EFFECTS OF FERTILIZER ADDITION AND DEBRIS REMOVAL ON LEAF-LITTER SPIDER COMMUNITIES AT TWO ELEVATIONS

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ABSTRACT.   This study investigates the indirect effects of primary productivity enhancement via fertilization, and the direct effects of environmental differences at two elevations, on the density and species richness of leaf-litter spiders. Litter was sampled in tabonuco forest (340–360 m elevation) and elfin forest (1051 m elevation) within the Luquillo Experimental Forest Long Term Ecological Research (LTER) site in Puerto Rico. Treatments consisted of three blocks with fertilization and control plots at both sites, and a one time removal of hurricane generated debris at tabonuco forest only. Treatments had no significant effect on spider density, species diversity, and species richness at either elevation. Elfin forest showed lower densities and lower species richness than tabonuco forest due to harsh environmental conditions. The thin litter layer and similar standing litter in the tabonuco forest suggest that spiders are limited by habitat, and also that they have successfully recolonized the debris cleared areas at this elevation. Harsh environmental conditions at elfin forest seem to be strong enough to counteract the effects of fertilizer addition on the measured variables. However, the high biomass of grasses in the fertilization plots at elfin forest could have caused an underestimation of spider densities. This study suggests that habitat availability is an important variable in bottom-up models for food web link control.

Keywords: Leaf-litter community, species diversity, primary productivity enhancement, tabonuco forest, Puerto Rico

Most studies of indirect effects of primary productivity enhancement on spider densities, or studies on spider recolonization patterns, have focused on above-ground spiders because they are easy to manipulate and count (Vince et al. 1981; Ehman & MacMahon 1996). Prey density may be affected by the bottom-up effects of nutrient addition in a food web (Power 1992). For example, the density of spiders of the Gulf of California is correlated negatively with island size (Polis & Hurd 1995). Higher marine productivity input to smaller islands, due to exposition of larger superficial area of small islands compared to larger ones, permits the support of higher arthropod prey densities and a higher density of web building spiders (Polis & Hurd 1995). In a salt marsh fertilization experiment, spiders showed a numerical response to an increased density of herbivores in the fertilization plots (Vince et al. 1981).

An increase in prey triggers a density independent aggregational and reproductive nu-

merical response in web-building spiders (Riechert & Lockley 1984; Wise 1993). These responses are said to be density independent because spiders have longer generation times and lower fecundity than most of their prey, and therefore can not track their prey populations closely (Riechert & Lockley 1984).

Spiders can quickly recolonize shrubs from which they are excluded by manipulation (Ehman & MacMahon 1996). Differences in the recolonization pattern, with an initial colonist inhibiting the establishment of others (see Drake 1991; Law & Morton 1993), have been shown to be an important factor in community composition development (Ehmann & MacMahon 1996).

As generalist predators, spiders constitute a very important group structuring leaf-litter communities (Clarke & Grant 1968; Moulder & Reichle 1972; Pfeiffer 1996). Leaf-litter arthropod communities can vary seasonally (Frith & Frith 1990), and along elevational gradients (Olson 1994). Variation in invertebrate abundance can also be related to availability of nutrients (Uetz 1976; Olson 1994) and fluctuations in environmental conditions

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(Frith & Frith 1990). The poorer the available nutrients and/or the harsher the environment, the lower the abundance.

In this study I focus on leaf-litter spiders to address the following questions: (1) How do harsh environmental conditions and lower primary productivity at one of two elevations of a tropical rain forest adversely affect litter spiders density and richness of species? (2) How does enhanced productivity at the two elevations, via fertilizer addition, favor higher densities of spiders?, and (3) How is species composition affected by recolonization of spider depleted sites?

I sampled litter spiders at two elevations in the Luquillo Experimental Forest (LEF). These two areas have subjected to fertilization treatments since 1989, after the strike of Hurricane Hugo. The low elevation site includes plots where all hurricane-generated debris was experimentally removed; and as a result, almost all invertebrates were also removed.

