VISITATION AND FRUIT CONSUMPTION BY BIRDS AT A REPRODUCTIVE *FICUS PERTUSA* AT LA SELVA BIOLOGICAL STATION

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Abstract. The reproductive success of fruiting tropical trees depends in part on seed dispersers. Plant species in seasonal tropical ecosystems that fruit during dry season scarcity are crucial to sustaining frugivores that are important seed dispersers for many tree species throughout the year. Fig species provide a constant food supply by producing copious fruits, with individuals within species fruiting asynchronously, a reproductive strategy that makes them keystone species in tropical ecosystems. We studied the seed dispersal of a fruiting *Ficus pertusa* by observing and identifying its avian visitors. During 20 hours of observations over two days, we documented 2862 visits, comprising 52 bird species, which consumed a total of 3050 figs. Clay-colored and Pale-vented Robins together consumed 53% of total fruits and represented 31% of total visits. By providing fruits for many bird species during the dry season, *F. pertusa* may sustain populations of seed dispersers important for its own reproduction and that of many other plant species.

Keywords: Keystone species, seed dispersal

INTRODUCTION

The reproductive success of fruiting trees depends in part on dispersal of seeds (Howe and Smallwood 1982). In tropical ecosystems, the survival of seeds is often maximized when the seeds are dispersed away from the parent plant, reducing both intraspecific competition and density-dependent seed predation and herbivory (Janzen 1970 and Connell 1971). In Costa Rica, 85% of canopy trees and 98% of sub-canopy trees rely on vertebrates to disperse their seeds (Howe and Smallwood 1982). Birds represent 45% of Costa Rica's canopy vertebrate dispersers and 68% of sub-canopy vertebrate dispersers (Leigh and Windsor 1982). To ensure that seeds are dispersed, and not degraded within the digestive systems of dispersers, plants either produce large seeds that dispersers regurgitate or small seeds that are defecated (Murray et al. 1994).

Many animals depend on fruiting trees. In the tropics, however, most trees fruit only in the wet season and therefore support frugivores intermittently (Janzen 1983). Plant species that fruit during the dry season, a time of fruit scarcity, are crucial to sustaining frugivorous animals that are important seed dispersers for many species throughout the year (Howe 1984). Failure to support seed dispersers during the dry season

would have strong negative consequences for all trees whose propagules are dispersed by those species. Thus, plant species that sustain frugivores (many of whom are effective dispersers) during periods of resource scarcity are considered keystone species (Gilbert 1980).

Asynchronous fruit production among individuals of sub-canopy fig species, as well as their large fruit crops, provide a continuous food source for frugivores (Tello 2003). We studied a fruiting individual of the subcanopy fig *Ficus pertusa* at La Selva Biological Station, Costa Rica. Many bird species of varying sizes are capable of feeding on the fruits of *F. pertusa*, due to the fruits' intermediate size (*c*. 1 cm diameter). While there are no distinct seasons at La Selva, February-April is relatively dry (Moore and Stephenson 2003). We expected that this *F. pertusa* individual, fruiting in the dry season, would be visited by many bird species; our goal was to document all avian frugivores that visited it over a two-day period.

METHODS

We observed bird visitation to a *F. pertusa* tree *c.* 10 m north of the cafeteria at La Selva Biological Station, Costa Rica, on 13-15 February 2007. The fig tree was *c.* 8 m tall, with three main branches, and started fruiting three days prior to the study. The two weeks after a *F. pertusa* fruits is the peak time for avian visitors; after this period, only 30% of the tree's fruits remain available (Tello 2003). We made morning and afternoon observations on 13 February (1200 -1700), 14 February (0600 - 1100 and 1200-1700), and 15 February (0600-1100), for a total of 20 hours.

