

We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

6,900

Open access books available

185,000

International authors and editors

200M

Downloads

Our authors are among the

154

Countries delivered to

TOP 1%

most cited scientists

12.2%

Contributors from top 500 universities



WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com



Vertical Arthropod Dynamics across Organic Matter Fractions in Relation to Microclimate and Plant Phenology

María F. Barberena-Arias and Elvira Cuevas

Abstract

Plant diversity is a key factor influencing belowground dynamics including microclimate and decomposer arthropod communities. This study addresses the effect of individual plant species on belowground arthropods by focusing on seasonal variations in precipitation, temperature and arthropods along the vertical organic matter profile. In the Guanica Dry Forest, Puerto Rico, microclimate was described and 5 plant species and 10 trees/species were selected. Under each tree, for one year, temperature was measured and samples collected along the organic matter fractions. Collected arthropods were standardized to ind/m², identified to Order/Family and assigned to morphotypes. The annual temperature pattern was similar for all species and OM fractions. Arthropod abundance was similar among plant species and higher in humus than in litter fractions. Richness and species composition were different among plant species and OM fractions. All plant species and OM fractions showed low arthropod abundance and richness, and similar arthropod species composition in the dry season, while in the wet season abundance and richness were higher and species composition varied across plant species and OM fractions. These data suggest that arthropods form specific assemblages under plant species and stages of decomposition that, during the dry season, represent a subgroup adapted to extreme environmental conditions.

Keywords: Berlese funnels, decomposition, extreme conditions, plant structure, seasonal dynamics

1. Introduction

Individual trees modify the below microclimate, resources and associated biodiversity [1]. Examples of trees modifying the below microclimate include trees serve as wind shelters [2], canopies intercept rainfall [3] and solar radiation [2, 4–6] resulting in calm drier and warmer below microclimate in comparison to nearby open areas. Through leaf fall, trees influence belowground microclimate and litter quantity and quality, for example dark litter warms more than light-colored litter [7], deciduous species show a pulse in litter production [8] and litter C: N and C:P ratios directly influence soil N and P [9] and N transformation rates [10]. In addition, physicochemical changes that happen during litter decomposition [11] are

paralleled in the vertical stratification of the organic matter (OM) [12]. As a consequence, trees produce spatial variation in microenvironments and a patchy distribution of litter that is vertically stratified into progressive decomposition stages [13].

The distribution of trees results in a patchy distribution of litter and associated organisms [14–16]. For example, microarthropods were more abundant in aspen than in pine [17] earthworms were abundant under *Qualea* and completely absent under *Dicorynia guianensis* [15] and *Heliconia caribaea* [18]. On the other hand, OM in early decomposition was dominated by cellulolytic bacteria, omnipotent fungi and collembolans while later on, by proteolytic bacteria, no-lygnolytic fungi, diplopoda and isopoda [19]. Cryptostigmata and collembolans dominated late decomposition [20], while others report Cryptostigmata diversity to be independent of the decomposition stage [21] but mites and collembolans species composition changed simultaneously with a decrease in collembolan abundance as decomposition proceeded [22]. In Guanica, enzymatic activity and microbe diversity were consistently different between *Tabebuia*, an evergreen facultative deciduous species, and *Ficus* and *Pisonia*, two deciduous species [23]. In this forest, arthropod species composition was different among tree species, and this difference was better explained by detritivores that covaried with the physicochemical characteristics of mature green leaves [24].

With the overwhelming impact of human activities on biodiversity [25, 26], an enormous amount of studies (e.g. [25, 27–30] are only few examples) have addressed the relationship between diversity and ecosystem processes at the stand and local scales, but few happen at the individual tree species scale [23, 24, 31]. Therefore, we evaluated how aboveground diversity, specifically individual tree species, modify microclimate and litter, and the relation to the dynamics and diversity of belowground arthropods in the vertical organic matter profile. For this, we selected isolated individual trees, such as those found in the Guanica dwarf forest, that provide the ideal setting to study tree species in complete isolation [24].

2. Methodology

2.1 Study site

The study was conducted in the Guánica dry forest, a Biosphere Reserve established in 80's (for the specific location, please see **Figure 1** in [31]) that has been disturbed by humans (urbanization, selective logging and charcoal pits) [32, 33] and hurricanes such as Hurricane Maria in 2017, but at the time of the study, the eyes of less severe hurricanes, such as Hortense (1995) and Georges (1998), had crossed the forest [34]. Average temperature is 25.1°C and precipitation is 860 mm (range 288–1348 mm) but the monthly distribution of the rain is highly erratic [35]. In average, there are 6 dry months (3–8 mo.) that occur as one major dry period from December to April and a minor one from June to August [36]. The forest presents several vegetation associations [37–39], the coastal vegetation is an open forest that occurs on limestone hills with rock depressions that accumulate highly fertile organic matter [33] where trees grow dwarf and isolated from neighbor trees by exposed rock [39]. Here five representative tree species were selected: *Coccoloba uvifera* (evergreen) and *Conocarpus erectus* (evergreen) both present near the cliff shore, and *Tabebuia heterophylla* (facultative deciduous), *Pisonia albida* (obligate deciduous) and *Ficus citrifolia* (deciduous) which are present from the coast to the upper ridges in the forest. Ten trees belonging to each species were selected for a total of 50 trees which represent the sampling units. Under each tree,

organic matter samples were collected and divided into fractions showing progressive stages of decomposition that were loose litter (recently fallen leaves), old litter (fragmented leaves) and humus. During the study (from September 2004 to November 2005), the structure of each tree was measured once while microclimate was measured and arthropods were collected under each tree for one year encompassing wet and dry periods, the wet period received unusual high precipitation. The data for each fraction was kept separately.

2.2 Mesoclimate

Mesoclimate was characterized by using data obtained from the NRCS [40] and RAWS sites [41]. The first site is a SCAN (Soil Climate Analysis Network) weather station that is located in an open area in the forest and up 165 m from the coastal plateau while the second site is a RAWS (Remote Automated Weather Stations) weather station located near the coast but the data for the study period is too fragmentary. Temperature and precipitation were taken from the SCAN site, except for October 2005, that is missing and was then was calculated by difference between the previous and next month. This datum was corroborated with the RAWS site. This information is presented in **Figure 1**.

2.3 Microclimate

Microclimate data was obtained from data loggers. For each of the study species, three (out of five) trees were selected to ensure trees were interspersed within the study area and therefore represented the local variation. Data loggers were placed under each tree as follows: one HOBO temperature/humidity data logger was placed at 25 cm above ground, and will be referred as understory temperature throughout the chapter, one TidBit temperature data logger was placed in the old litter fraction (~2.5 cm depth) and one TidBit temperature data logger was placed in the humus fraction (~4.5 cm depth). Data loggers collected temperature data every hour from September 2004 to November 2005. Although the HOBO data logger collected temperature and humidity, only temperature is presented because the humidity sensor shorted out as it was exposed to a salty environment and produced unreliable data.

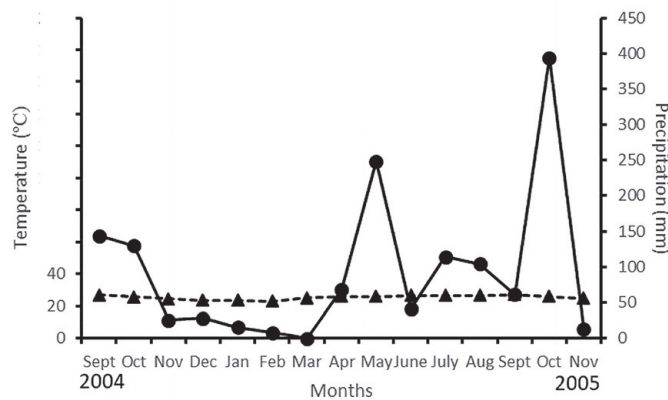


Figure 1. Diagram showing the relation between average monthly temperature (dashed line) and total monthly precipitation (solid line) in the Guánica forest during the study period. When the solid line is below the dashed one, this indicates water deficit (dry period), when the solid line is above the dashed one this indicates water availability (wet period), and when precipitation surpasses 100 mm, this indicates water surplus. Please note that months begin in September 2004.

2.4 Tree species characterization

Each tree was characterized by measuring tree height, canopy area, organic matter dry mass and depth. Tree height was measured as the distance between the ground and the highest canopy point in vertical orientation, and canopy length and width were measured in horizontal orientation. Canopy area was calculated from length and width. Organic matter dry mass and fraction depth were measured separately for each tree and fraction in November 2004, February, April, June, September and November 2005.

2.5 Arthropods

Arthropod collections were performed under each tree on November 2004, February, April, June, and September 2005. During each sampling, one 10 cm x 10 cm sample/tree/species was collected, and the sample was separated into three fractions: loose litter, old litter and humus. Each fraction was kept separately and placed in a Berlese funnel for one week for arthropod extraction using light [42]. This sampling design gave 5 species x 10 trees x 3 fractions x 5 samplings = 750 samples. Collected arthropods were taxonomically identified to the lowest category possible, either class, subclass, order or suborder, and classified as adult or immature, and assigned to a morphospecies. Collembolans were not assigned to morphotypes since variation in the morphology can only be seen in mounted slides and by a specialist. The abundance of each morphospecies was recorded and standardized to number of individuals per square meter. Morphospecies composition was used as a surrogate for species composition.

2.6 Statistical analyses

Anovas were used to evaluate differences in tree structure and organic matter among plant species. Also, a two-way Anova was used to establish the effect of plant species and fraction on the modulation of temperature. Modulation was estimated as the maximum, minimum and daily range in temperature. To assess the effect of tree structure on temperature modulation we used spearman rank correlations. To assess the effect of time (sampling dates), plant species and fraction on the abundance and richness of arthropods three-way AOV were used. The abundance of arthropod morphotypes was used in a Multi-Response Permutation Procedure (MRPP) to evaluate the effect of time, plant species and fraction on the species composition of adult arthropods. MRPP is a non-parametric test that calculates a distance matrix of average observed distance within predefined groups and compares it to an average distance expected by chance. Within group distance is used to calculate A, a homogeneity parameter of within group variability that ranges between zero and one. In community ecology, values close to zero are common and suggest a heterogenous community that can still be different from other communities [24, 43–45].

3. Results and discussion

3.1 Mesoclimate

During the study, temperature decreased from September to February, and then it increased again (**Figure 1**) and total precipitation was 1575 mm, and was distributed as follows: 480 mm from September to October 2004 producing wet

conditions at the end of 2004, 120 mm between November 2004 and April 2005 producing dry conditions at the beginning of 2005, and 975 mm between May and October 2005 producing wet conditions in the second half of 2005 that were interrupted by a short water deficit in June 2005 (**Figure 1**). In general, during the study, the pattern was similar to the one historically established for the Guanica forest [36, 46] with some variations. Historically, the dry season runs from January to July interrupted by a small pulse in precipitation in May, and then follows a wet season from August to December with water surplus during September. This study encompassed two wet periods and one dry period, there was water surplus in September and October 2004, followed by dry months up to April 2005 indicating 6 consecutive months of water deficit. Then, there were wet conditions after April 2005 with three pulses of water surplus in May, July and October 2005. This indicates that during the study, precipitation was atypical because dry conditions lasted 6 consecutive months while Lugo et al. [36] found that, for this forest, dry conditions usually last 3–4 consecutive months. In addition, historically the wet season usually presents one pulse of water surplus but during wet 2005 there were three pulses in precipitation. These data confirm that precipitation in Guánica is highly erratic [35] and show that the 2004–2005 months encompassed in this study represent extreme dry conditions followed by extreme wet conditions.