METHODS

Study site.—This study was conducted in the tabonuco and elfin forests found in the Luquillo Experimental Forest Long-term Ecological Research (LTER) site in Puerto Rico. The tabonuco forest area is located near El Verde Field Station, at the eastern part of Puerto Rico (18°20′N, 65°49′W) and it is at an elevation between 340–360 m (Zimmerman et al. 1995). It is classified as a subtropical wet forest (Ewel & Whitmore 1973). This area is dominated by *Dacroydes excelsa* Vahl, known as tabonuco, and *Prestoea montana* Nichols, known as the sierra palm (Walker et al. 1996).

The tabonuco forest was heavily damaged by Hurricane Hugo in September 1989 (Sanford et al. 1991). The mass of fine litter (defined as all leaf, wood <1 cm in diameter, and miscellaneous plant material) that resulted from the hurricane was almost 400 times the daily average at El Verde and Bisley (Lodge et al. 1991). Input of nutrients via litterfall appears to have altered nutrient cycles, increasing forest productivity and nutrient availability (Sanford et al. 1991). Canopy cover and height also decreased dramatically (Brokaw & Grear 1991). Invertebrate populations were greatly reduced (Alvarez & Willig 1993; Willig & Camilo 1991).

One of the elfin forest areas of the Luquillo Mountains is located at Pico del Este (18°16′N, 65°45′W), which is a summit area at 1051 m of elevation. Its vegetation is classified as lower montane rain forest (Ewel & Whitmore 1973). The dominant species are *Tabebuia rigida* Urban, *Ocotea spathulata* Mez, and *Calyptranthes krugii* Kiaersk (Walker et al. 1996). This forest was heavily defoliated by Hurricane Hugo (Brokaw & Grear 1991). Compared to pre-hurricane levels, mean annual litterfall was 1.9 times higher, and the annual fine litterfall input of N (1.5×), P (1.7×) and K (3.1×) times higher (Lodge et al. 1991). Aside from these damages, there were no large structural changes at Pico del Este (Walker et al. 1996).

Structural and dynamic features of the tabonuco forest are very different from the high altitude elfin forest. The number of trees per hectare, basal area, and soil organic matter are higher in the elfin forest; while specific leaf area, canopy height, tree diameter range, forest volume and biomass, and species diversity are higher at the tabonuco forest (Weaver & Murphy 1990). Tree ingrowth and mortality, tree growth (includes biomass, volume, and diameter), litterfall, amount of loose litter, litter turnover, herbivory, and net primary productivity are higher at the tabonuco forest (Weaver & Murphy 1990). Climatic conditions in the elfin forest at Pico del Este such as high humidity, soil saturation, relatively low temperatures, high winds, and soil leaching are thought to be influential to its structural and dynamic features (Weaver et al. 1986, Weaver & Murphy 1990).

Experimental design.—The experimental blocks in the tabonuco forest were chosen at random. Each block was divided in three experimental plots measuring 20 × 20 m each (Zimmerman et al. 1995). Plots were located on ridge tops to minimize water flow between plots (G.R. Camilo pers. comm.). The three treatments were: (1) one-time total debris removal, (2) fertilization, and (3) control. The one-time debris removal treatment occurred one month after the hurricane. Following the treatment, litter was allowed to accumulate naturally. Fertilizer treatment was first applied immediately after Hugo and then approximately every three months. Fertilizer was added at an annual rate of 300 kg/ha N, 100 kg/ha P, 100 kg/ha K, 8 kg/ha B, 15.4 kg/ha Cu, 2.2 kg/ha Fe, 25 kg/ha Mn, 26 kg/ha Zn and 19 kg/ha Mg (Walker et al. 1996). These rates

constitute N (3×), P (30×) and K (2×) the mean annual inputs from fine litterfall (Lodge et al. 1991). The control plot was left intact, with no debris removed and no fertilizer applied (Walker et al. 1996).