During each of the four 5-hour observation periods, two observers used binoculars to identify the species of every bird that visited the tree, for a total of 40 person hours. Each observer recorded bird visits to half of the tree. If a positive identification could not be made, morphological characteristics were recorded for identification later. On the first morning, we did not distinguish between Clay-colored and Pale-vented Robins, so we grouped these into "Robins" for some of our analyses.

We watched each visiting bird and recorded all feeding behaviors during its visit. The behaviors were categorized into five actions: peck (eating approximately half of a fruit), whole (eating an entire fruit), fly (flying away with an uneaten fruit still in its mouth), drop (dropping either a part or a whole fruit), and ground (eating either a part or a whole fig fruit from the ground under the tree). For more than one peck to be documented, a bird must have pecked more than one fruit.

For a whole fruit to be documented, a bird must have swallowed an entire fruit either in one bite, or in successive pecks.

We calculated the total number of visits, the total number of species that visited, and the total number of fruits consumed. For each species, we also calculated the percentage of total visits, percentage of total fruits consumed, and the average number of fruits consumed per visit. We divided our observations into one-hour intervals, using the average of two days of data for each interval, to assess the variation in visits and fruit consumption during the day, for all species combined, and separately for the five species that visited most often.

RESULTS

The *Ficus pertusa* individual had 2862 visits, over a total of 20 hours, by 52 species of birds, which consumed 3050 fruits. The top five visitors were Clay-colored and Pale-vented Robins, Passerini's Tanager, Golden-hooded Tanager, Olive-backed Euphonia, and Palm Tanager (Table 1). The top five fruit consumers were the same, except that the Black-cheeked Woodpecker took approximately the same number of figs as the Palm Tanager (Table 1). When we excluded the first five hours, in which Clay-colored and Pale-vented Robins were lumped, we found that Clay-colored Robins comprised 23% of total visits and 38% of total fruits eaten and that Pale-vented Robins comprised 9% of total visits and 16% of total fruits eaten. The total number of bird visits, and visits by the five most frequent visitors, decreased during the day (Fig. 1a, Fig. 1b). The relative abundance of species also changed throughout the day: the percentage of Robins, Olive-backed Euphonias, and Palm Tanagers decreased, while the percentage of Passerini's Tanagers and Golden-hooded Tanagers increased (Fig. 1c).

The total number of fruits consumed decreased during the day (Fig. 2a). While the fruit consumption of Passerini's Tanager and Golden-hooded Tanager remained constant, that of Olive-backed Euphonia and Palm Tanager decreased slightly, and that of the Robins decreased drastically (Fig. 2b). The same trends were observed for the percentage of fruits consumed throughout the day. However, the increase in the percentage of fruits consumed by Passerini's Tanager and Golden-hooded Tanager was stronger than their increase in fruit consumption (Fig. 2c).

TABLE 1. The species of birds that visited a fruiting *Ficus pertusa* at La Selva Biological Station, Costa Rica during a total of 20 hours of observations in the dry season. The percent of total visits (% Visits), the percent of fruits consumed (% Fruits), the number of total visits (Total Visits), the number of total fruits consumed (Total Fruits) and the number of fruits consumed per visit (Fruits/Visit) were calculated for each species (n=2862 total visits by all species). The five species with the most visits are in bold.

