Chapter 1

Physicochemical Foliar Traits Predict Assemblages of Litter/Humus Detritivore Arthropods

Maria Fernanda Barberena-Arias and Elvira Cuevas

Additional information is available at the end of the chapter

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Abstract

Plant functional traits influence the decomposition of their own residues occurring underneath individual plant species. Arthropods associated to litter are critical components influencing decomposition. Nevertheless, few studies have established a direct relation between plant traits and belowground arthropods. To address this relation at the individual plant species scale, this study was conducted in the Guánica dry forest, Puerto Rico, by selecting five tree species and ten isolated trees/species where variations due to neighbor trees are reduced. Mature green leaves, litter, and associated arthropods were sampled from November 2004 through September 2005. Collected arthropods were counted and classified, and abundances were standardized to ind/m^2. Arthropod abundance did not differ among plant species, but richness, and species and trophic composition were different among the plant species. Predators, omnivores, and sucking herbivores showed a similar species composition among plant species, while detritivore was the only trophic groups with a different species composition among plants. These results are further supported by canonical correspondence analysis results showing that detritivore arthropod species composition covaries with the physicochemical characteristics of mature green leaves of plants. These findings support that the plant idiosyncratic characteristics affect the structure of litter/humus arthropods up to the first consumer level.

Keywords: CCA, detritivore, Guánica dry forest, NMS, plant functional traits, litter arthropods

1. Introduction

Idiosyncratic effects of plants (groups of characteristics of individual species or groups of species) are postulated to have a large impact on ecosystem processes occurring underneath

the individual plant species [1, 2]. Plants affect belowground dynamics through net primary productivity and quality of resources [3]; for example, litter decomposition rates were predicted by green leaf chemistry and toughness [4], nitrogen (N) and phosphorus (P) availability in the soil was affected by plant species [5], and soil N transformation rates were higher under *Acomastylis rossii* than under *Deschampsia cespitosa*. These data suggest that the distribution of tree species, within and among stands, results in a patchy distribution of litter and therefore in variations in decomposition, nutrients, and associated decomposer organisms [3, 6].

Arthropods associated to litter are critical components that influence decomposition dynamics [7–9]. This fauna responds to variations in litter quality and quantity as a result of changes in plant species identity. For example, mesostigmatid and prostigmatid mites and other microarthropods were more abundant in aspen leaves than in pine needles [10]. Also, the abundance of bacteria, fungi, and invertebrates was higher in quaking aspen stands than in red pine or white spruce stands [11]. Wardle and Lavelle [6] found that Amazonian endogeic earthworms were abundant under *Qualea* trees and completely absent under *Dicorynia guianensis* trees. In Puerto Rico, González and Zou [12] found that the density of anecic earthworms was higher in areas that were afar from *Heliconia caribaea* trees and similarly abundant in areas close and afar from *Dacryodes excelsa* trees. Furthermore, the chemistry of litter has been shown to differentially affect decomposer organisms; for example, high polyphenol inhibited microbial growth [13], and high tannin concentrations in *Quercus ilex* were toxic for two collembolan species [14].

Although plant species have been shown to influence belowground dynamics, and litter has been shown to influence associated fauna, few studies have established a direct relation between green leaf chemistry and the belowground arthropods in order to address how plant idiosyncratic effects differently influence the litter arthropod fauna diversity. There is a lack of information on how components of arthropod diversity (i.e., abundance, richness, species, as well as trophic composition) differently respond to these idiosyncratic effects. There is also a scarcity of studies at the individual plant species scale where neighbor tree effects are reduced. To accurately describe how plant species influence belowground arthropod diversity, isolated trees provide an excellent opportunity because the effects introduced by neighbor trees are reduced. The Guánica forest is a relict of dry forest located on the southwest extreme of the island of Puerto Rico. In this forest, the vegetation growing in the coastal plateau is an open forest with dwarf trees, and vegetation is interspersed between rocks preventing the overlap of trees, therefore creating monospecific islands. These characteristics make this an ideal system to study singletree effects in complete isolation, i.e., arthropods associated to organic matter under single trees belonging to five tree species. We hypothesize that arthropod abundance, richness, as well as species composition will be different among tree species, but trophic composition will be similar because plant species vary in their chemical and morphological characteristics of the litter they produce. Therefore, we expect that plant species will have sets of different associated litter arthropods, although the trophic groups that these arthropods represent will be similar.

2. Materials and methods

2.1. Study site

The study was conducted in the Guánica dry forest (17°57′56″N, 66°52′45″W), southwestern Puerto Rico. This forest was declared a UNESCO Biosphere Reserve in 1981 because of its extension, high plant diversity, and high occurrence of endemism and habitat for endangered organisms [15]. This forest occurs on limestone [16] where the calcareous rock has low water retention ability and pH ~ 7; the excess calcium in combination with water limitation immobilizes the available phosphorus [17, 18]. The mean annual rainfall is 869 mm (range 288–1348 mm) with a major dry period that runs from December to April [16], but the monthly distribution of the rain is highly erratic [18]. For the study period, the total accumulated rainfall was 1575 mm that was distributed as 480 mm for the wet 2004 season, 120 mm for the dry 2005 season, and 975 mm for the wet 2005 season [19, 20]. The specific study site was located in the coastal vegetation association that is an open forest with dwarf trees, and the ground is exposed to rocks.

2.2. Data collection

In the coastal plateau, five representative tree species were selected. The species were *Coccoloba uvifera* and *Conocarpus erectus* only present in the coastal plateau and *Ficus citrifolia*, *Pisonia albida*, and *Tabebuia heterophylla* species present from the coast to the upper ridges in the forest. Ten trees belonging to each of the five species were selected for a total of 50 trees, which represent the sampling units.

2.3. Tree species characterization

Each tree was characterized for leaf toughness and C, N, and P contents. Leaf toughness was measured in 20 adult leaves/tree by using a punchameter Chatillon® 516 Push/Pull Gauge. Toughness is the force necessary to punch a 3 mm hole through the leaf [21, 22]. Each leaf was pierced once and in areas avoiding leaf nerves and away from the leaf border. These data give an index of toughness and the units are in newton (N). C, N, and P were measured in green leaves. For each tree/species, we collected fully expanded adult leaves that were oven dried at 65°C for 1 week. Leaves from the same tree were pooled, ground, and sieved to 1 mm (18 mesh). Total C analyses were done at the laboratory of the International Institute for Tropical Forestry (IITF), in San Juan, Puerto Rico. Total N and P content assessments were done at the Plant Ecophysiology Laboratory of the Instituto Venezolano de Investigaciones Científicas (IVIC), in Caracas, Venezuela. For C, digestion was done by using a modified version of the Huang and Schulte methodology [23], concentration of total C was determined by the dry combustion method using a CNS analyzer Leco® CNS-2000, and then total C was determined by individual IR (infrared) detectors. For N, samples were digested with sulfuric acid and selenium as catalyst at 350°C for 2 h, and then N was determined with the micro-Kjeldahl

method [24]. For P, digestion was done with perchloric-sulfuric acid solution and determined by colorimetry using a modified Murphy and Riley methodology [25].