Each block in elfin forest consisted of pairs of plots, located on ridge tops, randomly assigned as control or fertilization (Walker et al. 1996). Debris removal treatment was not applied due to the small amount of Hurricane generated debris at this forest (Zimmerman pers. comm.). Each plot measures 9 × 14 m. Fertilizer was first applied in April 1990 and then every 3 months to the present (Walker et al. 1996). Fertilizer constitute N (15×), P (166×), and K (30×) the mean annual input from leaf litterfall (Lodge et al. 1991). For this study I used three adjacent blocks in elfin forest to compare with three blocks in the tabonuco forest.

The litter spider community was sampled five times at each site between February 1996–January 1997. Each sample consisted of four random 0.25 m^2 quadrants of leaf litter taken by hand from each experimental plot in each of three blocks at tabonuco forest and six randomly chosen plots at elfin forest. Leaf litter was then taken to the laboratory and placed in Berlese funnels for 5 days, or until dry, to extract invertebrates. After invertebrates were removed the processed litter was returned to the site of collection.

We placed four pitfall traps randomly in each plot in order to sample wandering nocturnal spiders and other invertebrates that may not retreat into the leaf litter by daytime. Traps consisted of containers with openings of 10 cm in diameter and 18 cm deep. Each container was filled to less than half of its capacity with a 70% ethanol -5% ethylene glycol solution. The opening was covered with disposable dish to exclude rain water. The traps were left on the sites for two days.

Spider samples obtained from Berlese and pitfall traps were preserved in 70% ethanol and were sorted by family and genus, and identified to species whenever possible using the appropriate literature (Petrunkevitch 1929, 1930a, 1930b; Bryant 1942; Chickering 1967, 1968, 1969, 1972a, 1972b). Juveniles were identified to family level only. Family and generic names follow Platnick (1989). Collected specimens were deposited in the Biology Mu-

seum of the University of Puerto Rico, Río Piedras Campus.

ANOVAs for a two-factor split plot design laid off in localities (based on Ott 1993) were performed to determine differences in square root transformed density data (Zar 1984) and the number of species present between treatments and localities. Subplots within a locality were tested for treatment and time of sampling effects. In addition, two-factor repeated measures ANOVA (Ott 1993) were performed on data from tabonuco forest to include data from the debris removal treatment, which is excluded in the split plot ANOVA.

The Morisita-Horn index was used to estimate the similarity (family level) among sites (Horn 1966; Wolda 1983; Russel-Smith & Stork 1995). A Multidimensional Scaling analysis was performed on the similarity matrix obtained from the index calculations to have a graphic representation of the dissimilarities between plots. A Principal Components Analysis was performed on data from all sites to determine which families are more important to the dissimilarities between plots.

RESULTS

Density of spiders.—A split plot ANOVA performed on data from both sites showed that there is no effect of treatment on spider density, but there is significant difference between localities (Table 1a). Densities per plot ranged from 0–15 ind./m^2 at elfin forest and from 5–118 ind./m^2 at tabonuco forest (Fig. 1). A repeated measures ANOVA performed on data from tabonuco forest to account for debris removal treatment effects revealed no difference in density of spiders between treatments, but revealed effects of time (Table 1b). Peak densities occurred between September and October (Fig. 1).