Common Name	Scientific Name	% Visits	% Fruits	Total Visits	Total Fruits	Fruits/ Visit
Balitmore Oriole	*Icterus g. galbula*	0.35	0.02	1	0.50	0.50
Bananaquit	*Coereba flaveola*	0.21	0.18	6	5.50	0.92
Black-and-white Warbler	*Mniotilta varia*	0.	0	1	0	0
Black-cheeked Woodpecker	*Melanerpes pucherani*	1.57	5.05	45	154.00	3.42
Black-faced Grosbeak	*Caryothraustes poliogaster*	0.25	0.72	7	22.00	3.14
Black-throated Trogon	*Trogan rufus*	0.04	0	1	0	0
Blue Dacnis	*Dacnis cayana*	0.73	0.74	21	22.5	1.07
Blue-black Grosbeak	*Cyanocompsa cyanoides*	0.25	0.16	7	5.00	0.71
Blue-gray Tanager	*Thraupis episcopus*	2.03	1.95	58	59.5	1.03
Bronze-tailed Plumeleteer	*Chalybura urochrysia*	0.04	0	1	0	0
Buff-throated Saltator	*Saltator maximus*	1.15	1.80	33	55.00	1.67
Chestnut-sided Warbler	*Dendroica pensylvanica*	1.15	1.30	33	39.50	1.20
Cinnamon Becard	*Pachyramphus cinnamomeus*	0.21	0.16	6	5.00	0.83
Clay-colored & Pale-vented Robin	***Turdus assimilis & Turdus obsoletus***	**31.45**	**52.7**	**900**	**1607.50**	**1.79**
Collared Aracari	*Pteroglossus torquatus*	0.35	0	1	0	0
Common-Tody Flycatcher	*Todirostrum cinereum*	0.14	0.26	4	8.00	2.00
Dusky-faced Tanager	*Mitrospingus palmarum*	0.11	0.08	3	2.50	0.83
Golden-hooded Tanager	***Tangara larvata***	**14.61**	**15.97**	**418**	**487.00**	**1.17**
Gray-capped Flycatcher	*Myiozetetes granadensis*	0.18	0.12	5	3.50	0.70
Great Kiskadee	*Pitangus sulphuratus*	1.50	1.99	43	61.00	1.42
Green Honeycreeper	*Chlorophanes spiza*	2.10	1.98	60	60.50	1.01
Mealy Parrot	*Amazona autumnalis*	0.21	0.59	6	18.00	3.00
Montezuma's Oropendola	*Psarocolius montezuma*	0.04	0.03	1	1.00	1.00
Olive-backed Euphonia	***Euphonia gouldi***	**8.81**	**8.97**	**252**	**273.50**	**1.09**
Orange-chinned Parakeet	*Brotogeris jugularis*	0.98	2.97	28	90.20	3.23
Palm Tanager	***Thraupis palmarum***	**4.86**	**4.75**	**139**	**145.00**	**1.04**
Passerini's Tanager	***Ramphocelus passerinii***	**20.23**	**21.79**	**579**	**664.50**	**1.15**
Plain-colored Tanager	*Tangara inornata*	0.87	0.74	25	22.50	0.90
Red-legged Honeycreeper	*Cyanerpes cyaneus*	0.04	0	1	0	0
Rufous-tailed Hummingbird	*Amazilia rutila*	0.49	0	14	0	0
Scarlet-thighed Dacnis	*Dacnis venusta*	0.25	0.33	7	10.00	1.43
Shining Honeycreeper	*Cyanerpes lucidus*	0.28	0.26	8	8.00	1.00
Silver-throated Tanager	*Tangara icterocephala*	0.38	0.26	11	8.00	0.73
Snowy Cotinga	*Carpodectes antoniae*	0.07	0.07	2	2.00	1.00
Summer Tanager	*Piranga rubra*	0.04	0.03	1	1.00	1.00
Social Flycatcher	*Myiozetetes granadensis*	1.19	1.13	32	34.50	1.08
Tennessee Warbler	*Vermivora peregrina*	2.13	1.74	61	53.00	0.87
Variable Seedeater	*Sporophila torqueola*	0.63	0.93	18	28.50	1.58
Violaceous Trogon	*Trogan violaceus*	0.07	0.03	2	1.00	0.50
White-collared Manakin	*Manacus candei*	0.18	0.20	5	6.00	1.20
Yellow-crowned Euphonia	*Euphonia luteicapilla*	0.14	0.20	4	6.00	1.50
Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	0.07	0.03	2	1.00	0.50
Unknown		0.35	0.15	10	4.5	0.45