2.4. Arthropod species

Arthropod collections were performed on November 2004 and February, April, June, and September 2005. During each sampling, one 10 cm × 10 cm sample/tree/species was collected, and the sample was separated into three fractions: loose litter (upper whole leaves), old litter, and humus. Each fraction was kept separately and placed in a berlese funnel for 1 week for arthropod extraction using light [26]. This sampling design gave 5 species × 10 trees × 3 fractions × 5 samplings = 750 samples. Collected arthropods were taxonomically identified to the lowest category possible, either class, subclass, order, or suborder, classified as adult or immature, and assigned to a morphospecies and to a trophic category. The abundance of each morphospecies was recorded and standardized to a number of individuals per square meter. Morphospecies were used as surrogate for species and thus used for richness and species composition. Richness is reported as a number of morphotypes per 100 cm^2. Trophic categories were assigned based on the feeding habit of the collected individual (immature/adult), and although some groups include organisms with a variety of feeding habits, we assigned trophic categories based on the predominant feeding habit of the group, e.g., detritivore, fungivore, omnivore, predator, and sucking herbivore. Detritivores feed directly on the organic matter including microbes (e.g., Blattodea, Diplopoda, Oribatida) [27]; fungivores feed on fungi growing on the litter (i.e., Collembola); omnivores use a variety of resources in the forest either to feed or for nest construction (e.g., Hymenoptera, Isoptera); predators feed on a variety of preys (e.g., Araneae, Chilopoda), and sucking herbivores feed on plant sap by making a hole where they insert their stylet (e.g., Thysanoptera and Homoptera). Not all collected arthropods fall within these categories; as a consequence they were excluded from the analysis. When immatures from these categories live and feed on litter, they were grouped in the corresponding category. For example, dipteran larvae mainly feed on decomposing litter, and thus collected larvae were grouped in the detritivore category, but as adults these dipterans may be hematophagous or licking, and then collected adults were grouped in the corresponding category. It should be clarified that collembolans were not assigned to morphotypes since variation in the morphology can only be seen in mounted slides and by a specialist. A total of 11 trophic categories were created [28], but only detritivores, sucking herbivores, predators, fungivores, and omnivores are directly related to the dynamics of the litter/humus cover and will be considered in detail.

2.5. Data analyses

Analyses of variance (ANOVAs) were performed to establish differences in specific leaf area (SLA), toughness, C, N, and P among plant species. ANOVAs were also used to evaluate the effect of plant species on the abundance and richness of arthropods. Although the distribution of data was not normal and transformations failed to normalize the data, analyses of variance were preferred over nonparametric tests. Analyses of variance were preferred because sample size was large ($n > 30$), and they allow to evaluate interactions among factors; if nonparametric statistics were used, then each factor had to be evaluated separately, and interactions would not be

considered. Abundance of arthropod morphotypes was used in a nonmetric multidimensional scaling (NMS) in combination with a multi-response permutation procedure (MRPP) to evaluate the effect of plant species on the species composition of adult arthropods. NMS is a nonparametric multivariate analysis that calculates a distance matrix using the Sorensen distance (Dist = 1–2 W/(A + B)); this distance is appropriate for the biological data because it does not take into account shared absences [29]. Based on the distance matrix, NMS generates a three-axis graph that locates sampling units in the graph area by discriminating them based on similarity so that sampling units that are close in the graph have similar species composition. It is important to clarify that given that NMS uses three axes to locate sampling units in the graph area, but only the two most explanatory axes are shown in the graph, then some statistical different sampling units may appear close in the two axes graph, but may actually be away over the third not represented axis. NMS used 50 sampling units (trees) × 143 arthropod species where matrix contents are arthropod abundance. MRPP is a nonparametric test that establishes differences among a priori factors using a distance matrix as the data set. With these data, MRPP calculates the average observed distance within predefined groups, compares this average distance to an average distance expected by chance, and tests whether the difference between observed and expected averages is due to the chance [29]. MRPP uses within group distance and calculates a measure within group homogeneity, A, that ranges between −1 and +1. When A = 1, homogeneity is highest, and all items within the group are identical; in community ecology values for A are commonly below 0.1, even when the observed distance differs significantly from the expected, meaning that a group can be heterogeneous and still be different from other groups. Heterogeneous groups have low average similarity values and can be significantly different from other groups. MRPP used 50 trees × plant species category matrix. Detritivores were further analyzed by performing a canonical correspondence analysis (CCA) that evaluated the relationship between species and environment matrices, specifically to explain structure in the arthropod detritivore community by using explanatory plant species variables [30]. The species matrix was 50 trees × 52 detritivore arthropod species where matrix contents are arthropod abundance, and the environment matrix was 50 trees × 3 variables where matrix contents were C (mg/g), N (mg/g), and P (mg/g). SLA and toughness were excluded from CCA because both correlated with other environmental variables (e.g., N). In CCA, rows and columns were standardized by centering and normalizing, scaling for ordination scores optimized detritivore species, and sampling unit scores are linear combinations of variables. The null hypothesis was no relationship between matrices where rejection of the null hypothesis indicates that both matrices covary [31], Monte Carlo tests had 100 randomizations, reported correlation coefficients are intraset correlations, and the joint biplot allows a direct spatial interpretation of the relationship between variables and sampling units [29].