3.2 Microclimate

3.2.1 Variation among tree species

There was a significant effect of plant species and fraction on maximum, minimum and temperature range (**Table 1, Figure 2**). Understory maxima temperatures ranged between 35.9°C and 34.9°C and followed the pattern *Conocarpus* > *Pisonia* > *Tabebuia*, *Ficus*, *Coccoloba* while minima followed the pattern *Tabebuia* ≥ *Coccoloba*, *Ficus*, *Pisonia* ≥ *Conocarpus*. Therefore, in the understory, temperature daily range was largest in *Conocarpus* intermediate in *Pisonia* and smallest in *Ficus*, *Tabebuia*, *Coccoloba*. In the litter, maxima temperatures ranged between 37.8°C and 30.2°C, and followed the pattern *Conocarpus* > *Ficus*, *Pisonia* > *Pisonia*, *Tabebuia* > *Coccoloba*. Minima temperatures were *Pisonia* ≥ *Ficus* ≥ *Conocarpus* ≥ *Tabebuia* ≥ *Coccoloba*, therefore temperature daily range in the litter was largest in *Conocarpus*, intermediate in *Ficus* followed by *Pisonia* and *Tabebuia*, and smallest in *Coccoloba*. In the humus, maxima ranged between 31.7°C and 28.2°C and the pattern was *Conocarpus*, *Ficus* > *Pisonia*, *Tabebuia* > *Coccoloba* and in the humus between. Minima were *Conocarpus* > *Pisonia* > *Tabebuia* > *Ficus* and *Coccoloba*. Therefore, humus

Factor	DF	Maxima		Minima		Range	
		F	p	F	p	F	p
Species	4	576	<0.001	26	<0.001	447	<0.001
Fraction	2	2767	<0.001	3138	<0.001	5624	<0.001
Species x fraction	8	149	<0.001	27	<0.001	142	<0.001
Error	18,995						
Total	19,009						

Table 1.
Effect of plant species and fraction (location: understory, litter, humus) on the magnitude of temperature fluctuations during the study period. Anovas were run using daily maximum, minimum and temperature range. There were 435 days (from September 8, 2004 to November 16, 2005).

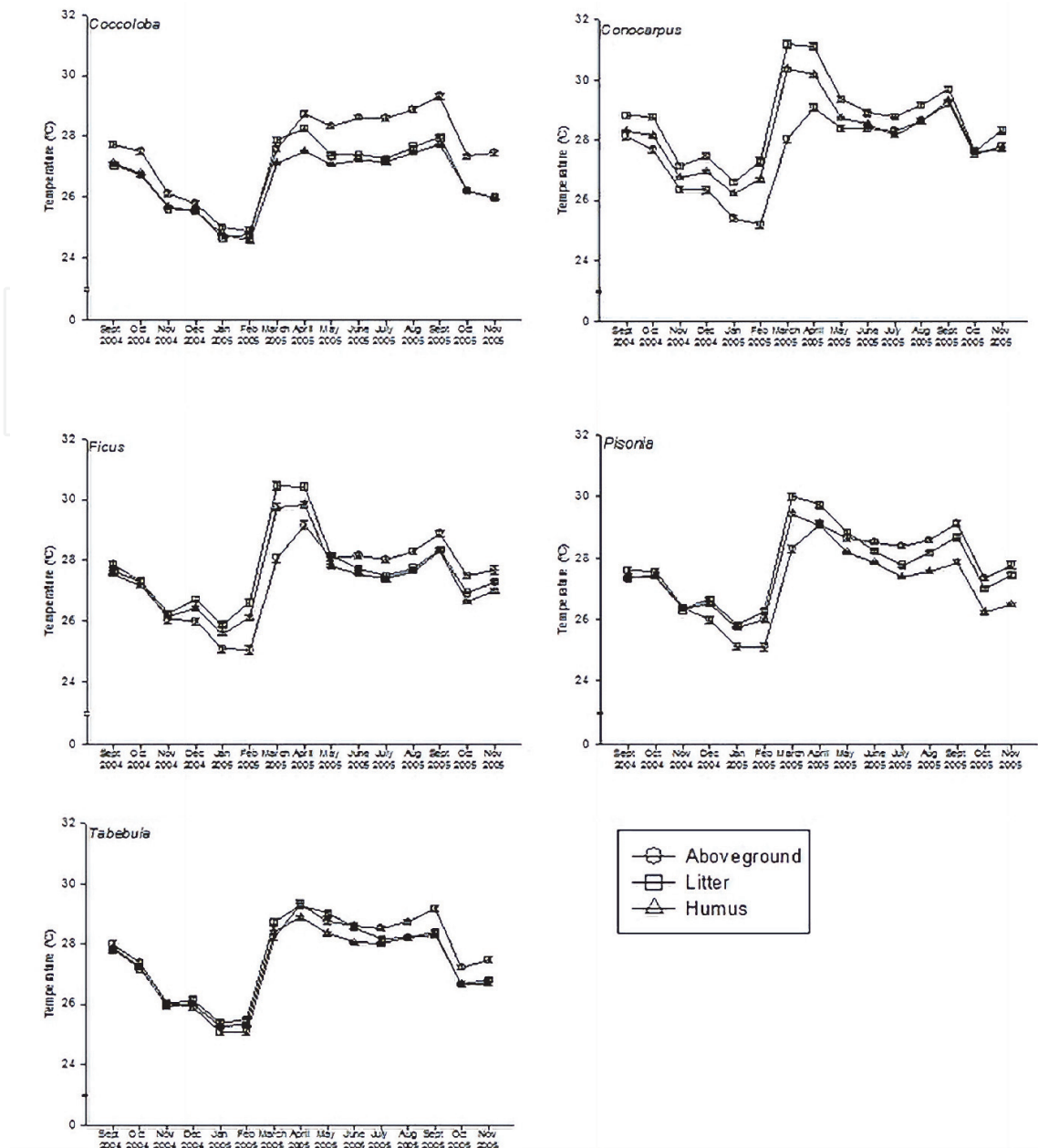


Figure 2. Mean monthly temperature (\pm s.e.) in the understory, litter and humus below the five tree species. (understory: ~ 25 cm understory, Litter: inside the old litter fraction ~ 2.5 cm depth, Humus: inside the humus fraction ~ 4.5 cm depth). Symbols represent mean values and whiskers represent standard error.

temperature daily range showed the pattern *Ficus* > *Conocarpus* > *Tabebuia* > *Pisonia* > *Coccoloba*.

Throughfall and stem flow are affected by tree size and differentially moisten soil under canopies [47] while surrounding rock similarly warms the OM underneath trees [48]. In this study temperature range was largest in the litter suggesting that the buffer capacity of humidity was absent in litter (upper OM) and present in humus (deeper OM). On the other hand, among the five species, *Coccoloba* has the largest leaves and *Conocarpus* the smallest ones, and canopy openness is intermediate in *Tabebuia*, *Ficus* and *Pisonia* [49] suggesting that tree characteristics play a role in modulating temperature fluctuations.

3.2.2 Variations among seasons

As expected, we found that the pattern of temperature fluctuations under all species (**Figure 2**) was similar to the pattern of mesoclimate temperature

fluctuations (**Figure 1**) (Kolmogorov Smirnov, $p = 1.00$), e.g. lower temperatures in January and February in comparison to the remaining months. Also, understory air temperature under the five species was consistently higher than temperature from the mesoclimate site by 2.13°C on average. This is due to differences in altitude, the mesoclimate SCAN site was located 165 masl while trees were located at 0 masl, and since temperature decreases by $\sim 1^{\circ}\text{C}$ for every 100 m in altitude, therefore this resulted in the consistent higher temperatures under the trees. Across months, understory, litter and humus temperature fluctuations were similar for all species, and the largest temperature increase occurred from February to March, an increase of 2.98°C (**Figure 2**). Our data is consistent with the historical pattern described for this forest [36] and with other studies that established that different vegetation associations within a geographic area follow similar fluctuations [50] because fluctuations at the regional scale drive the seasonal pattern at smaller scales, i.e. tree understory temperature.

In all species, through time, daily range significantly varied in all fractions and was larger from December 2004 to March 2005 (**Figure 3**). In *Coccoloba*, *Pisonia* and *Tabebuia* daily variation was largest in the understory and progressively smaller in litter and humus, while in *Conocarpus* and *Ficus* daily variation was largest in the litter particularly in March 2005. During the first quarter of the year, Puerto Rico is affected by cold temperate fronts that decrease average minimum temperatures from December to March [51] but do not affect maxima temperatures producing larger daily variations for all species when compared to remaining months. The largest variation in daily temperature occurred in March 2005 (**Figure 3**), when there was no precipitation (**Figure 1**).

Therefore, in Guanica, months of water deficit (**Figure 1**) coincide with cool months suggesting that mesoclimate drives the decrease in rainfall and minima temperatures while plant species modulate maxima temperatures. In addition, temperature fluctuations in the soil are buffered by soil moisture [52] and isothermal karst rocks warm OM [48] therefore water deficit [53] in combination with an increase in temperature better explain the largest daily variations found in March 2005.

3.3 Tree species characterization

On average, *Pisonia* trees were 2.0 m height, *Coccoloba*'s were 1.8 m and *Ficus*' 1.8 m, and significantly taller than *Tabebuia*'s and *Conocarpus*' that were 1.2 m and 1.1 m respectively (**Figure 4**). Canopies were significantly larger in *Coccoloba*, 155 m^2 , than in the other species (**Figure 4**) therefore *Coccoloba* trees were tall and large, *Ficus* and *Pisonia*'s were tall and small, and *Conocarpus* and *Tabebuia*'s were short and small. Litter weight varied among species and through time (**Figure 5**), there was a trend for *Coccoloba* to have the largest litter mass and *Tabebuia* to have the lowest. Litter depth tended to be higher in *Pisonia* particularly at the beginning of the dry season, i.e. January 2005 (**Figure 5**). On the other hand, humus weight and depth were similar among species and months suggesting that although new litter is produced, there is an effect of past accumulation. In Guánica, the ground surface is irregular presenting small depressions of varying sizes [33], then variations in humus may be due to changes in size of the exact sampling points and not because of changes in soil organic matter per se.

Across months, litter fractions varied significantly (**Figure 5**). For example, litter depth under *Coccoloba* was highest in November 2004 and lowest in June 2005, while it was highest in *Pisonia* during the dry months possibly because this species is deciduous and drops the leaves during the dry season [54, 55]. *Ficus* tended to have large litter depth in the wet months; as a facultative deciduous