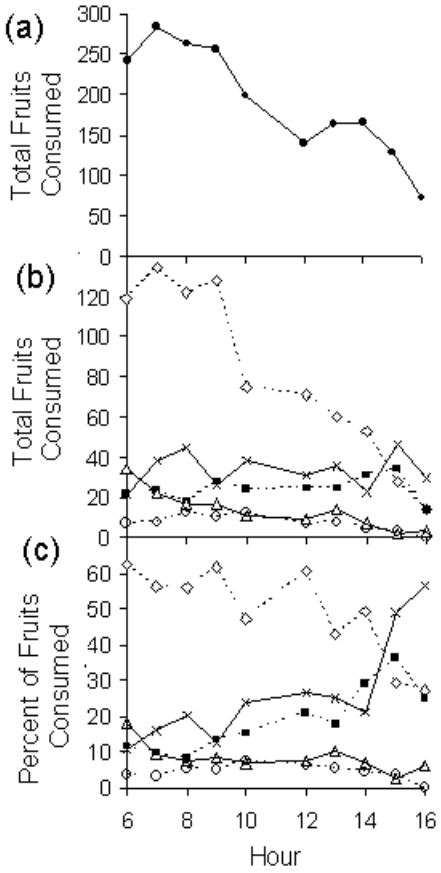

Figure 1. (a) The total number of avian visits per hour, (b) the number of visits per hour for each of the five bird species with the most visits, and (c) percent of total visits for each of the five bird species with the most visits, to a fruiting *Ficus pertusa* at La Selva Biological Station, Costa Rica. Values are averages in one-hour periods during observations on two mornings (0600-1200) and two afternoons (1200-1700), during the dry season (n=20 one-hour intervals). For panels (b) and (c), open diamonds (◊) represent Robins, dark squares (■) are Golden-hooded Tanagers, open triangles (Δ) are Olived-backed Euphonias, open circles (○) are Palm Tanagers, and crosses (x) are Passerini's Tanagers.

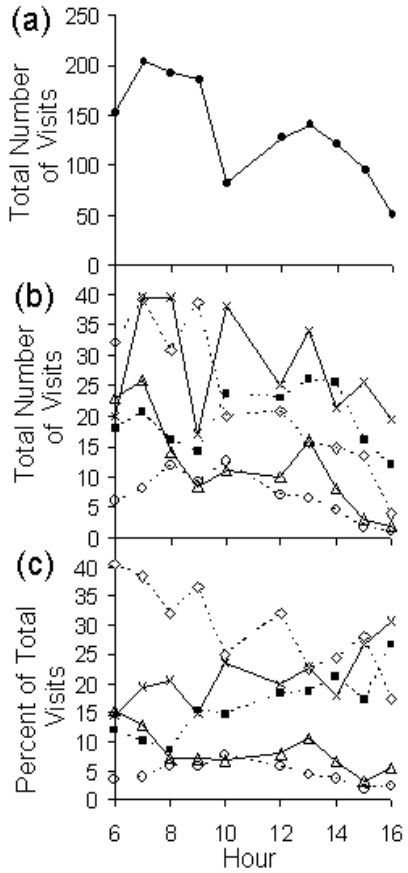

Figure 2. (a) Total number of fruits consumed per hour by avian dispersers, (b) number of fruits consumed per hour by each of the five bird species with the most visits, (c) and percent of total fruits consumed by each of the five bird species with the most visits to a fruiting *Ficus pertusa* at La Selva Biological Station, Costa Rica. Values are averages in one-hour periods during observations on two mornings (0600-1200) and two afternoons (1200-1700), during the dry season (n=20 one-hour intervals). For panels (b) and (c), open diamonds (◊) represent Robins, dark squares (■) are Golden-hooded Tanagers, open triangles (Δ) are Olived-backed Euphonias, open circles (○) are Palm Tanagers, and crosses (x) are Passerini's Tanagers.