3. Results

3.1. Plant species characterization

Specific leaf area was significantly different among plant species and followed the pattern *Ficus* > *Pisonia* > *Tabebuia* > *Conocarpus* > *Coccoloba* (**Table 1**). Leaf toughness was significantly different among plant species (**Table 1**) with tougher leaves in *Coccoloba* (383.7 ± 65.9 N) and

	Coccoloba	*Conocarpus*	*Ficus*	*Pisonia*	*Tabebuia*
Green leaves					
Specific leaf area (cm^2/g)	65 (±4)e	79 (±13)d	110 (±16)a	103 (±13)b	84 (±12)c
Toughness (N)	384 (±41)a	212 (±34)c	170 (±30)d	110 (±11)e	343 (±42)b
Carbon (mg/g)	502.5 (±5.7)a	481.9 (±32)b	473.0 (±10.1)b	507.1 (±9.6)a	498.8 (±4.8)a
Nitrogen (mg/g)	16.2 (±2.0)b	12.9 (±1.5)c	17.0 (±2.0)b	20.4 (±2.1)a	17.8 (±1.8)b
Phosphorus (mg/g)	0.9 (±0.3)a	1.1 (±0.6)a	1.0 (±0.1)a	1.0 (±0.2)a	0.6 (±0.1)b
C:N	31 (±4)b	38 (±3)a	28 (±4)c	25 (±3)d	28 (±3)c
C:P	589 (±200)b	550 (±262)b	493 (±36)b	541 (±164)b	796 (±149)a
N:P	19 (±8)bc	15 (±7)c	18 (±2)bc	22 (±8)b	28 (±5)a

Lowercase letters indicate significant differences among plant species for a specific trait.

Table 1. Physicochemical foliar traits of the five tree species in this study: values represent average (±sd) (n = 10 trees/species).

Tabebuia (343.1 ± 75.4 N) and tender leaves in *Pisonia* (110.3 ± 33.4 N) than in the other species. Leaf toughness followed the pattern *Coccoloba* > *Tabebuia* > *Conocarpus* > *Ficus* > *Pisonia* suggesting that there is a continuum; at one end *Coccoloba* had tough leaves, and at the other end, *Ficus* and *Pisonia* had tender leaves, while *Conocarpus* and *Tabebuia* had intermediate toughness leaves. Nutrients varied among plant species, and the degree of difference among species varied according to the specific nutrient. *Coccoloba*, *Tabebuia*, and *Pisonia* had significantly higher C than *Conocarpus* and *Ficus* (**Table 1**). Nitrogen was highest in *Pisonia* and followed the pattern *Pisonia* > *Tabebuia* – *Ficus* > *Coccoloba* > *Conocarpus*, and the C:N ratio inversely mirrored N concentration and followed the pattern *Conocarpus* > *Coccoloba* > *Tabebuia* – *Ficus* > *Pisonia* (**Table 1**). In addition, *Tabebuia* had lower P than *Coccoloba*, *Conocarpus*, *Pisonia*, and *Ficus*, and the C:P was highest in *Tabebuia*.

3.2. Arthropod abundance and richness

Plant species significantly affected arthropod richness (ANOVA, $F = 3.39$, $p < 0.001$) but not arthropod abundance (ANOVA, $F = 1.65$, $p = 0.16$). Average richness of microarthropods (the number of adult morphotypes) was significantly higher in *Ficus* and *Pisonia* than in *Tabebuia*, *Conocarpus*, and *Coccoloba* (**Figure 1A**). A total of 22 orders were collected, and 16 were common to all plant species; *Coccoloba* had no unique order, while Trichoptera was unique to *Conocarpus* and Chilopoda to *Ficus*, and Symphyla and Protura were shared by *Pisonia* and *Tabebuia* but absent in the other plant species (**Table 2**). Although total abundance was not significantly different among species, four orders showed significantly different abundances among plant species (**Table 2**). Acari was the most abundant order, and it was higher in *Coccoloba*, *Ficus*, and *Tabebuia* than in *Pisonia* and *Conocarpus*. Psocoptera abundance was higher in *Conocarpus* and *Ficus* than in *Pisonia*, *Coccoloba*, and *Tabebuia*. Diplopoda abundance was highest in *Pisonia*, and Pseudoscorpiones was more abundant in *Ficus* and *Coccoloba* than in *Pisonia*, *Tabebuia*, and *Conocarpus*.

