slope, soil type). Soil chemistry was determined for composite samples of regularly spaced soil cores (six cores/plot). Samples were drawn from 0–10 cm depth. After being air-dried, sieved (2 mm), and ground, samples were analyzed at the Institute of Soil Science and Forest Nutrition, University of Göttingen, Germany, for total C with a CHN analyzer, and total P by HNO₃-pressure extraction and ICP-AES (Veldkamp *et al.* 2003, Schwendenmann & Veldkamp 2005). At our site, total P and extractable P are poorly associated with one another, perhaps as an artifact of soil drying; total P is probably a better time-integrated predictor of availability (Powers *et al.* 2005). Soil stocks of C and P were calculated from mean concentrations, adjusted by mean values for bulk density on each soil type. In each plot, leaf litterfall was collected every 2 weeks in nine evenly-spaced pairs of 0.25 m² litter traps, one a mesh bag 0.8 m above the ground, the other a ground-level square from which the larger litter items were collected. Litter nutrients were

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analyzed in the Department of Environmental Sciences, University of Virginia. We performed a modified Kjeldahl digestion on the oven-dried (< 70°C), ground leaf litter to determine P concentration. Leaf litter C concentrations were determined by dry combustion.

Invertebrate densities were sampled using pitfall traps; methods follow Bestelmeyer *et al.* (2000). Ten traps were used at each of the 15 plots; the traps were half-filled with 70% ethanol and left in the field for 96 h with trapping timed for simultaneous collection across edaphic types. The depth of leaf litter for each trap was assessed as the mean litter depth measured by inserting a wire vertically through the litter layer at four points adjacent to the trap (20 cm from the trap edge in each cardinal direction).

Macroscopic litter-dwelling animals—those visible to the naked eye—were counted and sorted to the taxonomic level required to establish adult trophic level when possible. For some common taxa, this was established by identification to order. Most beetles were assigned to trophic level based on family associations; bark beetles and rove beetles accounted for the majority of beetles. A small fraction of specimens were unable to be categorized by trophic level, because of a broad diet or lack of information about their natural history; these were excluded from trophic groups, but included in the measurement of overall density. Animals known to primarily consume other animals were classified as predators. Statistical analyses were performed using JMP (version 5.1.2, SAS Institute, Inc.). No transformations on data were performed. We use the term detritivore in the most general sense, including animals feeding directly upon detritus as well as microbial grazers. We created a correlation matrix to observe the relationships among faunal, litter, and nutrient variables, and performed multiple regressions using invertebrate density as the independent variable. We also present some of these results with simple linear regression.

RESULTS

We collected and identified 5080 individual invertebrates from 15 plots, and calculated the density using the mean number of indi-

viduals per trap. Springtails (Collembola, 59%) and bark beetles (Scolytidae, 34%) were the principal detritivores, and rove beetles (Staphylinidae, 24%) and spiders (Araneae, 54%) were the main predators.

Invertebrate densities were negatively related to soil C:P (Table 1; Fig. 1a; $P = 0.01$, $F_{1,12} = 6.43$) and litter C:P (Fig. 1b; $P = 0.02$, $F_{1,12} = 6.4$). Soil C:P and leaf-litter C:P were closely linked to one another (Fig. 1c; $P = 0.009$, $F_{1,13} = 9.5$). Litter depth did not explain invertebrate densities (Fig. 1d). Multiple regression of invertebrate density as a function of soil C:P and leaf-litter C:P (adjusted $R^2 = 0.33$, $P = 0.036$; $F_{2,12} = 4.4$) did not explain more variance than either variable alone, whereas multiple regression with litter depth, soil C:P and leaf-litter C:P as independent variables appreciably increased the correlation coefficient (adjusted $R^2 = 0.47$, $P = 0.018$; $F_{3,11} = 5.2$). The ratio of detritivores per predator was significantly negatively related to soil C:P ($R^2 = 0.38$; $P = 0.01$; $F_{1,13} = 8.04$; $y = -0.03 \times + 14.4$) and with a similar relationship to litter C:P that was marginally nonsignificant ($R^2 = 0.24$; $P = 0.06$; $F_{1,13} = 4.09$).

DISCUSSION

Our results suggest that much of the variation in the density of litter invertebrates across a rain forest landscape can be explained by the effects of nutrient limitation. While predation or parasitism can be important to the density of detritivores in lowland tropical forest leaf litter at some scales (Franks & Bossert 1983, Letourneau & Dyer 1998, Beard *et al.* 2003, Kaspari & O'Donnell 2003), it appears that resource ratios can determine within-landscape variation in the density of the invertebrate fauna overall.

To our knowledge, this is the first demonstration of explicit links among soil stoichiometry, litter stoichiometry and the density of invertebrate litter fauna in a tropical rain forest. Although most primary production is consumed by detritivores and not by herbivores, detrital food webs have been largely ignored in empirical studies and models of forest processes (Moore *et al.* 2004). Nutrient-driven spatial heterogeneity in the detrital food webs of tropical rain

TABLE 1. Correlation matrix of litter invertebrate fauna and litter properties.

