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Temporal Dynamics of Arthropods on Six Tree Species in Dry Woodlands on the Caribbean Island of Puerto Rico

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ABSTRACT. The seasonal dynamics of foliage arthropod populations are poorly studied in tropical dry forests despite the importance of these studies for understanding arthropod population responses to environmental change. We monitored the abundance, temporal distributions, and body size of arthropods in five naturalized alien and one native tree species to characterize arthropod seasonality in dry novel *Prosopis–Leucaena* woodlands in Puerto Rico. A branch clipping method was used monthly to sample foliage arthropod abundance over 39 mo. Seasonal patterns of rainfall and abundance within various arthropod taxa were highly variable from year to year. Abundance for most taxa did not show significant seasonality over the 3 yr, although most taxa had abundance peaks each year. However, Homoptera displayed high seasonality with significant temporal aggregations in each year. Formicidae, Orthoptera, and Coleoptera showed high variation in abundance between wet and dry periods, whereas Hemiptera were consistently more abundant in the wet period. Seasonal differences in mean abundance were found only in a few taxa on *Tamarindus indica* L., *Bucida buceras* L., *Pithecellobium dulce*, and (Roxburgh) Benth. Mean arthropod abundance varied among tree species, with highest numbers on *Prosopis juliflora*, (Swartz) De Candolle, *Pi. dulce*, *Leucaena leucocephala*, and (Lamarck) de Wit. Abundance of Araneae, Orthoptera, Coleoptera, Lepidoptera larvae, and all arthropods showed weak relationships with one or more climatic variables (rainfall, maximum temperature, or relative humidity). Body size of arthropods was usually largest during the dry periods. Overall, total foliage arthropod abundance showed no consistent seasonality among years, which may become a more common trend in dry forests and woodlands in the Caribbean if seasonality of rainfall becomes less predictable.

Key Words: alien tree species, body size, dry woodland, rainfall effect, temporal dynamics

Studies documenting temporal population dynamics of arthropod communities are important because they provide a better understanding of underlying ecological processes operating within tropical dry forests and woodlands. Understanding the nature of the faunal dynamics becomes especially important as ecosystems change through ecological homogenization, increased globalization of commerce, and climate change. Furthermore, understanding patterns of temporal arthropod dynamics is important because arthropods play a key role in tropical forests mediating many ecological processes (Wall and Moore 1999). Seasonal variation in arthropod abundance is a common phenomenon in tropical ecosystems with distinct wet and dry seasons (Pinheiro et al. 2002). This arthropod seasonality may be explained by the interaction of multiple abiotic and biotic factors (Didham and Springate 2003). Abiotic environmental factors such as rainfall, temperature, and humidity can have a strong influence in temporal fluctuations of arthropod populations throughout the year (Grimbacher and Stork 2009, Vasconcellos et al. 2010, Silva et al. 2011). However, rainfall appears to be the most important climatic factor influencing seasonality of arthropod abundance in tropical areas (Wolda 1988). Arthropod population dynamics are also influenced by biotic factors such as food availability, host tree phenology, predation, parasitism, and interspecific resource competition (Didham and Springate 2003, Richards and Coley 2007). For herbivorous species, however, the phenology of host plants, particularly the production of new leaves during the wet season, exerts a stronger influence on population dynamics (Richards and Coley 2007).

Arthropod body size is expected to vary seasonally with fluctuations in some of the abiotic and biotic factors that contribute to seasonality in arthropod abundance (Chown and Gaston 2010). Body size appears to have a strong influence on structure of animal assemblages

(Blackburn and Gaston 1994), and a number of factors may influence body size of a species, including: 1) the quantity and quality of resources used by a species (Novotny and Basset 1999), 2) physiology and microclimate (Schoener and Janzen 1968, Chown and Klok 2003), and 3) predation (Berger et al. 2006). Thus, a variety of factors can potentially contribute to seasonal variation in arthropod size, and therefore, documentation of temporal dynamics of arthropod size may provide insights into some of the underlying factors. In addition, documenting changes in the body size distributions of different taxa may provide insights into determinants of seasonal abundance patterns in arthropods (Chown and Gaston 2010). Moreover, understanding how arthropod size varies seasonally can provide important information on variation in prey availability or biomass for studies of insectivore populations and food web dynamics (Reagan and Waide 1996).

Studies documenting the interannual population dynamics of arthropod assemblages on specific tree species are particularly important for evaluating responses of arthropods to environmental change (e.g., Tylianakis et al. 2008). However, little is known about seasonality of arthropod abundance on specific tree species (Wagner 2001, Schowalter and Ganio 2003), especially for naturalized alien tree species in the tropics or subtropics. Despite the fact that some alien tree species are now dominant floristic elements in new or novel Neotropical forests or woodlands (Lugo 2004, Lugo and Helmer 2004), there are few studies of arthropod seasonality on alien trees, and most are restricted to trees grown in seminatural conditions, such as plantations (Banerjee 1981, Nyeko et al. 2002). Some of these alien-dominated novel woodlands have low tree species richness and occur in overgrown or abandoned pastures on seasonally dry tropical or subtropical sites in which various N-fixing leguminous trees predominate. For example, these