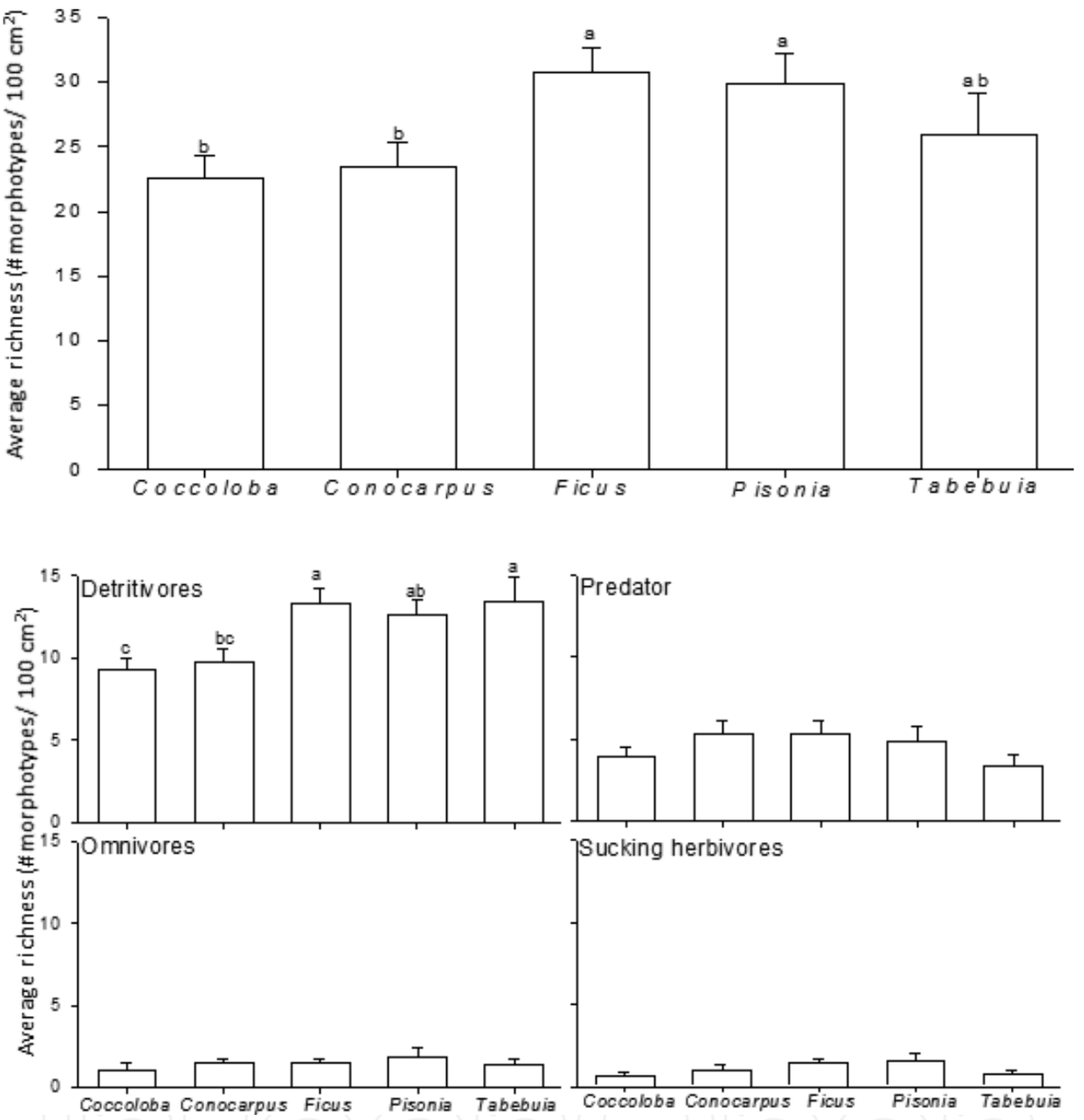

Figure 1. Average number of adult morphotypes (±s.e.) collected under the five tree species (A, upper). Average number of morphotypes (±s.e.) per trophic category collected under the five tree species (B, lower). Lowercase letters indicate significant differences among plant species.

3.3. Arthropod species composition

The species composition of all arthropods (based on adult morphotypes) was significantly different among plant species (MRPP, T = −10.878, A = 0.006, p = 0.000). Using arthropod species composition, NMS and MRPP grouped sampling units (i.e., 50 trees representing 10 trees/species × 5 study species) into three clusters: the first cluster grouped *Ficus*, *Pisonia*, and *Tabebuia*, the second one had *Conocarpus*, and the third one had *Coccoloba* (**Figure 2A**). *Coccoloba*

	Coccoloba	*Conocarpus*	*Ficus*	*Pisonia*	*Tabebuia*
Acari	837 (±1300)a	431 (±743)b	869 (±1505)a	595 (±1240)ab	959 (±2623)a
Homoptera	95 (±634)	38 (±264)	55 (±234)	103 (±658)	108 (±670)
Collembola	43 (±194)	56 (±198)	103 (±513)	115 (±524)	63 (±311)
Araneae	28 (±77)	38 (±96)	59 (±150)	53 (±204)	32 (±106)
Diptera	31 (±63)	31 (±68)	49 (±97)	56 (±146)	37 (±73)
Hymenoptera	56 (±298)	17 (±69)	31 (±98)	47 (±196)	32 (±128)
Psocoptera	11 (±46)b	42 (±132)a	45 (±111)a	33 (±87)ab	14 (±49)b
Coleoptera	41 (±218)	25 (±83)	33 (±106)	21 (±53)	15 (±56)
Pseudoscorpiones	37 (±99)a	13 (±39)c	33 (±68)a	29 (±82)ab	16 (±49)bc
Isopoda	10 (±55)	33 (±238)	21 (±80)	25 (±84)	8 (±50)
Thysanoptera	4 (±20)	12 (±49)	22 (±63)	27 (±155)	3 (±16)
Thysanura	9 (±68)	17 (±66)	15 (±64)	5 (±50)	5 (±31)
Diplopoda	1 (±12)b	2 (±14)b	1 (±12)b	15 (±71)a	3 (±16)b
Hemiptera	3 (±20)	7 (±35)	5 (±21)	3 (±16)	4 (±23)
Blattodea	1 (±12)	3 (±16)	5 (±21)	1 (±8)	1 (±12)
Opiliones	1 (±12)	2 (±18)	1 (±16)	1 (±8)	1 (±12)
Diplura	3 (±33)		1 (±8)	1 (±8)	1 (±8)
Lepidoptera	1 (±8)	2 (±18)		1 (±8)	1 (±12)
Symphyla				4 (±35)	7 (±74)
Protura				1 (±8)	1 (±12)
Trichoptera		1 (±8)			
Chilopoda			2 (±14)		
Total	67 (±194)	43 (±98)	75 (±200)	57 (±131)	66 (±212)

Lowercase letters indicate significant differences among plant species for the specific class/order.

Table 2. Mean abundance (±sd) (ind/m^2) of collected arthropods classified into taxonomic categories (class or order), under the five tree species.

had 17 unique morphotypes, and *Conocarpus* had 20 unique morphotypes, while *Pisonia* and *Ficus* shared 39 morphotypes, *Ficus* and *Tabebuia* shared 33, and *Pisonia* and *Tabebuia* shared 28 morphotypes [28].

3.4. Arthropod trophic groups

Of all the trophic groups, only the species composition of detritivore arthropods (MRPP, T = −11.040, A = 0.014, p = 0.000) was significantly different among plant species (**Figure 2B**). For predators (MRPP, T = 0.593, A = −0.002, p = 0.705), omnivores (MRPP, T = 0.278, A = −0.005, p = 0.578), and sucking herbivores (MRPP, T = −0.296, A = 0.008, p = 0.345), the species composition based on morphotypes did not change significantly among plant species. For detritivores, average abundance (ANOVA, F = 3.36, p = 0.01) and richness (ANOVA, F = 3.27, p = 0.01) were significantly different among plant species, while average abundance

