THE RELATIONSHIP BETWEEN LEAF LITTER COMPOSITION AND ASSOCIATED INVERTEBRATE DIVERSITY IN A TROPICAL WET FOREST

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Abstract: Many critical ecosystem functions of forests are rooted in the leaf litter and its associated invertebrate community. However, there is little consensus in the literature about how litter characteristics affect associated invertebrate communities. We hypothesized that morphological and structural diversity of the leaf litter would be positively correlated with invertebrate morphotype richness. To test for these relationships, we sampled the forest litter along two trails at the Estación Biológica La Selva, Costa Rica, and characterized richness and evenness of the litter and the litter invertebrates. Invertebrate morphotype richness was positively correlated with leaf morphotype richness and evenness, although there was no such correlation with litter structural richness or evenness. Our findings demonstrate that there are significant links between leaf litter composition and litter invertebrate communities.

Key words: macroinvertebrate, detrital community

INTRODUCTION

In tropical forests, rates of nutrient cycling and primary production are much faster than in temperate forests (Lavelle et al. 1993). Trees take up nutrients as soon as they are they are made available by detritivore communities and associated macroinvertebrate communities (Lavelle et al. 1993, Hättenschwiler and Gasser 2005). Because soil and litter organisms vary in their contributions to decomposition rates (Hättenschwiler and Gasser 2005, Sulkava and Huhta 1998), the diversity and species richness of litter communities may influence forest nutrient cycling and energy fluxes.

Researchers have sought to isolate the factors that control community composition of invertebrate litter fauna, but there is little consensus in the literature on the relationship between the diversity of leaf litter and the invertebrate community. While some have found positive correlations between plant species richness and litter invertebrate richness (Chen and Wise 1999, Hansen 2000, Hooper et al. 2000), others have not (Siemann et al. 1998, Hooper et al. 2000). Rather than litter species diversity, the structural diversity of leaf litter may be more important in driving invertebrate richness (Sulkava and Huhta 1998). As an explanation for inconsistencies in the literature, Hooper et al. (2000) suggest that the

type of effect that one community has on another can vary depending on the particular species present.

We examined relationships between leaf litter characteristics and the associated invertebrate community. We predicted that invertebrate richness and evenness would be positively correlated with richness and evenness of plant species within the leaf litter as well as with richness and evenness of the litter's structural components.

METHODS

Field methods.

We conducted our study on 13-14 February, 2007 in primary tropical wet forest at the La Selva Biological Station, Costa Rica. We sampled invertebrates from five randomly selected locations along the Camino Experimental Sur trail and six along the Sendero Surá trail. Locations on each trail were 10 - 20 m apart and 3 - 6 m from the trail edge. At each of the 11 locations, we installed one pitfall trap (65 mm diameter) filled with soapy water and left it for 15 hours (overnight) before collecting the invertebrates. We also collected approximately two liters of litter from each location and left the litter samples in Berlese funnels for 24 hours to extract the invertebrates. We pooled invertebrates collected by these two methods, sorted them into morphotypes, and counted abundances of individuals in each morphotype.

At each location, we also collected all leaf litter from a 1 m x 0.5 m plot. We sorted the litter into eight structural categories (fruits, leaves, leaf fragments, palm fragments, sticks ≤ 0.5 cm in diameter, sticks > 0.5 cm in diameter, bark, and woody fragments). We subsequently sorted the fruits and leaves into morphotypes, and measured mass (to the nearest 0.01 g) per sample of each structural category and morphotype.

Statistical analysis.

For each location, we calculated richness and evenness[1] for each of the following variables: invertebrate morphotypes, litter structural categories, and leaf morphotypes. To test for a possible trail effect, we performed a MANOVA to compare leaf richness, leaf evenness, invertebrate richness, and invertebrate evenness (dependent variables) between the two trails (independent variable). We found no significant differences between trails ($F_{4,6}$ = 0.73, P = 0.60)

[1] We calculated richness S as the total number of morphotypes found in a sample. We calculated evenness J using the Shannon-Weiner formula below:

$$J = -\sum_{i=1}^{S} \frac{Pi \ln(Pi)}{\ln(S)}$$

where P_i equals the proportion of total individuals in the ith species.

and combined data from the two trails for all analyses.