Species richness.—Based on adult individuals, there was a total of 31 species and 19 families identified from the two forest types (Table 2). A total of 27 species was found at tabonuco forest (Table 2). The dominant species in all treatments was *Modisimus montanus*, followed by *Theotima radiata*, and *Masteria petrunkevitchi*. When juveniles and adults were taken together, the dominant family was Pholcidae (Table 2). *Modisimus montanus* is the only adult species collected in the Pholcidae, therefore the juvenile individuals are probably of the same species.
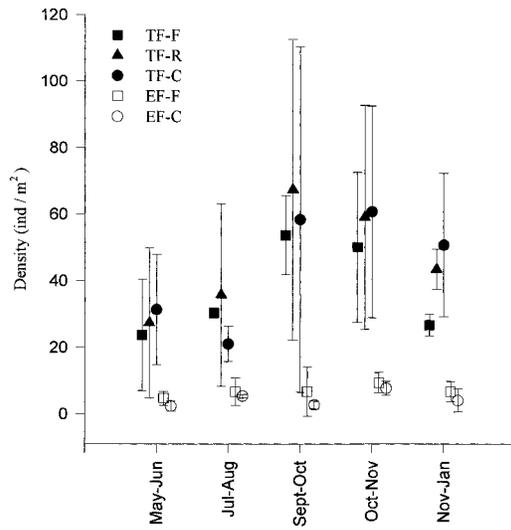
Figure 1.—Density of spiders per treatment plot, elevation, and sampling date. TF = tabonuco, EF = elfin, F = fertilization, R = debris removal, C = control.

Data from elfin forest yielded 16 species, four of these were found only at elfin forest; and all four of these were collected only once (Table 2). Pooled data for adult individuals

from both treatments show that *Mysmena caribbaea* is the dominant species at this locality, followed closely by *Oningis minutus* and *Corinna jayuyae* (Table 2). *Theotina radiata* and *M. petrunkevitchi* were virtually absent at elfin forest. When juveniles are taken in consideration, along with adults, the dominant families are Pholcidae (presumably *M. montanus*) and Salticidae (most adults represented by *O. minutus*) (Table 2). Of the seven species collected only in pitfall traps at tabonuco forest, *Agriognatha gloriae* was a web builder not typical of the litter, but of the understory. At elfin forest there were two species captured only in pitfall traps (Table 2). Of the two species, a poorly-preserved male specimen of the genus *Tetragnatha* is typical of the understory.

A split plot ANOVA showed that the number of species differed between localities but not between treatments (Table 3a). The number of species was higher at tabonuco forest (see Table 2). A repeated measures ANOVA, performed on data from tabonuco forest to account for debris removal effects, revealed no effect of this treatment on the number of species (Table 3b).

Community similarity.—The Morisita-

Table 1.—ANOVA analysis for the effects of treatment, time of sampling, and elevation on the density of leaf litter spiders. TF = tabonuco, EF = elfin.

Source	df	Mean square	F	P
A. Split plot ANOVA to compare treatment and time of sampling effects between TF and EF. Debris removal was excluded from this analysis.				
Between localities				
Time	4	5.402	1.72	>0.25
TF vs EF	1	228.32	72.64	<0.0025
Time × (TF vs EF)	4	3.143		
Within localities				
Treatment	1	0.025	0.01	0.904
Treatment × Time	4	0.546	0.32	0.865
Error	45	1.723		
B. Repeated measures ANOVA to compare effects of treatment (including debris removal) and time of sampling (Time) at the plots of tabonuco forest.				
Between blocks				
Treatment	2	1.334	1.46	>0.25
Plots in treatment	6	0.910		
Within blocks				
Time	4	11.66	3.01	0.035
Time × Treatment	8	0.935	0.24	0.979
Error	24	3.88		

Horn community similarity index was calculated using pooled data for family from all sampling times. Table 4 shows the similarity matrix obtained from this analysis. Multidimensional Scaling Analysis of the matrix shows good separation of sites based on locality (Fig. 2). Plots from the same elevation and treatment tend to be most closely related, with the exception of the tabonuco forest, where removal plots show the greatest variation in species composition (Fig. 2). Principal Component Analysis show that the first axis accounts for 92% of the variance between plots. The family with the highest absolute loading in this axis is Pholcidae (0.98), followed by Ochyroceratidae (0.15) and Heteropodidae (−0.085). Axis 2 accounts for 4.2% of the variance between plots, with the highest absolute loading values for Ctenidae (−0.73), Heteropodidae (−0.66) and Pholcidae (−0.35). Axis 1 shows a clear separation of plots by elevation, except for two plots from tabonuco forest (control #2 and debris removal #3) that appear together with the plots from elfin forest (Fig. 3). These two plots from tabonuco forest have a lower density of Pholcidae than the rest of the plots from this elevation. Axis 2 clearly separates one of the fertilized plots from elfin forest from all the other plots (Fig. 3). The prevalence of families with negative eigenvector values (namely Oonopidae, Ctenidae and Heteropodidae) is responsible for this separation.