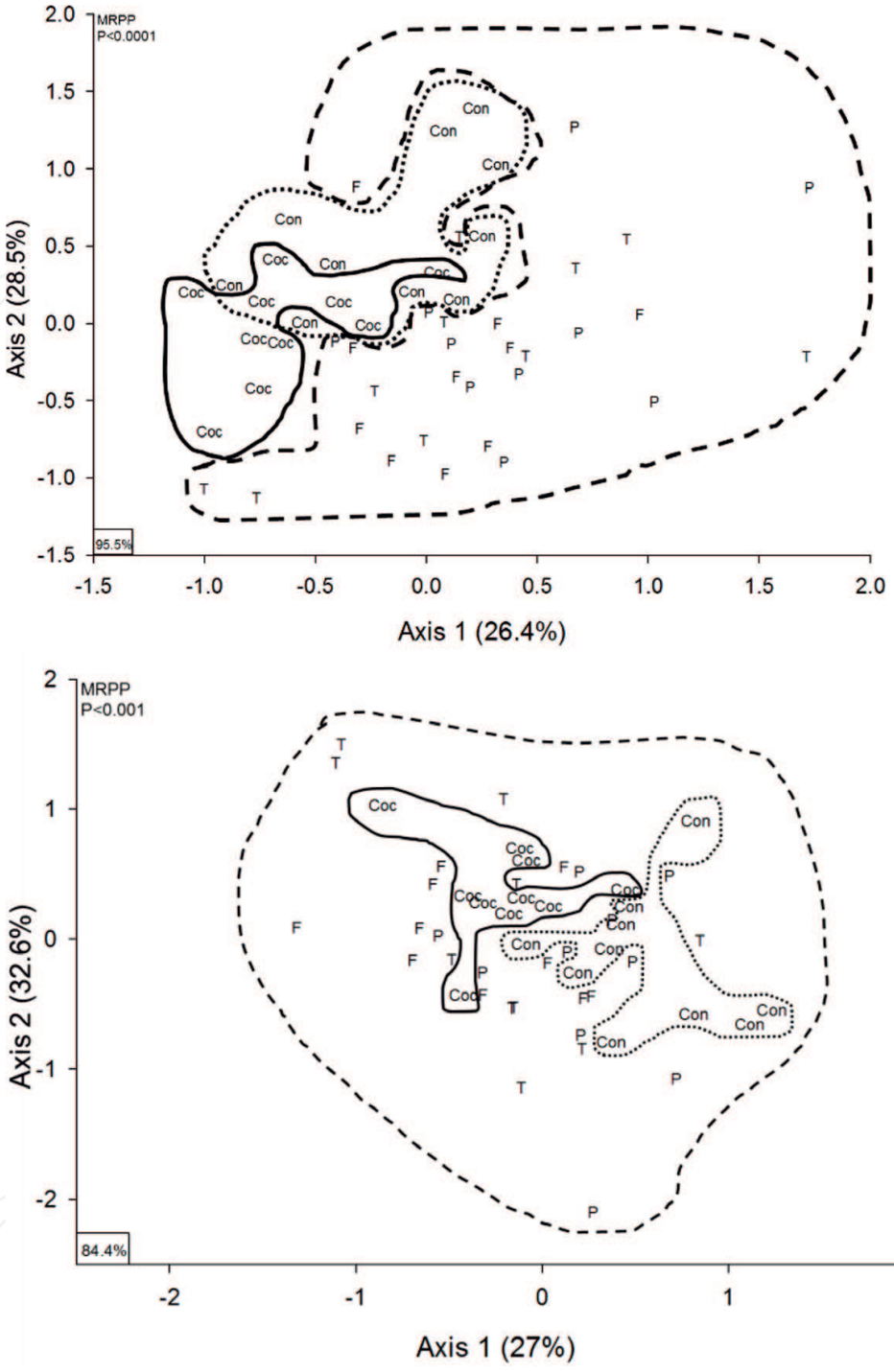

Figure 2. Nonmetric multidimensional scaling (NMDS) ordination of the 50 sampling units (5 tree species × 10 tress/species) based on arthropod species composition similarity (A, upper). NMDS ordination of the 50 sampling units based on detritivore species composition (B, lower). Coc represents *Coccoloba*, Con represents *Conocarpus*, Fic represents *Ficus*, Pis represents *Pisonia*, and Tab represents *Tabebuia*. Lines group significant different clusters: the solid line groups the *Coccoloba* cluster; the dotted line groups the *Conocarpus* cluster; and the long-dashed line groups the *Ficus* + *Pisonia* + *Tabebuia* cluster. Detritivore species composition was significantly different in *Coccoloba* when compared to *Conocarpus* (A = 0.0067, p = 0.0033), *Ficus* (A = 0.0110, p = 0.0000), *Pisonia* (A = 0.0104, p = 0.0000), and *Tabebuia* (A = 0.0121, p = 0.0000). Similarly, detritivore species composition in *Conocarpus* was significantly different when compared to *Ficus* (A = 0.0152, p = 0.0000), *Pisonia* (A = 0.0139, p = 0.0000), and *Tabebuia* (A = 0.0168, p = 0.0000). *Ficus* and *Pisonia* had similar detritivore species composition (A = −0.0004, p = 0.5606), as well as *Ficus* and *Tabebuia* (A = 0.0005, p = 0.3070) and *Pisonia* and *Tabebuia* (A = 0.0024, p = 0.0600). Since for each plant species the arthropod data set was used to perform four comparisons, only p-values smaller than 0.0125 were considered significantly different.

	Coccoloba	*Conocarpus*	*Ficus*	*Pisonia*	*Tabebuia*
Detritivore	583 (±976)ab	341 (±575)b	567 (±970	409 (±711)b	710 (±1727)a
Sucking herbivore	99 (±633)	53 (±269)	77 (±239)	132 (±783)	111 (±676)
Predator	76 (±148)	67 (±169)	108 (±177)	91 (±227)	53 (±118)
Fungivore	52 (±206)	75 (±221)	118 (±520)	120 (±526)	87 (±318)
Omnivore	51 (±297)	15 (±68)	22 (±82)	42 (±195)	25 (±125)
Vestigial mouth	5 (±23)b	4 (±20)b	11 (±38)a	5 (±23)b	3 (±16)b
Chewing herbivore	8 (±34)a	2 (±14)b	1 (±12)b	3 (±18)b	1 (±12)b
Hematophagous	4 (±23)	5 (±28)	5 (±23)	7 (±26)	2 (±14)
Plant exudates	4 (±23)	5 (±24)	4 (±20)	7 (±34)	8 (±30)
Licking	1 (±12)	1 (±8)	3 (±16)	1 (±12)	1 (±8)
Nectarivore	0 (±0)	0 (±0)	1 (±12)	1 (±8)	0 (±0)

Lowercase letters indicate significant differences among plant species for the specific trophic category.

Table 3. Mean abundance (±s.d.) (ind/m^2) of arthropods grouped into trophic categories under the five tree species.

and richness of the remaining trophic groups did not vary significantly among plant species (**Table 3**) (**Figure 1B**). Detritivore abundance followed the pattern *Tabebuia* > *Coccoloba* and *Ficus* > *Pisonia* and *Conocarpus* (**Table 3**), while richness followed the pattern *Ficus* and *Tabebuia* > *Pisonia* > *Conocarpus* > *Coccoloba* (**Figure 1B**). The species composition of detritivore arthropods produced the same three clusters that were formed in the species composition of all arthropods. The first cluster was formed by *Ficus*, *Pisonia*, and *Tabebuia*, the second one was formed by *Conocarpus*, and the third one by *Coccoloba*.