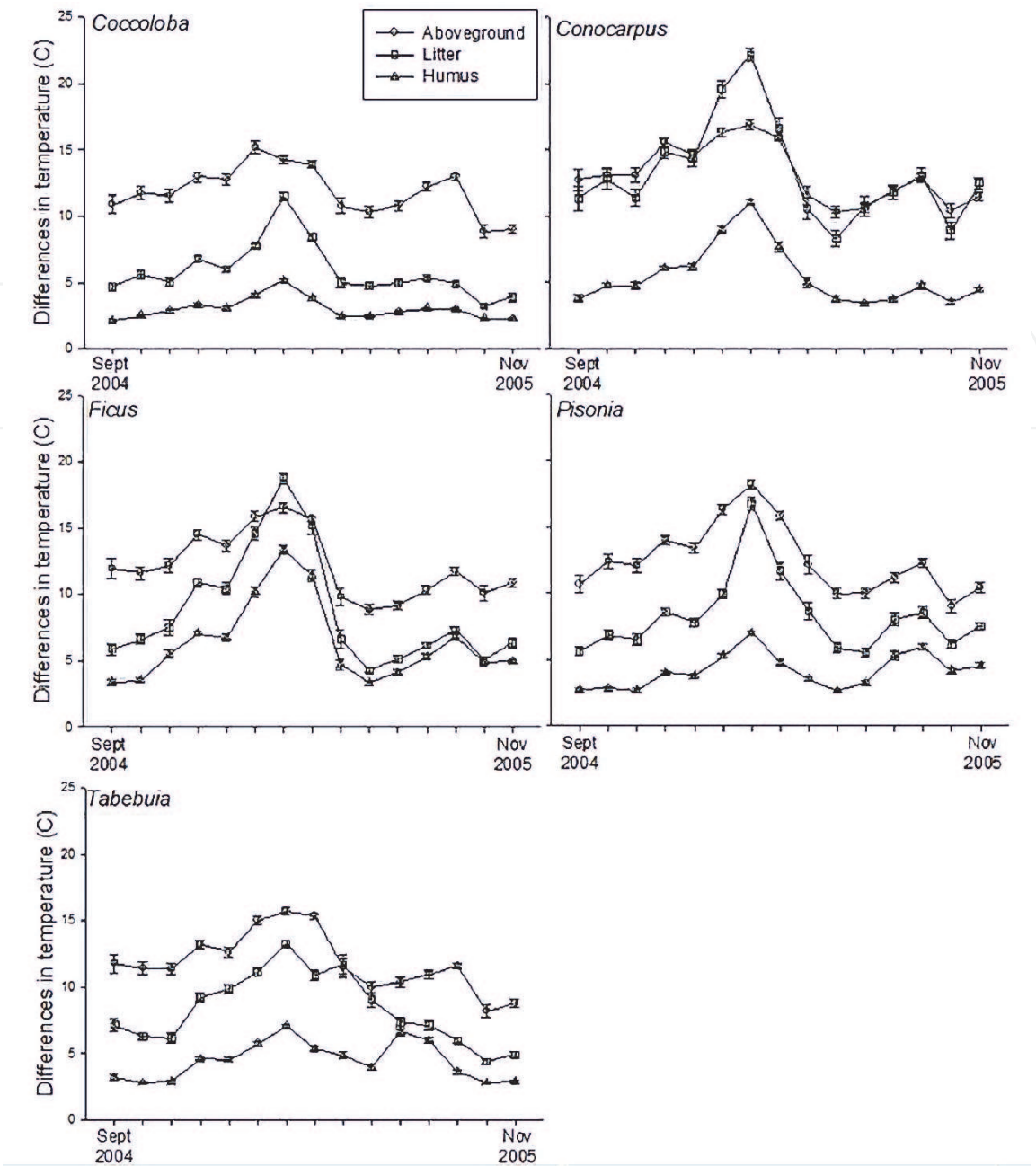


Figure 3. Mean daily temperature range per month below the five tree species and for each of the three depths. Daily range was calculated as $T_{max} - T_{min}/day$. Symbols represent mean values and whiskers represent standard error.

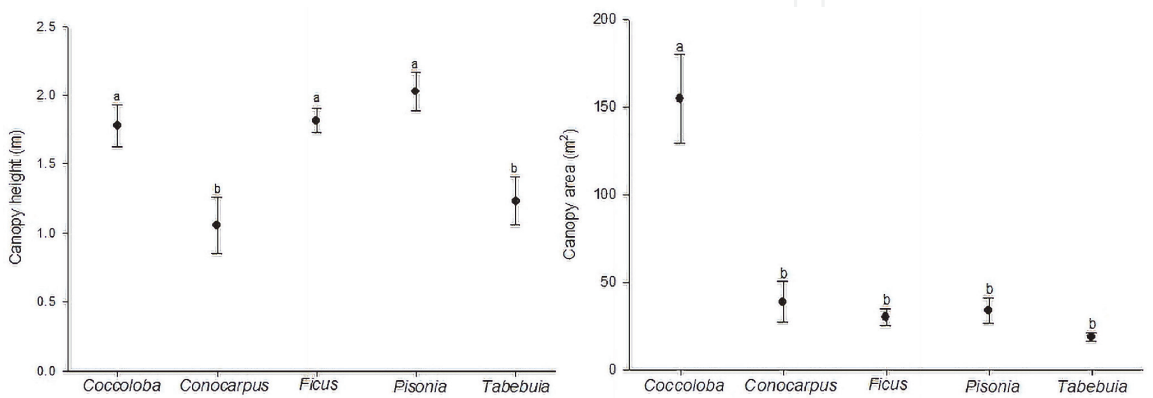


Figure 4. Average canopy height (m) and average canopy area (m^2) for the five species. Dots represent means, whiskers represent standard error, and lower-case letters indicate significant differences.

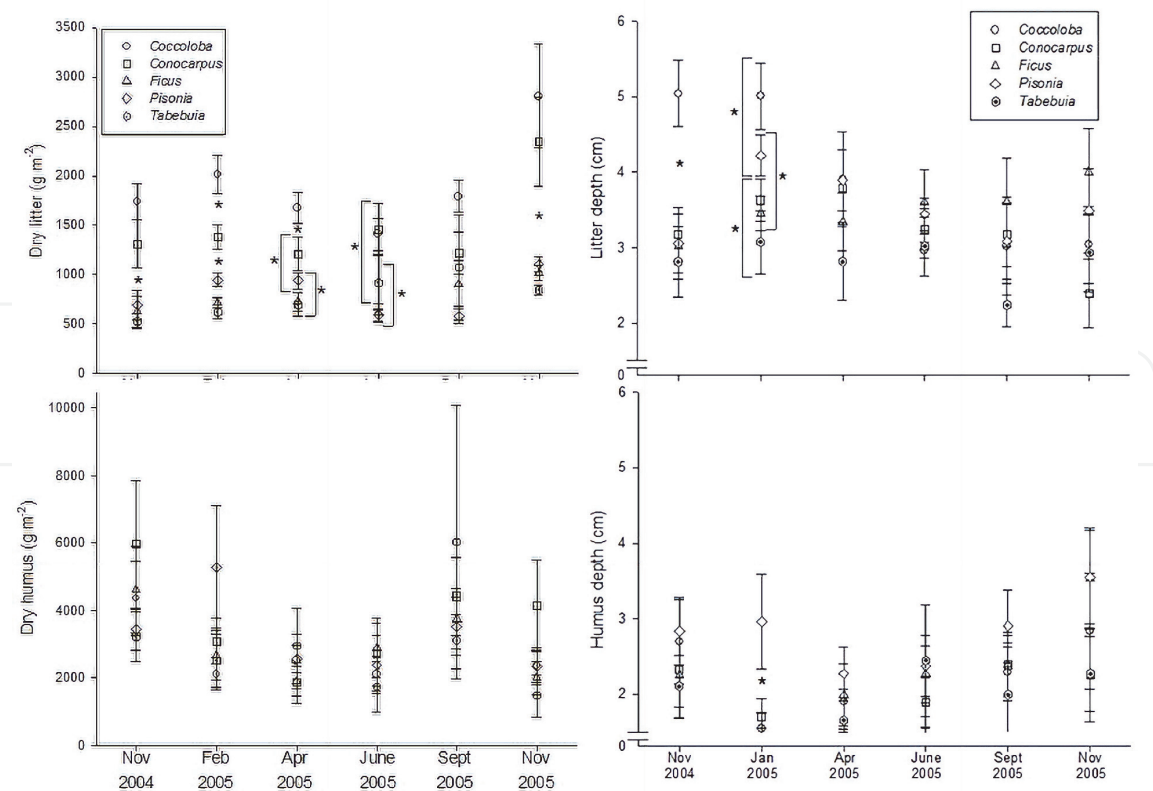


Figure 5. Average litter and humus dry weight (g m^{-2}) and depth (cm) for the five tree species and in each of the six sampling dates. Symbols indicate the mean and whiskers indicate standard error. Asterisks indicate significant differences among plant species within censuses.

species, it drops the leaves during the dry season [54, 55] but these leaves had a slower decomposition possibly in relation to milky sap that deters feeding organisms than did *Pisonia*. *Tabebuia* and *Conocarpus* consistently had small litter depth possibly due to low production of litter fall. Our results are consistent with Lugo et al. [36] who found that litter production increased during the dry season because of deciduous species and because decomposition was arrested (due to water deficit). Humus is a stable fraction of soil organic matter, and loose and old litters are the dynamic fractions, then any change in soil organic matter depth can be attributed to changes in litter.

3.4 Tree species and microclimate

In summary, we have shown that microclimate fluctuations follow the seasonal pattern of mesoclimate, that maxima and temperature range, tree height, canopy area and litter are different among plant species. Different tree species characteristics correlated significantly with temperature, and these correlations varied seasonally (Table 2). In general, understory air temperature correlated with tree characteristics in the dry season but not in the wet season, while litter and humus temperatures correlated with tree characteristics in both seasons and with litter mass only in the wet season. Canopy size correlated significantly with understory maximum temperature in February 2005 when deciduous species drop the leaves [37] suggesting that more open canopies allowed for higher maximum temperatures in the dry season. On the other hand, litter mass and depth correlated with litter temperature suggesting that the quantity of organic matter and its water holding capacity is important for buffering litter temperature during the wet season.

Canopy area significantly correlated with temperature, for example maximum temperature was highest in *Conocarpus*, a species with small canopies while species

February 2005			September 2005			
	Maxima	Minima	Range	Maxima	Minima	Range
Understory	<ul style="list-style-type: none">• Canopy size**• Tree volume***		<ul style="list-style-type: none">• Canopy size**• Tree volume***			
Litter	<ul style="list-style-type: none">• Canopy size***• Tree volume***• Tree height*	<ul style="list-style-type: none">• Tree height***• Litter depth***	<ul style="list-style-type: none">• Canopy size***• Tree height***• Tree volume***• Litter depth***	<ul style="list-style-type: none">• Canopy size***• Tree volume***• Litter depth***• Litter mass***	<ul style="list-style-type: none">• Tree volume***• Litter mass***	<ul style="list-style-type: none">• Canopy size***• Tree volume***• Litter mass***
Humus	<ul style="list-style-type: none">• Canopy size***• Tree volume***		<ul style="list-style-type: none">• Canopy size***• Tree volume***	<ul style="list-style-type: none">• Canopy size***• Tree height***• Tree volume***• Litter depth***• Litter mass***	<ul style="list-style-type: none">• Canopy size***• Tree volume***• Litter depth***• Litter mass***	<ul style="list-style-type: none">• Canopy size***• Tree height***• Tree volume***• Litter mass***

Only significant correlations are shown, and asterisks next to the variable indicate level of significance: *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$. February and September 2005 are shown as representatives of dry and wet periods.

Table 2. Spearman rank order correlations among maximum, minimum and range in temperature and tree characteristics (height, size, volume, organic matter depth and volume).

with similar canopy areas such as *Ficus*, *Pisonia* and *Tabebuia* had lower maximum temperatures, and *Coccoloba* had taller trees with larger canopy areas which possibly resulted in less understory heating and lower temperatures. Leaf area and leaf orientation result in light differentially entering plant canopies producing different degrees of heating of understory air [1, 52]. Therefore, our data suggest that the size of the tree (canopy and height – volume) influence the microclimate created underneath it but not in a linear additive way, rather tree characteristics interact and influence microclimate underneath the tree in complex ways, suggesting that the tree is an integrate that modulates the understory microclimate.

3.5 Arthropods

3.5.1 Litter fractions

A total of 8702 arthropods representing 22 orders and 301 morphotypes were collected. Arthropod abundance and richness were significantly different among fractions (**Table 3**). Overall *Tabebuia* and *Ficus* had similarly higher abundance, followed by *Pisonia* and *Coccoloba*, and abundance was lowest in *Conocarpus*. In general, there was a trend for lower arthropod abundance in loose litter and highest in humus except in *Coccoloba* where old litter had higher abundance than the other two fractions (**Figure 6**). Overall, richness was highest in *Ficus* and *Pisonia*, followed by *Tabebuia*, and lowest in *Coccoloba* and *Conocarpus*, but among fractions the trend for lower richness in loose litter and higher in humus was similar as for abundance (**Figure 6**). These data suggest that for arthropod abundance and

Factor	DF	Abundance		Richness	
		F	p	F	p
Date	4	9.36	<0.001	41.68	<0.001
Species	4	1.65	0.16	3.39	0.01
Fraction	2	40.83	<0.001	66.13	<0.001
Date x species	16	0.90	0.57	1.52	0.09
Date x fraction	8	2.92	0.00	7.23	<0.001
Species x fraction	8	2.59	0.01	1.93	0.05
Date x species x fraction	32	0.79	0.79	0.93	0.58
Residual	675				
Total	749				

Table 3.
Three-way analysis of variance for the effect of date, species and fraction on the abundance and richness of arthropods.