We used multiple pair-wise correlations to test the relationships between invertebrate abundance, richness, and evenness for 45 combinations of litter and invertebrate variables (Table 1). To address our primary hypothesis, we tested the effects of leaf richness, leaf evenness, litter structure richness, litter evenness, and litter mass on invertebrate richness, invertebrate evenness, and invertebrate abundance with 15 separate pair-wise correlations. While our hypothesis predicts that all of these variables would be positively correlated, we anticipated noise in our data, due to idiosyncracies among invertebrate species in their behavior and resource requirements. Because different groups of invertebrates might respond to litter gradients differently, we tested the effects of the leaf and litter predictor variables on the abundances of two dominant invertebrate morphotypes (each comprising >20% of total invertebrate abundance; Fig. 2) and with abundances of predatory arachnids (a possible key functional group). We also tested the individual effects of five dominant litter structural components and morphotypes on invertebrate richness, evenness and abundance. We identified small sticks, large sticks, and leaf fragments as dominant components of the litter (each comprised >10% total litter mass), as well as one dominant leaf and one dominant fruit morphotype (each present in >5 sampling locations).

Lastly, we created two species-area curves to characterize leaf and invertebrate morphotype accumulation with increasing number of sampling locations using EcoSim 7.0 software (Gotelli and Entsminger 2005).

RESULTS

From 515 total individuals in our 11 samples, we identified 30 morphotypes of invertebrates, representing at least 9 orders (Table 2, Fig. 2). We recognized 16 leaf morphotypes and 6 fruit morphotypes.

Leaf richness and evenness were both positively correlated with invertebrate richness. No single component of the litter was correlated with invertebrate abundance or richness. Nor were leaf richness and abundance correlated with abundances of individual invertebrate taxa (Table 1).

The species-area curves for invertebrate and leaf morphotype richness both accumulate slowly, and neither reach an asymptote by the last sampling location (Fig. 1).

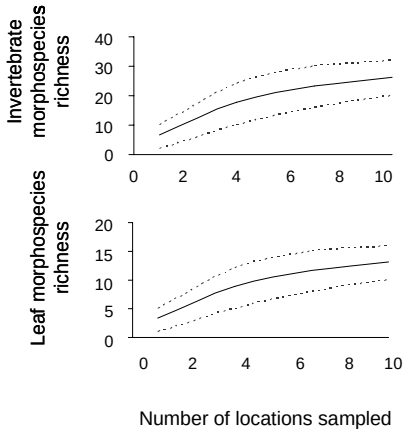

Fig. 1. Species-area curves for invertebrates and leaf litter from 11 sampling locations in old-growth forest floor at the Estación Biológica La Selva, Costa Rica. Numbers of arthropods in each sample ranged from 16 to 110 individuals.

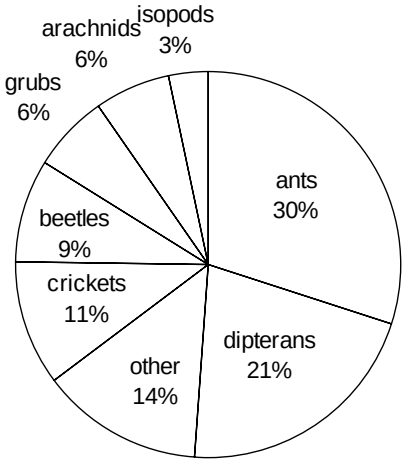

Fig. 2. Percent individual abundances of invertebrate morphotypes in samples from pitfall traps and Berlese funnels, in the tropical wet forest at the Estación Biológica La Selva, Costa Rica.