3.5. Plant species and detritivores

Given that only detritivore species composition was different among plant species, we used a CCA to determine which plant species characteristics influenced the detritivore community. CCA results indicate that the null hypothesis of no relation was rejected; therefore, there was a significant relation between the species and the environmental variables (see data analysis for further description). The eigenvalue for axis 1 is higher than expected by chance (p = 0.01, 998

Axis	Eigenvalue	Species-environment correlation	p-value	Cumulative percentage (%) of variance	Environmental variables	Correlation with axis 1
1	0.138	0.836	0.006	5.4	N	−0.446
2	0.109	0.763		9.6	P	0.803
3	0.058	0.632		11.8	C	−0.317

p-Values for axes 2 and 3 are not reported since the randomization test for these axes may bias the p-value [43].

Table 4. CCA results showing eigenvalues and species-environment correlations based on 999 Monte Carlo test runs with randomized data. Also, correlations (as intraset correlations) of environmental variables with axis 1 are reported.

randomizations), and this axis is correlated with environmental variables (p = 0.006) (**Table 4**). Axes 1 and 2 explained a total cumulative 9.6% of the variance, and both axes had 98.7% orthogonality. This significant relation indicates that both matrices covary suggesting that the detritivore community is structured by plant CNP (**Figure 3A**). Detritivore morphotypes that were common to all plant species (**Appendix 1**, **Figure 3B**) are located near the center of the

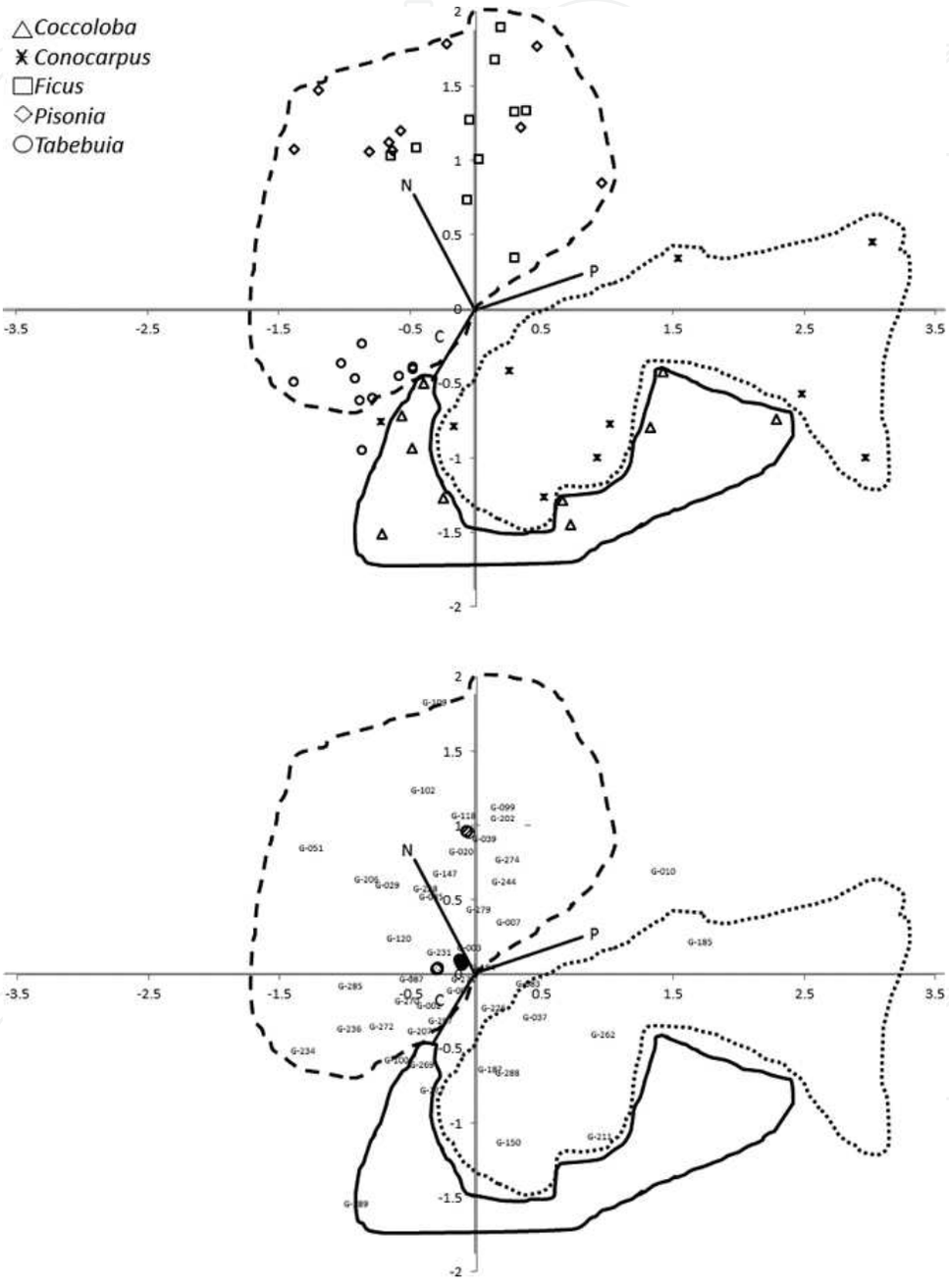

Figure 3. Ordination of the 50 sampling units using detritivore abundance as defined by canonical correspondence analysis; symbols represent tree species and lines represent significant clusters (A, upper), please see legend explanation in **Figure 1**. Ordination of the 50 sampling units using detritivore abundance as defined by CCA; symbols represent detritivore morphotypes overlaid over the CCA ordination (B, lower). (Symbols indicate morphotypes whose location overlaps: striped circle for G-119 and G-301, dotted circle for G-105 and G-188, and black circle for G-078 and G-280). The biplot overlay shows leaf N, P, and C vectors.

graph (near the intercept of X and Y) such as G-002, G-003, G-004, G-007, and G-274, while those that occurred only in high N species (e.g., *Ficus* and *Pisonia*) are located in the upper half of the graph such as G-109, G-102, G-118, G-301, and G-119. Those detritivores that occurred only under low P species (e.g., *Tabebuia*) include G-234, G-236, and G-272.