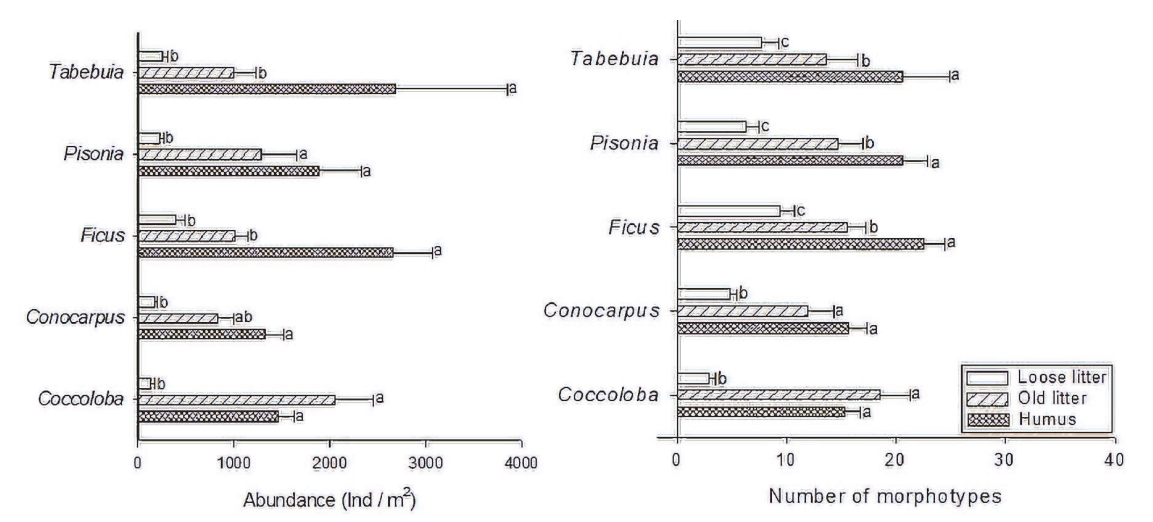


Figure 6.
Average arthropod abundance (\pm s.d.) (ind/m²) and average number of morphotypes (\pm s.e.) in each fraction for the five study species. Lower case letters indicate significant differences among fractions within species.

richness, the decomposition stage of the organic matter (paralleled in the vertical profile: loose, old, humus) is a determining factor as important as plant species identity [24]. Furthermore, the decomposition stage is advanced in humus where the biological activity is high and thus there are high available resources (e.g. higher nutrient availability in humus than in litter fractions, [11]) suggesting a higher abundance of decomposer microbes that, in the trophic food web theory would result in higher abundance of arthropods.

Hansen [12] found that large litter dwellers were positively associated with particular litter substrates, Berg et al. [22] similarly found that litter in different decomposition stages had sets of associated arthropods, and Prinzing et al. [56] found that even sexes within a mite species differentially used organic matter strata. At the same time, Hansen [12] proposed that a higher abundance and richness of arthropods would be found in strata with higher diversity of resources (i.e. litter). Our results support that specific groups are associated to specific litter strata, being more abundant where more resources are found, but not in the litter, instead in the humus fraction. Kardol et al. [57] suggest that plant–soil feedbacks are mediated by

microbes; specifically, they found that soil microbial pathogens affected the development of the future plant community because soils have a biotic legacy of past vegetation cover. Similarly, soils may have a biotic legacy of beneficial microbes that, as Wardle states, maximizes decomposition, and can have a positive historical feedback on the soil community. In addition, Bezemer et al. [58] found that plant–soil feedbacks are dependent on plant species. In our case, these data suggest that trees in the coastal plateau have been there for long enough to result in a biotic legacy that, under certain plant species favors some arthropods, while under other plant species other types of arthropods are favored.

3.5.2 Variations through time

Arthropod abundance and richness were significantly different among sampling dates (**Table 3**). Through time, arthropod abundance varied with a trend for a decreased abundance in the dry period (April 2005) and higher abundance in the wet period (**Figure 7**). In all species and all samplings, arthropod abundance was consistently low in loose litter while variations in old litter and humus explained significant differences. For example, in *Coccoloba*, *Ficus* and *Tabebuia* abundance peaked at the onset of the wet period (June 2005) while in *Conocarpus* and *Pisonia* peaked abundance was observed later in the wet period (September 2005). Similarly, for all plant species, arthropod richness was significantly low in the dry period and higher in the wet period (**Figure 8**). Also, in *Coccoloba*, *Ficus* and *Tabebuia* peaked richness occurred at the onset of the wet period (June 2005) while in *Conocarpus* and *Pisonia* it was later in the wet season (September 2005).

During the study, precipitation varied producing a wet 2004 period, a dry 2005 period and a wet 2005 period (**Figure 1**). Herrera [59] found that the abundance of soil fauna fluctuated seasonally influenced by the precipitation regime. Specifically, groups like ants and beetles were present during year-round but isopods and diplopods were more abundant at the end of the wet season while chilopods were present all the year but during the dry season they migrated vertically and thus were completely absent in the upper litter. On the other hand, Prather et al. [27] found that high soil moisture promoted arthropods while high temperature decreased arthropods. Our results show that arthropod abundance and richness follow a seasonal pattern tight to precipitation, and that arthropods tightly linked to litter are able to overcome drought although in such low abundance that does not support upper trophic levels [24].

Arthropod species composition was dynamic through time as it varied among plant species (**Figure 9**). Under wet conditions such as in November 2004, arthropod species composition was similar between *Coccoloba* and *Conocarpus* and among *Tabebuia*, *Ficus* and *Pisonia* who shared unique sets of associated arthropods. Similarly, in June and September 2005, a similar pattern was observed such that species composition was similar between *Coccoloba* and *Conocarpus*, and among *Ficus*, *Pisonia* and *Tabebuia*. On the other hand, at the onset of the dry period (February 2005) when water shortage peaked, differences among plant species were lost resulting in similar arthropod species composition among species (**Figure 9**). Therefore, in general, when water is available, arthropods formed two distinctive communities under different groups of plant species, while when water deficit happened, plant species shared a common set of arthropods.

From these data, we conclude that two major arthropod communities were formed, one with arthropods common to *Coccoloba* and *Conocarpus*, and one with arthropods common to *Ficus*, *Pisonia* and *Tabebuia*. The local distribution of trees shows that *Coccoloba* and *Conocarpus* are closer to the shore than the other three species, suggesting that plants near the coast share arthropods communities as do

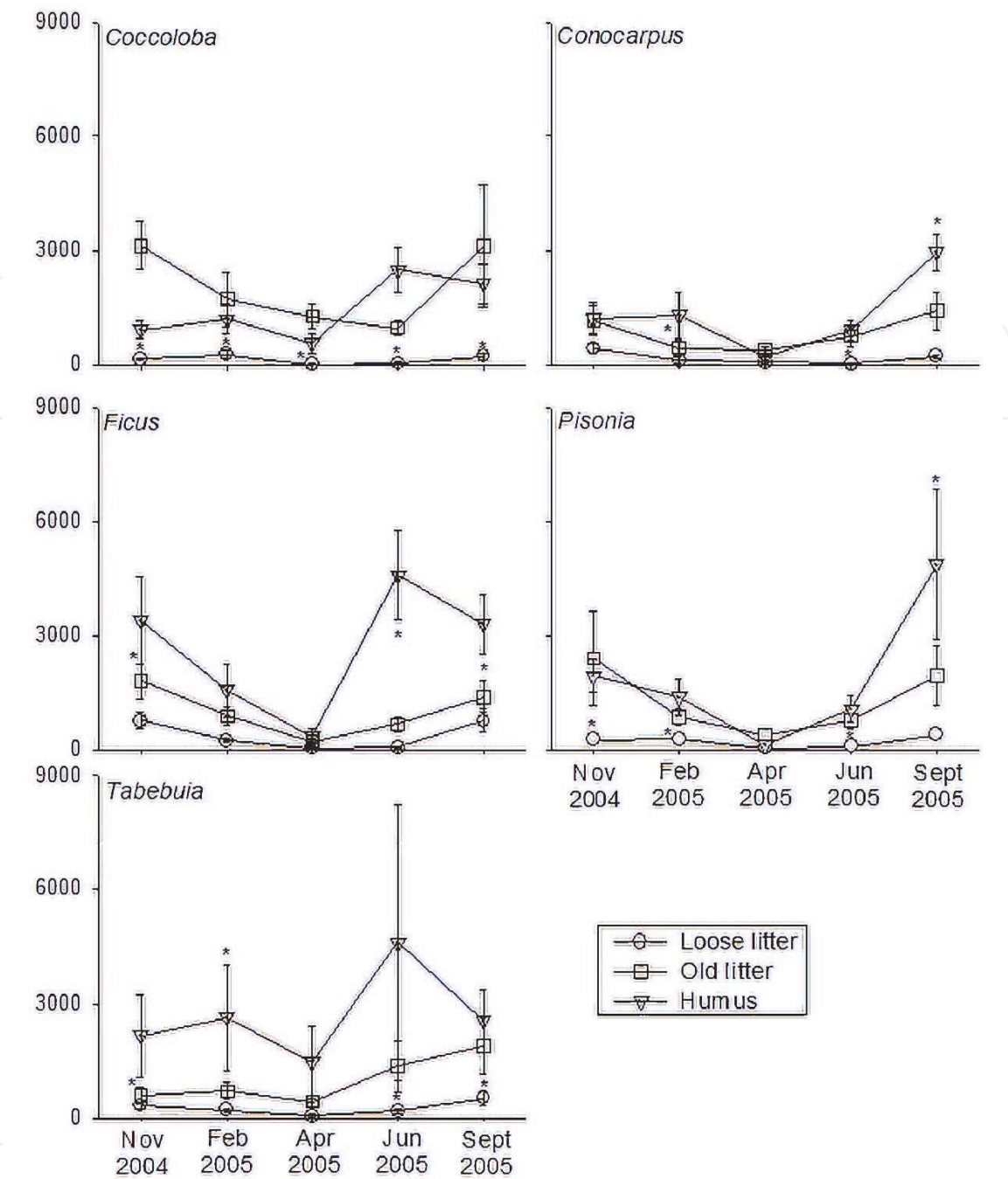


Figure 7. Mean arthropod abundance (\pm s.d.) (ind/m²) in each sampling date and in each fraction for the five study species. Asterisks indicate significant differences among fractions within species for the corresponding sampling date.

plants farther from the shore. Nevertheless, when extreme conditions happen, such as dry cool months in February 2005 (**Figure 1**), the arthropod community homogenizes because arthropod abundance was low and species composition becomes similar.