Table 1. Multiple pair-wise correlations between leaf litter characteristics (left column) and characteristics of the associated invertebrate community (top row) from samples in tropical wet forest at the Estación Biológica La Selva, Costa Rica. S and J represent richness and evenness, respectively. P-values are in parentheses below the correlation coefficients, and statistically significant correlations at alpha = 0.05 are in bold type.

	Invert S	Invert J	Invert abundance	Beetles	Ants	Arachnids
Leaf S	**0.78** **(0.005)**	-0.26 (0.43)	0.18 (0.60)	0.53 (0.10)	0.24 (0.47)	-0.17 (0.61)
Leaf J	**0.72** **(0.01)**	-0.32 (0.34)	0.28 (0.41)	0.45 (0.17)	0.05 (0.88)	-0.26 (0.43)
Structural S	-0.05 (0.89)	-0.32 (0.34)	0.16 (0.63)	0.23 (0.49)	0.09 (0.79)	-0.17 (0.62)
Structural J	0.36 (0.27)	-0.01 (0.99)	0.05 (0.88)	0.35 (0.29)	-0.19 (0.58)	-0.13 (0.70)
Litter mass	0.05 (0.88)	0.03 (0.92)	-0.17 (0.62)	0.05 (0.88)	-0.18 (0.59)	-0.40 (0.22)
Sm sticks	-0.08 (0.81)	0.30 (0.36)	-0.37 (0.26)			
Lg sticks	-0.27 (0.43)	0.30 (0.38)	-0.37 (0.27)			
Leaf fragments	0.37 (0.26)	-0.23 (0.51)	0.30 (0.37)			
Leaf 5	-0.11 (0.75)	-0.47 (0.14)	0.45 (0.16)			
Fruit 4	-0.14 (0.68)	-0.10 (0.76)	0.10 (0.76)			

Table 2. Litter arthropod morphotyes found in leaf litter of old-growth forest at the Estación Biológica La Selva, Costa Rica, in pitfall traps and Berlese funnels (total number of morphotypes = 30).

Category:	Number of morphotypes
Formicidae	11
Coleoptera	6
Araneae (spiders)	4
Gryllidae (crickets)	3
Isopoda	2
Diptera	1
Pseudoscorpionida	1
Annelida	1
Cicadellidae	1

DISCUSSION

As predicted, we discovered a strong positive correlation between morphotype diversity of the La Selva leaf litter and morphotype richness of the litter invertebrates. However, we did not find any correlation between litter structure and invertebrate richness, evenness, or abundance. It is possible that the invertebrate species we found are specialized according to food resources (i.e. leaf species) rather than habitat resources (i.e. structural components), and therefore increasing leaf species adds to the number of possible niches, while increasing litter structural components does not.

The strong negative correlation between invertebrate abundance and evenness suggests that adding individuals to a sample does not add more species, but rather adds more numbers of a few highly abundant species, thereby reducing evenness. Taxa that may have contributed to this effect include two invertebrate morphotypes, an ant and a dipteran, which together comprised 42.9% of all invertebrates.

In contrast to other studies (Chen and Wise 1999, Koivula et al. 1999, Hooper et al. 2000, Halaj and Wise 2002), we found no correlation between litter mass and invertebrate abundance. If La Selva litter experiences seasonal changes in its quantity and composition, our result may be the product of a lag in invertebrate response to dry season leaf-fall. Longer-term research that monitors the leaf litter community of La Selva over seasons could test this hypothesis.

A clearer relationship between litter structure or abundance and the invertebrate

community might emerge if our litter structure and abundance had varied more among samples. Future studies could explore the effects of litter that is more and less diverse than that found in this study, by experimentally manipulating the amount of leaf litter, and leaf litter structure, in the field. Overall, our study supports our hypothesis that invertebrate diversity responds to litter leaf richness. Further work is needed to uncover the underlying mechanisms.

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