DISCUSSION

Density of spiders.—The lack of a treatment response may be due to a lack of response from spider prey to treatments. Preliminary data for litter insects from the same experimental plots show no significant difference between treatments at tabonuco forest or elfin forest (E. Nazario pers. comm). Standing litter was similar for all treatments at a given elevation, even though litter fall was higher in fertilization plots at each elevation site (Walker et al. 1996). This suggest that there is a higher density of decomposers in the fertilization plots.

A factor opposing the bottom-up productivity enhancement effects on spiders relates to features of the litter. The structure and depth of the litter have been shown to be very important factors affecting the density and diversity of litter arthropods (Uetz 1979; Bult-

man & Uetz 1982, 1984). Spider density and diversity increase with higher litter depth and complexity (Uetz 1979; Bultman & Uetz 1982, 1984). Litter depth proved to be more important, in the short term, for spiders than nutrient content of the litter (Bultman & Uetz 1984). The fact that the litter layer is relatively thin at the tabonuco forest (Pfeiffer 1996) and elfin forest (pers. obs.), and that standing litter in our plots is similar in all treatments (Zimmerman et al. 1995; Walker et al. 1996), supports the statement that spiders are habitat limited in our plots. The constant and rapid turnover of leaf litter (La Caro & Rud 1985) may limit habitat for litter spiders. Because leaves are constantly decomposing, *M. montanus* will have to frequently switch to a new leaf.

Consumption by vertebrate predators is not a very important factor opposing the bottom-up productivity enhancement effects on litter spiders in the tabonuco forest (Pfeiffer 1996). Diurnal predators concentrate foraging activities to the arboreal layers (Reagan 1996); nocturnal predators forage in arboreal areas or near the ground (Stewart & Woolbright 1996). *Eleutherodactylus portoricensis* Schmidt is the only vertebrate that includes some litter arthropods in its diet (Stewart & Woolbright 1996). Non-anoline reptiles like the gecko *Sphaerodactylus klauberi* Grant (1 individual/ m^2) may account for the majority of litter arthropod consumption (Pfeiffer 1996), which include, in order of quantity, Acari, Araneae, Collembola, Isopoda, and Coleoptera (Thomas & Gaa Kessler 1996). However, unlike *Eleutherodactylus* frogs, we never collected *S. klauberi* in the litter.

The one time debris removal from experimental plots in 1989 eliminated almost all litter fauna and their respective habitats. The lack of differences in spider density, and the similarity of standing litter between treatments (Zimmerman et al. 1995), suggests that litter spiders were able to recolonize rapidly. Spiders near the debris removal plots had potential free habitat to colonize from the moment when leaf fall began to cover the forest floor once again. The similarity of standing litter between treatments (Zimmerman et al. 1995) meant equal leaf-litter habitat availability in all plots. The relatively small size of our study plots (20 m^2) permits rapid recruitment of col-

Table 2.—Pooled abundance for spider families and species found in all treatments at the sites of tabonuco (TF) and elfin (EF) forests. Data include total number adult and juvenile specimens collected in Berlese funnels for each family. Total number of individuals from a species is based on adult individuals only. Species found only in pitfall traps are indicated by an asterisk (F = fertilization, R = debris removal, C = control).