Both, arthropod abundance and richness (**Figures 7 and 8**) decreased at the onset of the dry period (February 2005) and were at a minimum in the middle of the period (April 2005), on the other hand species composition was similar at the onset but different in the middle of the dry season (**Figure 9**). Furthermore, litter depth was high at the onset of the dry season (**Figure 5**) because of new litter produced by plants as a response of water deficit (**Figure 1**). These results suggest that during the dry season, conditions are such that plants drop leaves and below-ground arthropods associated to plants represent a shared subgroup common to all

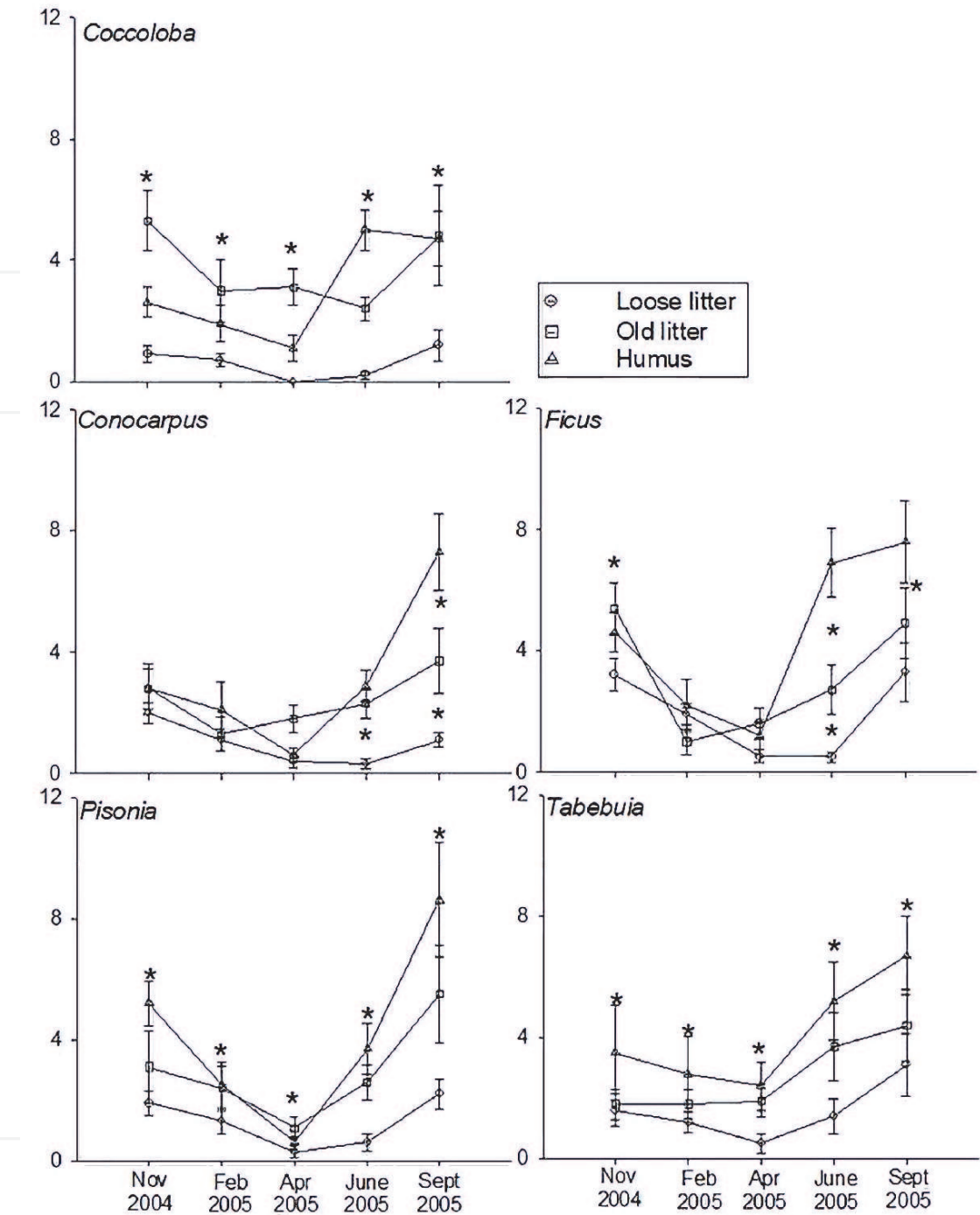


Figure 8. Average number of morphotypes in each sampling date and in each fraction for the five study species. Asterisks indicate significant differences among fractions within species for the corresponding sampling date.

plant species, while further into the dry season, arthropod abundance and richness are at the lowest such that only arthropods specific to plant species are present. Abundance and richness are not linearly related, nevertheless an increase in abundance results in more species, for example Prather et al. [27] found that for every 16 individuals a new species appears. From these data we can expect that a decrease in abundance results in loss of species, therefore, in our study the decrease in abundance at the beginning of the dry season may have resulted in a decrease in species such that only stress-tolerant arthropod species [27] were present in all plant species producing a homogenization of the arthropod community. A further decrease in abundance led to the minimum found in mid-dry season which might have produced further species loss so that only species adapted to the specific plant microhabitat remained resulting in a differentiation in arthropod community.

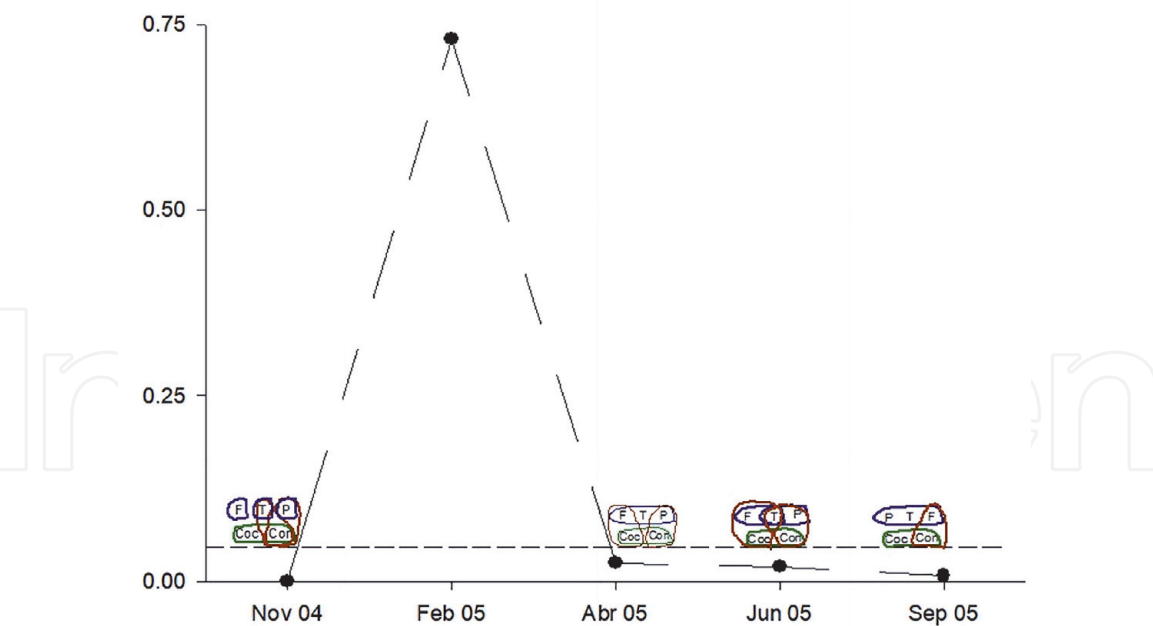


Figure 9. *p*-value results from MRPP (Multi-response permutation procedure) tests. MRPP evaluated whether there were significant differences in arthropod species composition among plant species in each sampling. The y-axis shows *p*-values, initials indicate plant species as follows Coc for Coccoloba, Con for Conocarpus, F for Ficus, P for Pisonia and T for Tabebuia. The short-dashed horizontal line indicates the critical value *p* = 0.05. Markers below the dashed line show significant differences among species. Significant differences are shown by circled color-coded initials.

Species	Nov 04 – Feb 05	Feb – Apr 05	Apr – June 05	June – Sept 05
Coccoloba	81(±8)**	96(±5)**	77(±7)	73(±9)*
Conocarpus	94(±3)*	94(±7)*	82(±9)	86(±9)*
Ficus	92(±5)*	91(±4)	91(±3)**	79(±6)
Pisonia	92(±4)*	94(±6)	89(±6)	89(±5)***
Tabebuia	94(±4)	94(±6)	88(±8)	85(±5)

Percent dissimilarity was calculated as $100 \times \text{dissimilarity}$. Dissimilarity was calculated using the Sorensen index $(1-2W/(A+B))$. W indicates the sum of abundances of common species between sampling units, and A and B indicate the sum of abundances of all species in each sampling unit. Asterisk indicates significant differences among consecutive sampling dates (**p* < 0.05, ***p* < 0.001, ****p* < 0.0001).

Table 4. Dissimilarity (%) of arthropod species composition (mean ± s.d.) associated to specific plant species among sampling dates.

Within each plant species, arthropod species composition significantly varied through time (**Table 4**). In *Coccoloba* and *Conocarpus*, species composition significantly changed between consecutive samplings except April to June 2005. These data suggest that for these two plants there is a high turnover of arthropod species, and that the arthropods present in April were a subset of the June arthropods. When comparing April and June 2005, in *Coccoloba*, abundance and species composition were similar and richness increased (**Table 4**, **Figures 7** and **8**) suggesting that at the onset of the wet season the majority of arthropods belong to the same species despite an increase in richness. In *Conocarpus*, when comparing April and June, arthropod abundance (**Figure 8**), richness (**Figure 9**) and species composition (**Table 4**) were similar suggesting that the transition between dry and wet months is dominated by a common set of arthropods.

In *Ficus*, the arthropod composition was similar through time except from November to February and from April to June (**Table 4**), suggesting that the major shifts in arthropod species occur between seasons (end wet period: November to February, end dry period: April to June). On the other hand, arthropod abundance and richness decreased to a minimum in the middle of the dry season (April 2005) (**Figures 8 and 9**) when litter increased (**Figure 5**) because this is a deciduous plant. These data suggest that arthropods present in *Ficus* respond to changing conditions, such as new litter or a change in precipitation.

In *Pisonia*, a similar pattern as in *Ficus* was observed but later in the wet period (June to September), arthropod abundance and richness increased in the wet period (**Figures 6 and 7**), and species composition was significantly different (**Table 4**). In addition, *Pisonia* is an obligate deciduous species that produces new litter in the dry season (**Figure 5**). These data suggest a possible time lag tied to increasing precipitation as arthropods present in *Pisonia* increased and litter depth decreased (**Figure 5**) probably explained by decomposition of new leaves and more arthropods at the onset of the wet season.

In *Tabebuia*, arthropod species composition and abundance were similar through time (**Figure 7 and Table 4**) while richness (**Figure 8**) significantly varied suggesting that there is a bulk of arthropods associated to this plant species that is present yearlong although some arthropod species vary through time but not enough to produce a different composition of arthropods.

For most plant species, these data show a shared pattern for a shift in arthropod communities between wet and dry seasons (November 2004 to February 2005), then arthropods in *Cocoloba* and *Conocarpus* continued to change as the dry season strengthened while arthropods in *Ficus* and *Pisonia* (deciduous plants with more open canopies by February 2005) changed with an increase in rainfall that triggers biological activity. *Tabebuia* was the only plant to show a consistent group of associated arthropods.

3.5.3 Variations across fractions

Abundance and richness of arthropods were significantly affected by sampling time and fraction (interaction term Date x Fraction in **Table 3**), suggesting that through time there is a dynamic movement of arthropods among fractions (**Figures 7 and 8**). In addition, for each plant species the composition of arthropods varied across the vertical organic matter profile (**Figure 10**).