	Total animals	Detritivores	Predators	Litter depth	Soil C:P	Litter C:P
Total Animal	–	0.994***	0.507	–0.029	–0.639**	–0.575*
Detritivores		–	0.441	–0.043	–0.663**	–0.588*
Predators			–	0.175	0.005	–0.035
Litter depth				–	0.456	0.480
Soil C:P					–	0.650**
Springtails	0.894***	0.894***	0.541*	0.149	–0.416	–0.482
Bark beetles	0.695**	0.709**	0.098	–0.370	–0.763***	–0.495
Spiders	0.673**	0.636**	0.705**	–0.254	–0.533*	–0.247
Rove beetles	0.143	0.099	0.444	0.678**	0.437	0.059

Values indicate r ; * indicates $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. The values used for all faunal variables are the mean values for individuals per trap. Correlations among taxonomic groups are excluded from analysis.

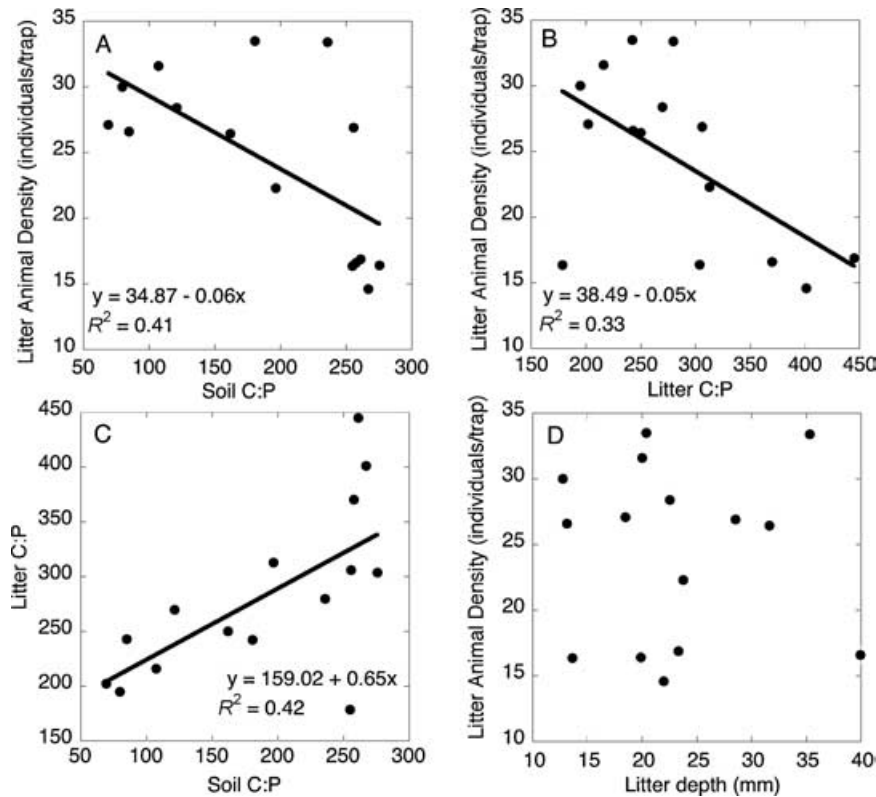


FIGURE 1. Relationships among litter animal density, soil, and litter C:P and litter depth. Environments richer in P have greater animal densities (A and B); the C:P of soil and litter are coupled (C); and litter depth is independent of animal density (D; $R^2 < 0.01$). Lines represent linear regressions, $P < 0.05$.

forests may explain community dynamics. Trophic cascades in forest floor detrital systems are thought to be far weaker than in other food webs (Shurin *et al.* 2002). However, soil C:P concentrations actually explained more variation in the forest floor community we studied than has been explained in any other study. Bottom-up trophic cascades could be a key factor structuring the hyperdiverse invertebrate communities in this biome.

The number detritivores per predator varied predictably with the C:P gradient, suggesting that nutrient concentrations or growth rates of detritivores may influence the density of the predator community (Sternler & Elser 2002). Elevated numbers of predators do not result in a decrease in detritivores, as they demonstrate a weak positive correlation. In higher P environments, the higher densities of detritivores may be regulated by two ways. First, the productivity of detritivores may be greater in higher P environments through many potential physiological mechanisms. Second, rates of predation might be lower in high P environments, potentially because the stoichiometry of the detritivores themselves may satiate predators more readily than in low P environments.

Tropical rain forests have long been seen as extremely complex systems where the drivers of density, diversity, and biomass must also be complex (Denslow & Chazdon 2002). At least for one tropical forest, faunal assemblage patterns and abundance can be predicted by remarkably simple and easily measured stoichiometric parameters.

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