Taxon	TF-F	TF-R	TF-C	EF-F	EF-C
Pholcidae	351	426	358	36	4
Modisimus montanus Pet.	67	87	79	8	1
Ochyroceratidae	32	91	48	4	4
Ochyrocera sp.	0	0	1	1	2
Theotima radiata Simon	23	72	37	0	0
Dipluridae	44	25	47	0	0
Masteria petrunkevitchi (Chickering)	18	8	11	0	0
Corinnidae	46	46	45	11	7
Corinna jayuyae Pet.	6	8	9	3	2
Trachelas bicolor Keyserling*	1	0	0	0	0
Heteropodidae	44	13	35	6	4
Pseudosparianthis jayuyae Pet.	7	0	4	1	2
Salticidae	20	23	36	12	28
Corythalia gloriae Pet.	5	4	8	0	0
Emanthis portoricensis Pet.	0	0	0	0	1
Oningis minutus Pet.	0	1	3	5	7
Oonopidae	17	3	22	7	2
Close to *Dysderina* sp.	1	0	0	0	1
Oonops ebenicus Chickering	4	1	7	1	0
Oonops sp.	1	0	1	0	0
Close to *Opopaea lutzi* Pet.	3	0	3	4	0
Stenoonops sp.*	2	0	0	0	0
Ctenidae	11	6	4	8	7
Celaetycheus strennus Bryant	0	1	0	4	1
Oligoctenus ottleyi Pet.	1	1	0	0	0
Symphytognathidae	0	5	2	9	5
Mysmena caribbaea Gertsch	0	2	2	9	4
Barychelidae	16	7	5	1	0
Trichopelma corozali (Pet.)	8	7	5	1	0
Caponidae	0	0	3	4	1
Nops blanda (Bryant)*	0	0	1	2	0
Hahniidae	0	2	7	0	0
Neohahnia ernesti (Simon)	0	2	0	0	0
Linyphiidae	0	7	0	0	0
Leptyphantes microserratus Pet.	0	6	0	0	0
Liocranidae	4	0	2	0	0
Phrurolithus insularus Pet.	3	0	2	0	0
Prodidomidae	1	0	1	0	0
Lygromma sp.*	1	0	0	0	0
Tetragnathidae	1	0	0	1	0
Agriognatha gloriae Pet.*	1	0	0	0	0
Tetragnatha sp.*	0	0	0	1	0
Theraphosidae	1	1	0	0	0
Ischnocolus culebrae Pet.*	0	1	0	0	0

Table 2.—Continued.

Taxon	TF-F	TF-R	TF-C	EF-F	EF-C
Theridiosomatidae	1	5	7	1	4
Baalzebub albinotatus (Pet.)	0	0	0	1	0
Chthonas sp.	0	2	3	0	0
Styposis luteus (Pet.)	0	0	0	0	1
Thomisidae	0	1	1	0	0
Epicaudus mutchleri Pet.	0	1	1	0	0

onizers from the surrounding habitat limited leaf litter.

Difference in density of litter spiders between tabonuco forest and elfin forest is consistent with a study that compared abundance and diversity of litter arthropods at different elevations in Panama (Olson 1994). In western Panamanian forests, species diversity and number of individuals decline in the upward transition to cloud forests (Olson 1994). This decline is associated with harsher environmental conditions (Weaver et al. 1986; Olson 1994), lower productivity (Weaver & Murphy 1990), and low resource availability (Olson 1994) at high elevations. Some harsh climatic conditions at elfin forest include high humid-

ity, moisture saturation, relatively low temperatures, high winds, and soil leaching (Weaver et al. 1986). Primary productivity (Weaver & Murphy 1990) and insect density (E. Nazario pers. comm.) are also lower at PE compared to EV. Leaf litterfall (Weaver & Murphy 1990) and standing litter (Walker et al. 1996) is also lower for PE. Thicker leaves at PE (Medina et al. 1981) should also be harder to curl than leaves at EV; and this could reduce the three-dimensional space of the litter, which is an important feature for spider habitat (Uetz 1979; Bultman & Uetz 1984).