4. Discussion

We found that *Pisonia* had the highest N and *Tabebuia* had lowest P. Also, *Ficus* had higher arthropod abundance, while *Pisonia* and *Ficus* had higher arthropod richness than the other plant species. Species composition of detritivore arthropods was different among plant species, and three clusters were formed: arthropod species composition under *Ficus*, *Pisonia*, and *Tabebuia*, species composition under *Coccoloba*, and species composition under *Conocarpus*. We also found that morphotypes that grouped *Ficus*, *Pisonia*, and *Tabebuia* were located toward the high N side of the vector, while those unique to *Coccoloba* and *Conocarpus* were at the low N side of the vector. These data suggest that physicochemical foliar traits of plants directly influence litter arthropods on the lower trophic levels of the decomposer food web.

4.1. Nutrients

When compared to species growing in other dry forests, the five tree species in this study are within the range for N and for P at the lower end [32] corroborating the data of Lugo and Murphy [17]. We found that green leaf nutrients varied among species. In Guánica, for a mature stand and pooled leaves from a sample, Lugo and Murphy [17] reported 16.4 mg/g N and 0.64 mg/g P. For N, our pooled average, 16.9 (±2.7) mg/g, was similar to Lugo and Murphy, while our average for P was higher, 0.92 (±0.2) mg/g, than in Lugo and Murphy. At the species level, N was higher in *Pisonia* and lower in *Conocarpus*, while the other three species were similar to the reported value. We found P to be similarly higher in all species when compared to *Tabebuia*. In addition, Lugo and Murphy reported that N:P ratio (on a dry weight basis) was 25, while in this study, we found the pooled average of N:P to be 20.4 suggesting that the plants near the coastal cliff grow with similar soil P limitation than plants uphill. For *Pisonia*, Medina and Cuevas [18] report nutrient concentration values that are similar to those found in this study, 18.9 mg/g N and 0.95 mg/g P. For *Tabebuia* growing in the Luquillo Experimental Forest (wet forest), Sánchez et al. [33] reported N 12–16 mg/g and P 0.8–1.3 mg/g. The similarity of N and P concentration in *Tabebuia* between two contrasting sites, such as dry and wet forests, shows the plasticity of the species to adapt to different climatic regimes. The P limitation in Guánica (dry forest) is due to the high P fixing capacity of the substrate, while the P limitation in Luquillo (wet forest) is due to highly weathered soils with low P availability due to iron (Fe) fixation.

4.2. Arthropods

Total arthropod abundance was similar among plant species, but four arthropod orders were more abundant under specific plant species. Milcu et al. [34] found that decomposer species

performed better under some plant species than under others because of resource quality and because of the presence of other decomposer species. These data suggest that the higher abundance of these four orders might be related to interactions with other soil fauna species and to resource quality. We also found that richness and identity of arthropods were different among plant species (38 morphotypes common to all plant species, 17 unique to *Coccoloba*, 20 to *Conocarpus*, 39 common to *Ficus* and *Pisonia*, and 33 to *Ficus* and *Tabebuia*) [28]. These data suggest that plant species identity differently influence the number and identity of arthropod species associated to the decomposing organic matter produced by each plant. De Deyn et al. [35] found that the identity of the plant species (i.e., resource quality) was the most important factor for soil nematode diversity; these findings support the idea that, similarly to nematodes, arthropod diversity is influenced by the plant species identity.

These data suggest that arthropods that depend directly on resource quality, and thus have a tight relationship with the resource, were significantly affected by the identity of plant species. In addition, it also suggests that arthropods in higher trophic levels, such as predators, are more generalist; that plant species identity effect does not cascade up; and that the exposed rocky terrain that separates the individual trees does not constitute a barrier for them to move among tree species.

4.3. Idiosyncratic effects

Aboveground plant species composition was the best predictor of arthropod assemblages [36], and arthropod species with specific requirements were associated to specific habitats [37]. Similarly, one can expect belowground arthropod assemblages to be best predicted by plant species and litter arthropod species to have specific nutrimental requirements. In our study, unique arthropod species in *Ficus* and *Pisonia* were located toward the high N vector, while unique arthropod species in *Coccoloba* and *Conocarpus* toward the low N vector. These data suggest that unique arthropod species respond to high nutritional content in high-quality plant species, while unique arthropod species respond to low nutritional content in low-quality plant species.

Litter decomposes faster in areas dominated by the plant species that produced it, the home-field advantage effect [38]. Home-field advantage has been related to the specialization of biota on litter produced by their plant through specialized enzymes, feeding on specialized fungi or animals using litter fragments in survival activities [39], and is also most pronounced in low-quality litter [40]. In decomposer food webs, lower trophic levels influence plant productivity more than higher trophic levels, and given that there is high redundancy within trophic groups, plant productivity is independent of what species are present as long as all of the trophic groups are present [41]. In addition, identity of plants affected the response of arthropods. For example, collembolans were positively affected by grasses and negatively by legumes, while earthworms were positively affected by legumes, suggesting that arthropod response varies depending on the group and nutrients [34]. Our data can be thus interpreted as arthropod species composition of lower trophic groups responds to variations in plant species characteristics, and the response depends upon the nutritional characteristics of the plant, in this case high or low N, which are correlated with the nutritional characteristics of the detritus the plant produces [4].

5. Conclusions

We expected that arthropod abundance, richness, and species as well as trophic composition would be differentially affected by the identity of the plant species. We found that the abundance of four arthropod orders was affected; also, total arthropod richness and species composition varied significantly specifically due to the response that detritivores had to physicochemical foliar traits (the only trophic group that differed among plant species). The CCA indicated that detritivore response is linked to aboveground nutritional content of plants. Wardle [3] suggests that the decomposing fauna is tightly associated to the detritus produced by plant species so that this association maximizes the decomposition and nutrient cycling. Therefore, differences in quality among plant species potentially influence litter-feeding arthropods. On the other hand, St. John et al. [42] found that mite assemblages were not affected by the identity of the grass species that mites inhabited neither in abundance, richness, or the composition. Our data support Wardle's ideas [3]. When pooled together our data suggest that litter arthropods in the lower trophic levels, such as detritivores (e.g., Acari, Psocoptera, and Diplopoda), perform better under specific plant species (therefore supporting Milcu et al.'s [34] findings) possibly because they are tied to resource quality (therefore supporting Wardle's ideas).

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Appendix 1

Average abundance (±s.d.) (ind/m^2) of detritivore arthropods identified to taxonomic categories under the five tree species.