In *Coccoloba*, there was a general trend for high turnover of arthropods which were more abundant and species composition was different among fractions in the wet season and similar in the dry season when abundance was lowest (**Figures 8–10**). In wet months, loose litter had 9–12 and old litter had 27–30 morphotypes and shared 1–4, while humus had 14–25 from which 12–16 occurred in old. Loose and humus fractions had 1 to none arthropods in common (Appendix I). These data show a unique arthropod community in loose litter mainly due to adult Diptera (unique to this fraction) that possibly pupated and emerged as adults at the moment of collection (e.g. in November: G-157, G-158, G-159, and in September: G-182, G-123, G-191, G-209) (Appendix I). On the other hand, humus species composition was unique in June due to a dominance of detritivore and predator species exclusive to this fraction, such as G-207, G-007, G-147, G-229 and G-263 (Appendix I). These data suggest that the beginning of the wet season triggers the biological activity in the humus fraction (as suggested by increased arthropod abundance and richness, and unique species composition), and that later in the wet season (September and November samplings) decomposer activity increases (as suggested by the presence of adult Diptera whose larvae feed on decomposing material, e.g. G-157, G-158 and G-159), and that a possible flush in aboveground biomass promotes herbivore activity that pupates in

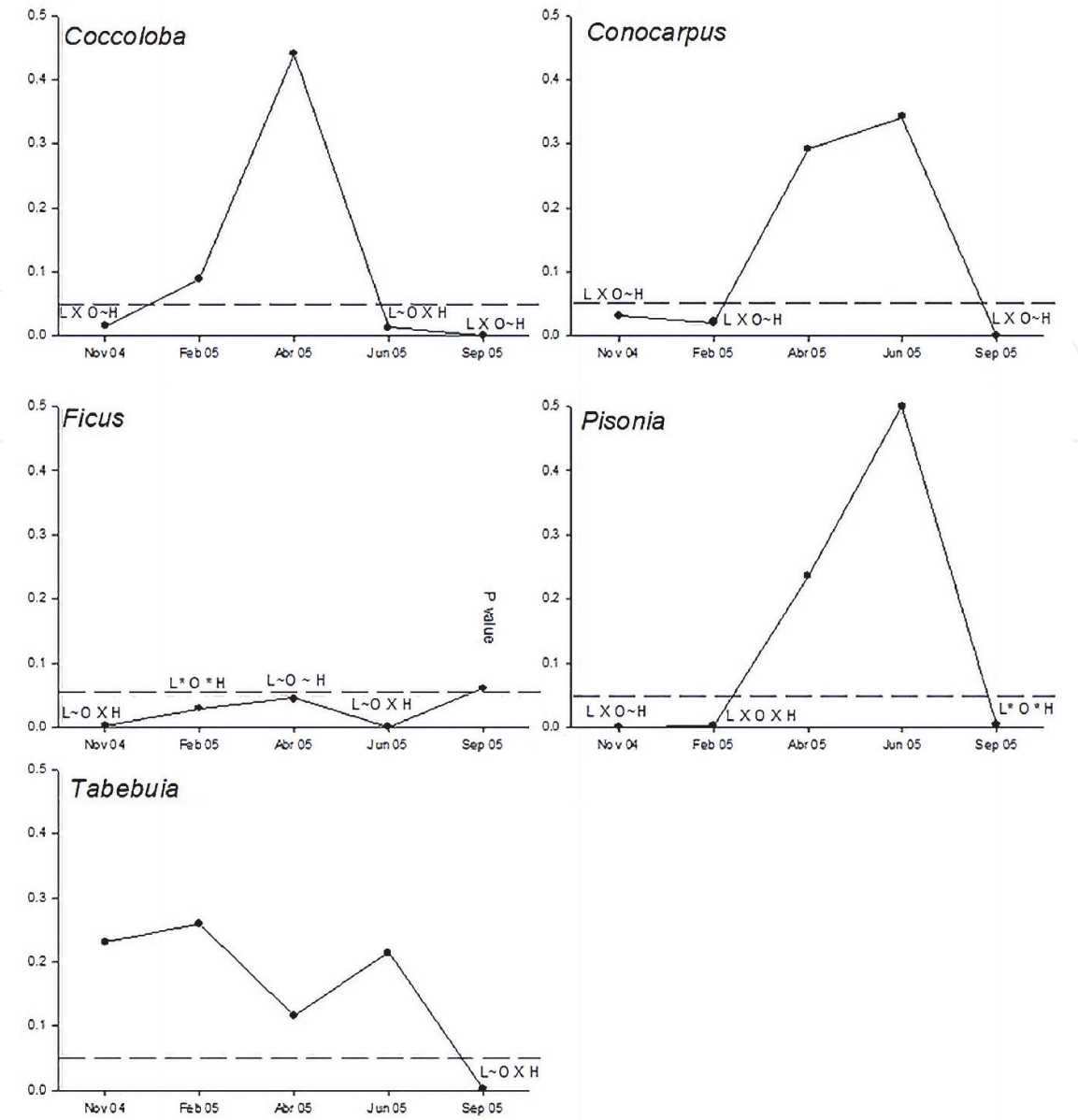


Figure 10. *p*-value results from MRPP tests. MRPP evaluated differences among fractions in arthropod species composition, for each plant species at each sampling separately. The y-axis shows *p*-values, initials indicate fractions as follows L for loose litter, O for old litter and H for humus. The short-dashed horizontal line indicates the critical value $p = 0.05$. The long-dashed line connects consecutive samplings. Markers below the dashed line show significant differences among fractions. Symbols indicate differences, 'X' indicates significant differences between the specified fractions, '~' indicates no significant difference, and '*' that two fractions are similar but different from the third one.

the ground (as suggested by the presence of adult Hymenoptera whose larvae are herbivores, e.g. G-168). The similarity in species composition among fractions during the dry period samplings (February and April) suggests that an increase in daily temperature (Figures 2 and 3) and drought represent stressors that mix the vertical stratification of the arthropod fauna. For example, in April loose litter had no arthropods, suggesting that remaining arthropods migrated downwards to avoid these extreme conditions.

In *Conocarpus*, also there was a general trend for high turnover of arthropods through time, but there was a consistent pattern for loose litter to have a low abundance arthropod community that is different from old litter and humus (Figures 7 and 8). In addition, when abundance was at a minimum in April 2005 (Figures 7 and 8), the species composition was similar (Figure 10). In November, February and September samplings, loose litter had unique species that were adult Diptera that possibly emerged at the moment of collection, and predators such as

Araneae and Opiliones (i.e. G-134 and G-101) (Appendix I). In April, abundance and richness were lowest especially in loose litter, and species composition was similar among fractions suggesting again that arthropods migrated downwards to avoid extreme conditions such as drought and heat. Although the wet period began in May (**Figure 1**), abundance and richness continued to be low in loose litter and species composition was similar among fractions. In June, loose litter had 3 morphotypes with very low abundance, two were detritivore mites (G-147 and G-100 - Appendix I) suggesting that the increase in precipitation may have promoted detritivore abundance but still not enough to propagate into the loose litter fraction, possibly because *Conocarpus* is a species that grows very near the shore cliff and may receive more salt spray and less effective rainfall so that it may take longer to respond to an increase in water supply.

In *Ficus*, in general, arthropod species composition was different through time and across fractions while abundance was higher in wet months and also in dry months when abundance decreased (**Figures 7, 8 and 10**). In November and June, humus had a specific set of associated arthropods that were mainly detritivores and predators (i.e. G-007, G-092, G-207, and G-244 - Appendix I). In February and April, species composition was marginally different, possibly due to the presence of adult Diptera in loose and old litter, and large detritivores (such as Psocoptera and Blattodea G-102 and G-228 - Appendix I) in old litter, while in humus there were basically small detritivores and predators (G-207, G-003 and G-220). A possible explanation for the presence of adult Diptera in old litter is that *Ficus* is a facultative deciduous species that progressively drops the leaves in dry conditions so that dipteran larvae that began pupating were then covered by new litter. In September, species composition mixed among fractions possibly due to the shared presence of highly abundant morphotypes such as G-078, G-037, G-105 and G-031 (Appendix I), mainly detritivores, suggesting that in mid wet season, there has been enough detritus production so that detritivores are promoted in the whole organic matter vertical profile resulting in a similar species composition among fractions.

In *Pisonia* also the general trend was for a different species composition when abundance is high in the wet season and it becomes similar when abundance decreases in the dry season (**Figures 7, 8 and 10**). In November, February and September, abundance and richness were comparatively high, and species composition was different among fractions. In loose litter, the majority of unique morphotypes were adult dipterans (e.g. G-157 and G-139) and adult coleopterans that as larvae are herbivores (e.g. G-146 and G-148) while old litter and humus shared basically abundant detritivore mites (G-037, G-007 and G-087) (Appendix I). In April and June, there was a similar composition of arthropod across fractions, possibly due to the extremely low abundance of arthropods. This may be the result of downwards migration of arthropods and a pulse of new litter because *Pisonia* is an obligate. These data suggest that extreme conditions that occur during the dry season mixed the stratification of arthropods in the vertical organic matter profile.

Tabebuia had a similar arthropod community across fractions through time although abundance was similar and richness increased in the wet season (**Figures 7, 8 and 10**). The similarity in species composition was possibly due to the shared presence of abundant morphotypes among fractions at each sampling date (e.g. in November G-037, G-003, G-002, G-001, in February G-078, G-188, in April G-037, G-078, in June G-078, G-002, G-004, G-105) (Appendix I). In September, there continued to be abundant shared morphotypes but the appearance of unique detritivore species in humus differentiate the species composition (e.g. as G-262, G-288, G-010, G-269). These data suggest that the arthropod fauna below *Tabebuia* actively moves among fractions and that, at mid wet season, enough detritus has been produced in order to differentiate active arthropods in each fraction.

4. Conclusions

We found abundance and richness to be highest in humus and species composition to be different among fractions suggesting that arthropod communities are segregated among plant species and are further stratified by decomposition stage. Also, abundance and richness were lowest in the dry months when arthropod communities homogenize while in the wet season there was a pattern for arthropods to form two distinctive groups, one formed by arthropods common to *Coccoloba* and *Conocarpus*, and a second group formed by arthropods common to *Ficus*, *Pisonia* and *Tabebuia*. Furthermore, under plant species, the seasonal distribution of arthropods among fractions in different decomposition stages was differentially affected by variations in microclimate and organic matter depth.

We found for 4 out of 5 plant species, that arthropod communities shift at the end of the wet season when water becomes scarce, and again at the onset of next wet season when temperature daily range was largest. In addition, we identified three patterns of arthropod dynamics across fractions.

First *Coccoloba* and *Conocarpus*, two species close to the shore cliff, showed stratification of arthropod communities across fractions except in dry months when arthropods migrate downwards to deep OM. Then at the beginning of the wet season, arthropods are a subgroup of those in the dry season, and as wet seasons continues, abundance increases and arthropods stratify across fractions.

Second *Ficus* and *Pisonia* both showed a seasonal increase in litter and distinct arthropod communities in wet and dry seasons. During the wet season arthropods are abundant and effectively stratify along OM fractions while in the dry season, in general, communities continue to be different across fractions despite a decrease in abundance, and at the onset of the wet season arthropods are a subgroup of those in the dry season. Nevertheless, *Conocarpus* and *Pisonia* present a time lag as compared to *Coccoloba*, in *Conocarpus* possibly related to less effective rain (proximity to the coastal cliff) and in *Pisonia* possibly related to the time that new litter takes to decompose enough to promote arthropods (as an obligate deciduous species).

Third in *Tabebuia*, litter depth was low all yearlong and temperature range was smaller, and we found arthropod species composition to be similar and abundance to vary through time, being always lowest in loose litter, also arthropod composition was similar across fractions suggesting that arthropods actively move among fractions.

Acknowledgements

This research was partially funded by CREST-Center for Applied Tropical Ecology and Conservation of the University of Puerto Rico at Rio Piedras Campus, grant NSF-HRD-0206200 through a fellowship to MFBA. Additional funding and logistic support was provided by the CREST-Center for Applied Tropical Ecology and Conservation of the University of Puerto Rico at Rio Piedras Campus, USDA Forest Service-International Institute of Tropical Forestry and the Guanica Dry Forest, a Biosphere Reserve staff.