Species richness.—Another study done at tabonuco forest found a total of 22 spider spe-

Table 3.—ANOVA analysis to compare the effects of treatment and time of sampling between tabonuco (TF) and elfin (EF) forest on the number of species.

Source	df	Mean square	F	*P*
A. Split plot ANOVA to compare treatment and time effects between elevations. Debris removal is excluded from the analysis.				
Between elevations				
Time	4	3.52	2.32	>0.10
TF vs EF	1	104.017	68.58	<0.0025
Time × (TF vs EF)	4	1.52		
Within elevations				
Treatment	1	3.75	0.17	0.68
Treatment × Time	4	3.08	1.94	0.12
Error	45	1.59		
B. Repeated measures ANOVA to compare treatment (debris removal included) and time of sampling at the plots of tabonuco forest.				
Between blocks				
Treatment	2	1.09	0.23	>0.25
Block	6	2.48		
Within blocks				
Time	4	2.86	1.47	0.24
Time × Treatment	8	2.01	1.03	0.43
Error	24	1.94		

Table 4.—Morisita-Horn community similarity index calculated for pooled data from each treatment plot. Numbers after treatment codes represent block number. Number of families per plot is given in the diagonal, shared species between plots are given in the upper right corner. Legend as in Table 1.

|	EF F1	EF F2	EF F3	EF C1	EF C2	EF C3	TF F1	TF F2	TF F3	TF R1	TF R2	TF R3	TF C1	TF C2	TF C3
EF-F1	10	6	6	8	5	7	8	8	6	9	9	8	7	8	9
EF-F2	0.76	7	6	7	5	5	5	5	5	6	6	6	5	6	7
EF-F3	0.60	0.50	8	8	4	6	6	5	6	7	6	7	6	7	8
EF-C1	0.86	0.70	0.76	10	5	8	7	7	7	9	8	9	8	9	10
EF-C2	0.82	0.81	0.52	0.81	5	4	5	5	5	5	5	5	4	5	5
EF-C3	0.64	0.47	0.60	0.81	0.72	8	6	6	6	8	7	8	7	7	8
TF-F1	0.79	0.79	0.60	0.62	0.74	0.45	13	8	10	9	8	9	8	9	11
TF-F2	0.65	0.77	0.36	0.45	0.58	0.28	0.86	10	8	9	9	8	7	9	9
TF-F3	0.73	0.87	0.48	0.59	0.77	0.44	0.92	0.92	10	9	8	8	8	9	10
TF-R1	0.74	0.82	0.39	0.57	0.67	0.35	0.85	0.91	0.93	12	10	11	9	10	12
TF-R2	0.69	0.82	0.32	0.47	0.60	0.26	0.82	0.94	0.93	0.97	11	10	8	9	10
TF-R3	0.81	0.84	0.52	0.79	0.87	0.66	0.77	0.70	0.8	0.74	0.69	14	9	9	12
TF-C1	0.71	0.88	0.40	0.59	0.69	0.41	0.86	0.89	0.96	0.94	0.94	0.76	10	8	10
TF-C2	0.77	0.72	0.62	0.74	0.84	0.69	0.85	0.76	0.82	0.75	0.67	0.84	0.72	11	11
TF-C3	0.74	0.82	0.55	0.63	0.67	0.38	0.91	0.93	0.95	0.94	0.92	0.78	0.92	0.82	16
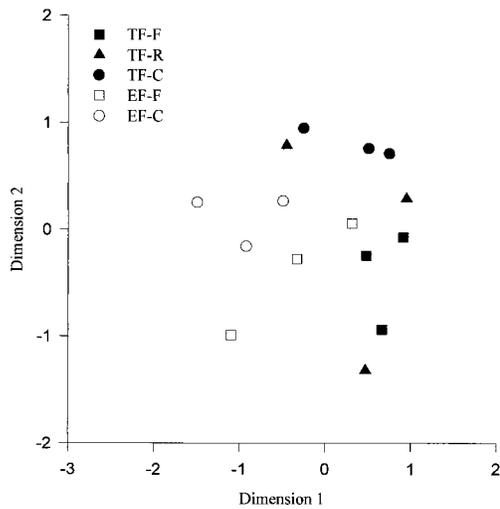
Figure 2.—Multi-dimensional Scaling Analysis on the Morisita-Horn community similarity index (stress = 0.222). TF = tabonuco, EF = elfin, F = fertilization, R = debris removal, C = control.
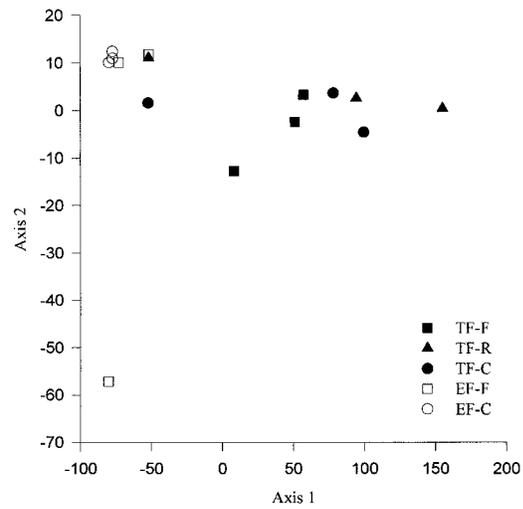