Class	**Order**	**Morpho.**	***Coccoloba***		***Conocarpus***		***Ficus***		***Pisonia***		***Tabebuia***	
Arachnida	Acari	G-037	2880	(±1642)	1390	(±837)	850	(±645)	770	(±525)	920	(±981)
Arachnida	Acari	G-078	1380	(±577)	470	(±467)	1530	(±1405)	680	(±569)	2070	(±2720)
Arachnida	Acari	G-007	750	(±924)	150	(±212)	470	(±353)	540	(±734)	230	(±206)
Arachnida	Acari	G-003	610	(±491)	190	(±228)	830	(±1136)	290	(±318)	490	(±409)
Arachnida	Acari	G-207	530	(±1470)	170	(±254)	560	(±1465)	100	(±200)	1170	(±2099)

Class	Order	Morpho.	*Coccoloba*		*Conocarpus*		*Ficus*		*Pisonia*		*Tabebuia*	
Arachnida	Acari	G-004	470	(±462)	320	(±385)	340	(±284)	490	(±431)	1330	(±3231)
Arachnida	Acari	G-002	460	(±723)	80	(±92)	340	(±299)	210	(±328)	1200	(±1624)
Arachnida	Acari	G-105	200	(±249)	90	(±120)	340	(±259)	280	(±220)	710	(±1186)
Arachnida	Acari	G-271	150	(±440)	120	(±114)	310	(±493)	40	(±126)	210	(±321)
Arachnida	Acari	G-274	50	(±108)	10	(±32)	250	(±756)	10	(±32)	30	(±48)
Arachnida	Acari	G-188	40	(±84)	40	(±84)	90	(±160)	130	(±279)	180	(±193)
Arachnida	Acari	G-147	30	(±67)	60	(±70)	380	(±278)	270	(±374)	160	(±143)
Arachnida	Acari	G-087	20	(±42)	90	(±185)	30	(±67)	130	(±189)	20	(±42)
Arachnida	Acari	G-244	20	(±42)	150	(±372)	210	(±354)	320	(±452)	140	(±158)
Malacostraca	Isopoda	G-010	10	(±32)	290	(±882)	30	(±48)	170	(±177)	20	(±63)
Arachnida	Acari	G-120	10	(±32)	30	(±67)	90	(±145)	110	(±185)	150	(±409)
Arachnida	Acari	G-231	10	(±32)	50	(±108)	60	(±84)	100	(±94)	60	(±84)
Arachnida	Acari	G-262	140	(±443)	30	(±95)	10	(±32)	—	—	110	(±348)
Arachnida	Acari	G-226	20	(±42)	110	(±99)	60	(±170)	—	—	130	(±211)
Arachnida	Acari	G-187	10	(±32)	50	(±127)	20	(±42)	—	—	60	(±84)
Malacostraca	Isopoda	G-184	20	(±42)	10	(±32)	—	—	30	(±67)	—	—
Arachnida	Acari	G-288	20	(±63)	20	(±63)	—	—	—	—	10	(±32)
Arachnida	Acari	G-279	10	(±32)	—	—	20	(±42)	20	(±63)	30	(±67)
Arachnida	Acari	G-280	20	(±63)	—	—	30	(±95)	10	(±32)	40	(±126)
Arachnida	Acari	G-202	10	(±32)	—	—	10	(±32)	60	(±107)	10	(±32)
Arachnida	Acari	G-185	20	(±63)	—	—	10	(±32)	—	—	—	—
Hexapoda	Blattodea	G-020	10	(±32)	—	—	10	(±32)	—	—	—	—
Arachnida	Acari	G-269	10	(±32)	—	—	—	—	—	—	40	(±97)
Hexapoda	Psocoptera	G-211	10	(±32)	—	—	—	—	—	—	—	—
Arachnida	Acari	G-277	10	(±32)	—	—	—	—	—	—	—	—
Arachnida	Acari	G-287	10	(±32)	—	—	—	—	—	—	—	—
Hexapoda	Psocoptera	G-029	—	—	10	(±32)	50	(±127)	70	(±134)	40	(±84)
Malacostraca	Isopoda	G-039	—	—	10	(±32)	50	(±158)	90	(±166)	—	—
Arachnida	Acari	G-100	—	—	10	(±32)	—	—	10	(±32)	30	(±48)
Arachnida	Acari	G-083	—	—	20	(±63)	—	—	—	—	30	(±95)
Arachnida	Acari	G-150	—	—	20	(±63)	—	—	—	—	10	(±32)
Hexapoda	Psocoptera	G-289	—	—	10	(±32)	—	—	—	—	—	—
Hexapoda	Psocoptera	G-102	—	—	—	—	90	(±129)	60	(±84)	10	(±32)
Hexapoda	Psocoptera	G-118	—	—	—	—	130	(±287)	10	(±32)	—	—
Malacostraca	Isopoda	G-085	—	—	—	—	40	(±97)	—	—	20	(±63)
Hexapoda	Blattodea	G-119	—	—	—	—	10	(±32)	—	—	—	—

Class	Order	Morpho.	*Coccoloba*		*Conocarpus*		*Ficus*		*Pisonia*		*Tabebuia*	
Hexapoda	Blattodea	G-228	—	—	—	—	20	(±42)	—	—	10	(±32)
Arachnida	Acari	G-270	—	—	—	—	10	(±32)	—	—	40	(±84)
Arachnida	Acari	G-301	—	—	—	—	10	(±32)	—	—	—	—
Arachnida	Acari	G-285	—	—	—	—	—	—	10	(±32)	20	(±42)
Symphyla		G-051	—	—	—	—	—	—	60	(±158)	10	(±32)
Diplopoda		G-099	—	—	—	—	—	—	10	(±32)	—	—
Arachnida	Acari	G-109	—	—	—	—	—	—	10	(±32)	—	—
Arachnida	Acari	G-206	—	—	—	—	—	—	10	(±32)	—	—
Hexapoda	Psocoptera	G-234	—	—	—	—	—	—	—	—	10	(±32)
Hexapoda	Psocoptera	G-236	—	—	—	—	—	—	—	—	10	(±32)
Arachnida	Acari	G-272	—	—	—	—	—	—	—	—	10	(±32)

Author details

Maria Fernanda Barberena-Arias[1]* and Elvira Cuevas[2]

*Address all correspondence to: mbarberena1@suagm.edu

1 School of Natural Sciences and Technology, Universidad del Turabo, Gurabo, Puerto Rico

2 Department of Biology, University of Puerto Rico, San Juan, Puerto Rico

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