Appendix I: Excerpt from appendix in Barberena-Arias (2008). Abundance (ind/m²) of adult morphotypes in each fraction and species, and for each of the samplings

Date	Order	Morpho	Coccoloba			Conocarpus			Ficus			Pisonia			Tabebuia		
		Type	L	O	H	L	O	H	L	O	H	L	O	H	L	O	H
Nov. 2004	Pseudosc.	G-001		700	200		100		100	300	200		200	300	200	200	200
Nov. 2004	Acari	G-002	100	1000			100								400	900	1300
Nov. 2004	Acari	G-003		900	400		400	400	100	1100	600	100	900	600	100	700	500
Nov. 2004	Acari	G-004		700	200		100	500	100	600	1000	100	100			400	1000
Nov. 2004	Acari	G-007		2500	300		100				1100		500	700			400
Nov. 2004	Isopoda	G-010		100			100	2800		300		100	100	1100			
Nov. 2004	Acari	G-031		1000													
Nov. 2004	Acari	G-037	100	7100	1900	100	1800	2300	100	400	1800		1500	1300	100	200	1800
Nov. 2004	Acari	G-078		600	700		200	200		300	3800			1600		100	4500
Nov. 2004	Isopoda	G-087					100						400	300		100	100
Nov. 2004	Coleoptera	G-092								200				300			
Nov. 2004	Opiliones	G-101		100	100	100							100			100	100
Nov. 2004	Psocoptera	G-102							300	400			100				
Nov. 2004	Diptera	G-123					100		100	200				100			
Nov. 2004	Araneae	G-134				200			500								
Nov. 2004	Acari	G-100															100
Nov. 2004	Diptera	G-139		100		200			100			100		100			
Nov. 2004	Acari	G-147										100					
Nov. 2004	Diptera	G-157	100			100						100					
Nov. 2004	Diptera	G-182		100				100									
Nov. 2004	Coleoptera	G-146										100					

Date	Order	Morpho	Coccoloba			Conocarpus			Ficus			Pisonia			Tabebuia		
			L	O	H	L	O	H	L	O	H	L	O	H	L	O	H
Nov. 2004	Coleoptera	G-148										100					
Nov. 2004	Diptera	G-158	100														
Nov. 2004	Diptera	G-159	100														
Feb. 2005	Acari	G-002		500	200					600	100	100	300			600	900
Feb. 2005	Acari	G-003		2300	400						1800	200	100	600		400	1300
Feb. 2005	Acari	G-004	100				100	1000	100		300		900	1100	200		300
Feb. 2005	Acari	G-007		1600	600		200				600		100	500			200
Feb. 2005	Acari	G-037		100	100	100	100	300	100		200			500			500
Feb. 2005	Acari	G-078		100	1700			300		100	100			400	100	100	2900
Feb. 2005	Psocoptera	G-102								100			400			100	
Feb. 2005	Araneae	G-134	200	500		400			300						200		
Nov. 2004	Hymenopt.	G-168	100														
Feb. 2005	Acari	G-188	100	100				200			100				100	100	100
Feb. 2005	Acari	G-207								100	4600						4600
Feb. 2005	Isopoda	G-010												200			100
Feb. 2005	Acari	G-100											100				
Feb. 2005	Diptera	G-139				100			100								100
Feb. 2005	Diptera	G-159								100			200				
Feb. 2005	Diptera	G-191										100			100		
Feb. 2005	Pseudosc.	G-220									200					100	100
Feb. 2005	Araneae	G-229		100			100										

Date	Order	Morpho Type	Coccoloba			Conocarpus			Ficus			Pisonia			Tabebuia		
			L	O	H	L	O	H	L	O	H	L	O	H	L	O	H
Feb. 2005	Pseudosc.	G-001						100									
Feb. 2005	Coleoptera	G-092									100						
Feb. 2005	Opiliones	G-101								100							
Feb. 2005	Diptera	G-209						100									
Feb. 2005	Blattodea	G-228															
Apr. 2005	Pseudosc.	G-001		200			100	100									
Apr. 2005	Acari	G-002		200	100					200	100					100	1700
Apr. 2005	Acari	G-003					300				1000						700
Apr. 2005	Acari	G-004		1100	300	100	100			100	100		600			500	9600
Apr. 2005	Acari	G-007								200				100			200
Apr. 2005	Acari	G-037		3400	700		1400	700		100	100		1000		200	300	300
Apr. 2005	Acari	G-078		800	400		100			500	100		300	300	100	1200	800
Apr. 2005	Acari	G-100														100	100
Apr. 2005	Araneae	G-134		100			200			200							
Apr. 2005	Diptera	G-139								100		100					
Apr. 2005	Acari	G-207		1000			100									200	100
Apr. 2005	Diptera	G-123		100													
Apr. 2005	Diptera	G-157									100						
Apr. 2005	Acari	G-188															100
Apr. 2005	Pseudosc.	G-220											100				
Apr. 2005	Blattodea	G-228														100	

Date	Order	Morpho	Coccoloba			Conocarpus			Ficus			Pisonia			Tabebuia		
			L	O	H	L	O	H	L	O	H	L	O	H	L	O	H
Apr. 2005	Acari	G-244							100								
Jun. 2005	Acari	G-002		500	400		200	200	200	400	1500	100	700	400	200	1200	1800
Jun. 2005	Acari	G-003			1000		100	100		100	2200			100		400	100
Jun. 2005	Acari	G-004		300	1800		400	300		300	500	100	600	600	300	100	900
Jun. 2005	Acari	G-007			1500			100			1900		100			400	500
Jun. 2005	Acari	G-031								300	1300			100		100	
Jun. 2005	Acari	G-037		4900	4100		1100	2200		100	3400		300	500		500	3400
Jun. 2005	Acari	G-078		500	4800		500	1700		300	5700	100	200	1000	100	300	5600
Jun. 2005	Acari	G-105		300	100			200		300	500		200		100	100	400
Jun. 2005	Araneae	G-134		100			100				100	100					100
Jun. 2005	Acari	G-147			200	100				300	2400		300	600	200	300	
Jun. 2005	Acari	G-207			3400		100	900			300		100	200	100	2900	
Jun. 2005	Araneae	G-229			200			100			100		100			300	
Jun. 2005	Acari	G-244						100			1200			100			
Jun. 2005	Acari	G-262			1400						100						
Jun. 2005	Pseudosc.	G-263			100			100		100	100		100			100	
Jun. 2005	Acari	G-269															300
Jun. 2005	Pseudosc.	G-001		100													
Jun. 2005	Acari	G-100				100											
Jun. 2005	Acari	G-188														100	
Sep. 2005	Acari	G-002		800	800			300	100	200		200	200	100	300	1100	1500

Date	Order	Morpho	Coccoloba			Conocarpus			Ficus			Pisonia			Tabebuia		
		Type	L	O	H	L	O	H	L	O	H	L	O	H	L	O	H
Sep. 2005	Acari	G-003		400	700		100	500			1400			300		400	300
Sep. 2005	Acari	G-007		400	600		600	500	200	100	600		800	2600		300	300
Sep. 2005	Acari	G-031		900	400	100	600	1100	200	1200	1000	500	1100	1000	300		700
Sep. 2005	Acari	G-037		4400	2000	100	2100	1600	300	600	1300		1000	1600	200	900	800
Sep. 2005	Acari	G-078		1100	3100		400	1300	100	400	3900	100	600	2200	200	800	3900
Sep. 2005	Acari	G-105	100	1300	200		700		1400	700	500	800	1700	100	700	5500	300
Sep. 2005	Acari	G-147		100			200	300	100	300	700		400	1300	100	400	600
Sep. 2005	Acari	G-188		200			200		400	100	300		100	1200	700	300	300
Sep. 2005	Acari	G-207		500	400		200	400	100	300	200	100	100	500	800	900	2100
Sep. 2005	Acari	G-244		100	100		100	1300	100	200	500		300	2800		500	900
Sep. 2005	Pseudosc.	G-001								100	100		200				
Sep. 2005	Acari	G-004			200			600		100	200		100	700			
Sep. 2005	Isopoda	G-087			100	200		600		300							
Sep. 2005	Araneae	G-134	100			100	100					100					
Sep. 2005	Araneae	G-229					100			200	100				100	100	
Sep. 2005	Acari	G-262															1100
Sep. 2005	Pseudosc.	G-263		300	100								100	100			
Sep. 2005	Acari	G-288			200			200									100
Sep. 2005	Isopoda	G-010															
Sep. 2005	Psocoptera	G-102								100			100				
Sep. 2005	Diptera	G-123	100									100					

Date	Order	Morpho	<i>Coccoloba</i>			<i>Conocarpus</i>			<i>Ficus</i>			<i>Pisonia</i>			<i>Tabebuia</i>		
			L	O	H	L	O	H	L	O	H	L	O	H	L	O	H
Sep. 2005	Diptera	G-182	100			100			100								
Sep. 2005	Pseudosc.	G-220				100											
Sep. 2005	Blattodea	G-228							100								
Sep. 2005	Acari	G-269	100														100
Sep. 2005	Diptera	G-157														100	
Sep. 2005	Diptera	G-191	100														
Sep. 2005	Diptera	G-209	100														

IntechOpen

Author details

María F. Barberena-Arias^{1*} and Elvira Cuevas²

1 Universidad Ana G. Méndez, Gurabo, Puerto Rico

2 University of Puerto Rico, San Juan, Puerto Rico

*Address all correspondence to: mbarberena1@uagm.edu

IntechOpen

© 2020 The Author(s). Licensee IntechOpen. This chapter is distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/3.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. 

References

- [1] Eviner VT, Chapin III FS. FUNCTIONAL MATRIX: A Conceptual Framework for Predicting Multiple Plant Effects on Ecosystem Processes. *Annu. Rev. Ecol. Evol. Syst.* 2003;34: 455–485. DOI: 10.1146/annurev.ecolsys.34.011802.132342
- [2] Van Miegrot H, Hysell MT, Johnson AD. Soil Microclimate and Chemistry of Spruce–Fir Tree Islands in Northern Utah. *Soil Science Society of America.* 2000;64:1515–1525. DOI: 10.2136/sssaj2000.6441515x
- [3] Haworth K, McPherson GR. Effects of *Quercus emoryi* trees on precipitation distribution and microclimate in a semi-arid savanna. *Journal of Arid Environments.* 1995;31: 153–170. DOI: 10.1006/jare.1995.0057
- [4] Belsky AJ, Amundson RG, Duxbury JM, Riha SJ, Ali AR, Mwonga SM. The Effects of Trees on Their Physical, Chemical and Biological Environments in a Semi-Arid Savanna in Kenya. *Journal of Applied Ecology.* 1989;26(3):1005–1024. DOI: 10.2307/2403708
- [5] Saxena M. Microclimate modification: calculating the effect of trees on air temperature. In: *Proceedings of the solar conference; 21–25 April 2001; Washington DC*
- [6] Lugo AE, McCormick JF. Influence of environmental stressors upon energy flow in a natural terrestrial ecosystem. In: Barrett GW, Rosenberg R, editors. *Stress effects on natural ecosystems*: Wiley; 1981. P.79–102. DOI: 10.1017/S0376892900015411
- [7] Hogg EW, Leiffers VJ. The impact of *Calamagrostis canadensis* on soil thermal regimes after logging in northern Alberta. *Canadian Journal of Forest Research.* 1991;21:387–394. DOI: 10.1139/x91-048.
- [8] Bullock SH, Mooney HA, Medina E. Seasonally dry tropical forests. 1st ed. Cambridge University Press; 1995. 439 p. DOI: 10.1017/CBO9780511753398.001.
- [9] Cuevas E, Lugo AE. Dynamics of organic matter and nutrient return from litterfall in stands of ten tropical tree plantation species. *Forest Ecology and Management.* 1998;112(3):263–279. DOI: 10.1016/S0378-1127(98)00410-1
- [10] Steltzer H, Bowman WD. Original Articles: Differential Influence of Plant Species on Soil Nitrogen Transformations Within Moist Meadow Alpine Tundra. *Ecosystems.* 1998;1:464–474. DOI: 10.1007/s100219900042
- [11] Swift MJ, Heal OW, Anderson JM. *Decomposition in Terrestrial Ecosystems*, volumen 5. 1st ed. University of California Press; 1979. 384 p.
- [12] Hansen RA. Diversity in the decomposing landscape. In: Coleman D, Hendrix P, editors. *Invertebrates as webmasters in ecosystems*. CABI; 2000. P. 203–219. DOI: 10.1079/9780851993942.0000
- [13] Ettema CH, Wardle DA. Spatial soil ecology. *Trends in Ecology & Evolution.* 2002;17(4):177–183. DOI: 10.1016/S0169-5347(02)02496-5
- [14] Wardle DA. *Communities and Ecosystems: Linking the Aboveground and Belowground*. 1st edition. Princeton University Press; 2002; 387 p.
- [15] Wardle DA, Lavelle P. Linkages between soil biota, plant litter quality and decomposition. In: Cadish G, Giller KE, editors. *Driven by nature: plant litter quality and decomposition*. CAB International; 1997. P. 107–123.
- [16] 1999 Chen B, Wise DH. Bottom-up limitation of predaceous arthropods in a

detritus-based terrestrial food web. Ecology. 1999;80:761-772. DOI: 10.2307/177015.