Figure 3.—The distribution of treatment plots in a two-dimensional morphospace, based on scores from the first two-family principal components axes. TF = tabonuco, EF = elfin, F = fertilization, R = debris removal, C = control.

cies in the leaf litter (Pfeiffer 1996). The higher number of species I found was the result of using pit-fall traps. The dominant species in tabonuco forest are consistent with the dominant species found by Pfeiffer (1996). The difference in dominant species I found between elevations has been found in other studies (Olson 1994), and is related to the same conditions that limit density (see previous section).

Community similarity.—Differences in community composition between elevations are related to differences in environmental conditions (Olson 1994). Dissimilarity between debris removal plots is indicative of random differences in the recolonization pattern at each of the plots, with an initial colonist species inhibiting the establishment of others (see Drake 1991; Law & Morton 1993). Differences in the initial colonists arriving to a spider depleted plot have been shown, in the short term, to be important in the process of community development (Ehmann & Mac-Mahon 1996). Principal Components Analysis showed that differences between plots was mainly explained by differences in the abundance of Pholcidae. Lower Pholcidae abundance in a tabonuco forest removal plot and a control plot (Fig. 3) grouped them with plots from elfin forest. The difference of Pholcidae abundance in these two plots is likely to be due to the heterogeneity between plots.

Higher numbers of individuals of some families at elfin forest compared to tabonuco forest (Table 2) are indicative of differences in community structure between both elevations. Dissimilarity between elevations is consistent with the steady changes in community composition, or species turnover, found in an elevational gradient in Panamian forests (Olson 1994). Analysis of species composition at the intermediate forests of El Yunque (palm and colorado forests) is necessary in order to determine if species turnover is constant.

Morisita-Horn analysis was also applied to determine similarity between mean annual density (MAD) data from Pfeiffer (1996) and my pooled treatments mean density per sample (PMD) data for tabonuco forest. The calculated index was 0.92. In order to determine how his data compare to mine in terms of density of individuals from each family, I ran a simple regression analysis. This analysis showed a high correlation of his data with mine ($r = 0.90$, $P < 0.0005$). However, Pfeiffer (1996) found a higher density of spiders than I did (MAD = $5.94 + 1.90 * $ PMD). The higher density of spiders found by Pfeiffer (1996) can be attributed to selection of sample sites away from rock surfaces and his use of a vacuum aspirator to obtain his samples. Our treatment plots were located along ridge tops.

This feature can minimize the already thin litter cover on the steeper areas, while concentrating litter on the relatively flat areas, consequently minimizing litter obtained for analysis.

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