Discussion

Over twenty hours, we observed 2862 visits from 52 species of birds. We documented visits from flocking birds common in this area, such as the Passerini's Tanager and the Buff-throated Saltator (Stiles and Skutch 1989), as well as occasional visits from the Violaceous Trogon and the Montezuma Oropendola. The top five visitors were Clay-colored and Pale-vented Robins, Passerini's Tanager, Golden-hooded Tanager, Olive-backed Euphonia, and Palm Tanager. When we examined the Robins separately, Clay-colored Robins accounted for 78% of total Robin visitors.

We believe the decrease in visitor frequency over the day is due to decreased foraging with increasing temperatures (Blake 1992). The relative abundances of the main visitors changed throughout the day, and these changes could be mediated by species interactions. As a hypothetical example, if Robins and Olive-backed Euphonia were competitively dominant, their decline in relative abundance during the day may have allowed more access by other species, such Passerini's Tanager and Golden-hooded Tanager. Over the course of the day, there was a decrease in the total number of fruits consumed, which may be attributable to the decline in consumption by Robins, which account for over half of total consumption.

Birds disperse the small seeds of fig trees via ingestion and defecation. We considered the number of seeds ingested to be an index of a bird's potential effectiveness as a disperser. Our top five visitors were also among the top fruit consumers: Robins, Passerini's Tanager, Golden-hooded Tanager, Olive-backed Euphonia, and Palm Tanager. Clay-colored Robins and Pale-vented Robins do not eat many seeds per visit, but they are likely important dispersers due to their high total number of visits. Other species, such as the Black-cheeked Woodpecker and Black-faced Grosbeak, did not visit the tree often, but they may be important dispersers because they consumed many seeds per visit. The importance of a bird species as a seed disperser will likely depend on both the frequency with which they visit as well as the number of seeds they consume per visit.

We have documented a single fig tree's avian seed visitors and potential dispersers. For a more complete picture of the fig tree's dispersers, future studies could examine visits from bats, primates, and terrestrial mammals.

This single fig tree provided nutrition for 52 species of birds over just twenty hours of observations during the fruit-poor dry season. In doing so, this tree may have

sustained seed dispersers important to its own reproduction, and that of other tree species.

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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).

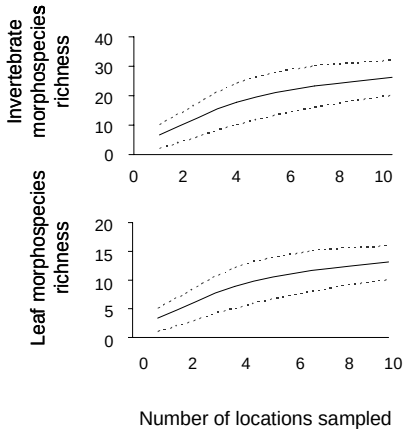

Fig. 1. Species-area curves for invertebrates and leaf litter from 11 sampling locations in old-growth forest floor at the Estación Biológica La Selva, Costa Rica. Numbers of arthropods in each sample ranged from 16 to 110 individuals.

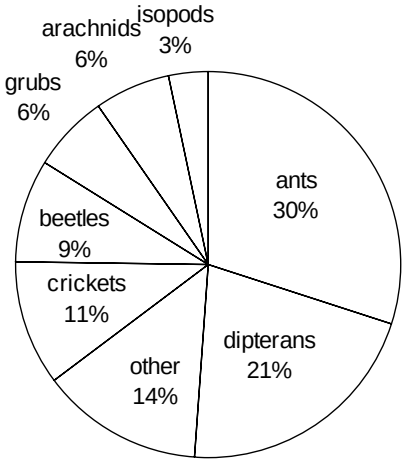

Fig. 2. Percent individual abundances of invertebrate morphotypes in samples from pitfall traps and Berlese funnels, in the tropical wet forest at the Estación Biológica La Selva, Costa Rica.

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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