[17] González G, Seastedt TR, Donato Z. Earthworms, arthropods and plant litter decomposition in aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*) forests in Colorado, USA. Pedobiologia. 2003;47:863-869. DOI: 10.1078/0031-4056-00272.

[18] González G, Zou X. Plant and litter influences on earthworm abundance and community structure in a tropical wet forest. Biotropica. 1999;31: 486-493. DOI: 10.1111/j.1744-7429.1999.tb00391.x

[19] Dilly O, Irmeler U. Succession in the food web during decomposition of leaf litter in a black alder (*Alnus glutinosa* (Gaertn.) L.) forest. Pedobiologia. 1998; 42:109-123.

[20] Irmeler U. Changes in the fauna and its contribution to mass loss and N release during leaf litter decomposition in two deciduous forests. Pedobiologia. 2000;44:105-118.

[21] Hasegawa M. Changes in Collembola and Cryptostigmata communities during the decomposition of pine needles. Pedobiologia. 1997;41: 225-241.

[22] Berg MP, Kniese JP, Bedaux JJM, Verhoef HA. Dynamics and stratification of functional groups of micro- and meso- arthropods in the organic layer of a Scots pine forest. Biology and fertility of soils 1998;26: 268-284. DOI: 10.1007/s003740050378

[23] Rivera-Rivera MJ, Acosta-Martínez V, Cuevas E. Tree Species and Precipitation Effect on the Soil Microbial Community Structure and Enzyme Activities in a Tropical Dry Forest Reserve. In: . Extremophilic Microbes and Metabolites - Diversity, Bioprospecting and Biotechnological

Applications. 2020. DOI: 10.5772/intechopen.82579

[24] Barberena-Arias MF, Cuevas E. Physicochemical Foliar Traits Predict Assemblages of Litter/ Humus Detritivore Arthropods. In: Tropical Forests - New Edition. Sudarshana P, Nageswara-Rao M, Soneji JR, editors. IntechOpen. 2018. DOI: 10.5772/intechopen.75076.

[25] Hooper DU, Chapin III FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs. 2005;75(1):3-35. DOI: 10.1890/04-0922

[26] Ebeling A, Rzanny M, Lange M, Eisenhauer N, Hertzog LR, Meyer ST, Weisser WW. Plant diversity induces shifts in the functional structure and diversity across trophic levels. Oikos. 2018;127(2):208-219. DOI: 10.1111/oik.04210

[27] Prather RM, Castillioni K, Welte EAR, Kaspari M, Souza L. Abiotic factors and plant biomass, not plant diversity, strongly shape grassland arthropods under drought conditions. Ecology. 2020;101(6):e03033. 10.1002/ecy.3033

[28] Welte E, Helzer C, Joern A. Impacts of plant diversity on arthropod communities and plant-herbivore network architecture. Ecosphere. 2017;8 (10):e01983. DOI: 10.1002/ecs2.1983

[29] De Deyn GB, Raaijmakers CE, Van Ruijven J, Berendse F, Van Der Putten WH. Plant species identity and diversity effects on different trophic levels of nematodes in the soil food web. Oikos. 2004;106(3):576-586. DOI: 10.1111/j.0030-1299.2004.13265.x

[30] Díaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A,

- Montserrat-Martí G, Grime JP, Zarrinkamar F, Asri Y, Band SR, Basconcelo S, Castro-Díez P, Funes G, Hamzehee B, Khoshnevi M, Pérez-Harguindeguy N, Pérez-Rontomé MC, Shirvany A, Vendramini F, Yazdani S, Abbas-Azimi R, Bogaard A, Boustani S, Charles M, Dehghan M, de Torres-Espuny L, Falczuk V, Guerrero-Campo J, Hynd A, Jones G, Kowsary E, Kazemi-Saeed F, Maestro-Martínez M, Romo-Díez A, Shaw S, Siavash B, Villar-Salvador P, Zak MR. The plant traits that drive ecosystems: evidence from three continents. *Journal of vegetation science*, 2004;15: 295-304. DOI: 10.1111/j.1654-1103.2004.tb02266.x
- [31] Rivera-Rivera MJ, Cuevas E. First Insights into the Resilience of the Soil Microbiome of a Tropical Dry Forest in Puerto Rico. In: Blumenberg M, Shaaban M, Elgaml A. *Microorganisms*. IntechOpen; 2020. DOI: 10.5772/intechopen.90395.
- [32] Murphy PG, Lugo AE. Dry forests of the subtropics: Guánica forest in context. *Acta científica*. 1990;4:15-24.
- [33] Lugo AE, Ramos O, Molina S, Scatena FN, Vélez-Rodríguez LL. A fifty-three year record of land use change in the Guánica forest Biosphere Reserve and its vicinity. IITF, USDA Forest Service, Rio Piedras, PR 13. 1996. p + maps + photos.
- [34] Dunphy BK, Murphy PG, Lugo AE. The tendency for trees to be multiple-stemmed in tropical and subtropical dry forests: Studies of Guanica forest, Puerto Rico. *Tropical Ecology*. 2000;41 (2): 161-167.
- [35] Medina E, Cuevas E. Propiedades fotosintéticas y eficiencia de uso de agua de plantas leñosas del bosque deciduo de Guánica: consideraciones generales y resultados preliminares. *Acta Científica*. 1990;4:25-36.
- [36] Lugo AE, González-Liboy JA, Cintrón B, Dugger K. Structure, productivity and transpiration of a subtropical dry forest in Puerto Rico. *Biotropica*. 1978;10:278-291. DOI: 10.2307/2387680
- [37] Cintrón B, Lugo AE. Litter fall in a subtropical dry forest: Guánica, Puerto Rico. *Acta científica*. 1990;4:37-50.
- [38] Farnsworth B. A guide to trails of Guánica. State forest and biosphere reserve. Departamento de recursos naturales de Puerto Rico. 1991.
- [39] Medina E, Cuevas E, Molina S, Lugo AE, Ramos O. Structural variability and species diversity of a dwarf Caribbean dry forest. *Caribbean Journal of Science*. 2010;46(2-3): 203-215.
- [40] NRCS National Water and Climate Center [Internet]. 2008. Available from <http://www.wcc.nrcs.usda.gov/scan/site.pl?sitenum=2067&state=pr>
- [41] RAWs Remote Automated Weather Stations - Western Regional Climate [Internet]. 2008. Available from <http://www.wrcc.dri.edu/wraws/prF.html>.
- [42] Barberena-Arias MF, González G, Cuevas E. Quantifying Variation of Soil Arthropods Using Different Sampling Protocols: Is Diversity Affected? In: Sudarshana P, Nageswara-Rao M, Soneji JR, editors. *Tropical Forests*. IntechOpen; 2012. DOI: 10.5772/30386.
- [43] McCune B, Grace JB. *Analysis of Ecological Communities*. 1st ed. Gleneden Beach: MjM Software Design; 2002. 300 p. ISBN: 0972129006
- [44] Legendre P, Legendre L. *Numerical Ecology—Developments in Environmental Modeling* 20. 1st ed. New York: Elsevier; 1998. ISBN: 0444892508
- [45] Peck J. *Multivariate Analysis for Community Ecologists*. 1st ed. Gleneden

Beach: MjM Software Design; 2010. 162 p. ISBN: 9780972129022

[46] Murphy PG, Lugo AE. Ecology of tropical dry forest. Annual Review of Ecology and Systematics. 1986;17:67-88. DOI: 10.1146/annurev.es.17.110186.000435

[47] Pressland AJ. Rainfall partitioning by an arid woodland (*Acacia aneura* F. Muell.) in south-western Queensland. Australian Journal of Botany. 1973;21: 235-245. DOI: 10.1071/BT9730235

[48] Clauser C, Huenges E. Thermal conductivity of rocks and minerals. In: Ahrens TJ, editor. Rock Physics and Phase Relations, A Handbook of Physical Constants, AGU Reference Shelf 3. 1995. P. 105-126. DOI: 10.1029/RF003p0105

[49] Barberena-Arias MF. Single tree species effects on temperature, nutrients and arthropod diversity in litter and humus in the Guánica dry forest [thesis]. San Juan PR, University of Puerto Rico. 2008.

[50] Ecosystem feedbacks on climate at the landscape scale. Philosophical Transactions of the Royal Society London B. 1998;353:5-18.

[51] Malmgren BA, Winter A. Climate zonation in Puerto Rico based on principal components analysis and an artificial neural network. Journal of climate. 1999;12:977-985. DOI: 10.1175/1520-0442(1999)012<0977:CZIPRB>2.0.CO;2

[52] Rosenberg NJ. Microclimate: the biological environment. Wiley Interscience; 1974. 528 p.

[53] Vandenbeldt RJ, Williams JH. The effect of soil surface temperature on the growth of millet in relation to the effect of *Faidherbia albida* trees. Agricultural and forest meteorology. 1992;60(1-2): 93-100. DOI: 10.1016/0168-1923(92)90076-G

[54] Axelrod F. A systematic vademecum to the vascular plants of Puerto Rico, Herbarium Manager UPRRP. 2007.

[55] Loigier AH. La flora de la Española, Universidad Central del Este, San Pedro de Macoris, R.D. Vols. I – VIII, Serie Científica 29. 1996

[56] Prinzing AP, Lentzsch P, Voigt F, Woas S. Habitat stratification stratifies a local population: Ecomorphological evidence from a bisexual, mobile invertebrate (*Carabodes labyrinthicus*; Acari). Annales Zoologici Fennici. 2004; 41(2):399-412. ISSN: 0003-455X

[57] Kardol P, Cornips NJ, van Kempen MM, Bakú-Schotman JMT, van der Putten WH. Microbe-mediated plant-soil feedback causes historical contingency effects in plant community assembly. Ecological Monographs. 2007; 77(2):147-162. DOI: 10.1890/06-0502

[58] Bezemer TM, Lawson CS, Hedlund K, Edwards AR, Brooks AJ, Igual JM, Mortimer SR, van der Putten WH. Plant species and functional group effects on abiotic and microbial soil properties and plant-soil feedback responses in two grasslands. Journal of Ecology. 2006;94:893-904. DOI: 10.1111/j.1365-2745.2006.01158.x

[59] Herrera F. Dinámica especial y temporal de la fauna del suelo en un mosaico de vegetación de la cordillera de la costa [tesis]. Caracas: IVIC Venezuela. 1997.