legume-dominated woodlands are common in the seasonally dry areas of Caribbean Islands (Beard 1949, Loveless and Asprey 1957, Kennaway and Helmer 2007, Helmer et al. 2008), where many of the dominant tree species include naturalized alien species in the genera *Acacia*, *Haematoxylum*, *Leucaena*, *Pithecellobium*, and *Prosopis*. On Puerto Rico and its satellite islands, the alien *Prosopis juliflora* (Swartz) De Candolle and *Leucaena leucocephala* (Lamarck) de Wit often predominate in open or dense drought-deciduous woodlands covering >18,882 ha (Kennaway and Helmer 2007). Our study takes advantage of the low tree species richness of these novel *Prosopis*–*Leucaena* woodlands on Puerto Rico to study variation in arthropod seasonality in six of the dominant tree species in this community.

Alien tree species in novel plant communities such as the *Prosopis*–*Leucaena* woodlands on Puerto Rico can play an important role in facilitating the establishment of other alien tree species as well as native and endemic species on degraded lands (Lugo 2004, Lugo et al. 2012). The successful establishment of some alien plant species has been attributed to lower foliage arthropod abundance than found on foliage of native species as predicted by the enemy release hypothesis. Enemy release is believed to occur when a plant species is moved beyond its native geographic range and leaves behind its specialized pests, thereby freeing the alien of its homeland pests and providing a competitive advantage over native species in human-disturbed habitats (Crawley 1997, Maron and Vilà 2001, Keane and Crawley 2002). Although support for the hypothesis is accumulating (Liu and Stiling 2006), some recent findings conflict with predictions (Fork 2010, Hartley et al. 2010). In addition, the effect of enemy release may be weakened for alien tree species with foliage, which is highly nutritious and palatable for arthropods as found in the novel *Prosopis*–*Leucaena* woodlands in Puerto Rico (Beltrán 2012, Beltrán and Wunderle 2013). In this latter study, the highest foliage arthropod abundance was found on the alien tree species with high nutrition content (i.e., high N) and palatability (i.e., low hemicellulose and lignin). Despite this information on foliage arthropod abundance in relation to certain foliage chemical traits of some common tree species in the *Prosopis*–*Leucaena* woodlands, little is known of the seasonal patterns of abundance of foliage arthropods or the factors contributing to patterns of abundance in these novel woodlands.

Studies of the patterns or seasonality of arthropod abundance and size on trees in the novel *Prosopis*–*Leucaena* woodlands may provide insights to some of the ecological processes mediated by arthropods in these newly evolving communities. These studies are also relevant for comparisons with natural forests and provide baseline for future comparisons given continuing changes in community composition as alien species invade and climate changes. Therefore, given the importance of documenting the temporal patterns of arthropod abundance and size in novel *Prosopis*–*Leucaena* woodlands, we sampled foliage arthropods monthly on the six most abundant tree species (five alien legumes and one native Combretaceae) in these woodlands for 39 mo in southwestern Puerto Rico. This approach facilitated addressing four interrelated questions: 1) Do the common arthropod taxa display high seasonality in abundance, with significant population peaks at specific times over a 3-yr period? We expected seasonal peaks in arthropod abundance given previous studies in seasonally dry forests (Tanaka and Tanaka 1982, Amorim et al. 2009, De Castro et al. 2012). 2) Which climatic variables (rainfall, maximum temperature, and relative humidity) are associated with the seasonal abundance of various arthropod taxa? We expected that populations of some arthropod taxa would vary with rainfall, temperature, and/or relative humidity given results from previous studies (Pinheiro et al. 2002, Vasconcellos et al. 2010, Silva et al. 2011). 3) Does overall arthropod abundance vary among different tree species and do various taxa show strong consistent seasonal variations in abundance on the different tree species? Given previous studies indicating that various arthropod taxa show species-specific preferences for certain plants (Basset 1996, Johnson 2000a, Tovar-Sánchez et al. 2003), we expected to find taxa-specific differences in abundance on the

different tree species. 4) Does arthropod body size change seasonally in a consistent pattern and are size changes restricted to different arthropod taxa? We expected that some arthropod taxa would show seasonal variation in size given previous studies documenting such changes (Chown and Klok 2003, Chown and Gaston 2010, Jahn et al. 2010).

Materials and Methods

Study Areas. This study was conducted in the Cabo Rojo National Wildlife Refuge (17° 59' N, 67° 10' W) and 8 km away at La Tinaja tract of the Cartagena Lagoon National Wildlife Refuge, in southwestern Puerto Rico. The refuges are located in the subtropical dry forest life zone and include secondary dry woodlands (Weaver and Schwagerl 2009).

Field work in the Cabo Rojo study site was done in the northeastern corner of the refuge (238 ha; <5–35 m elevation). Climate data for this site were gathered daily by U.S. Fish and Wildlife Service at the wildlife refuge headquarters (within 150 m of study site) and were used in all our climate analyses (see Data Analyses). The mean annual rainfall at this site prior to our study was 930 mm, with high year-to-year variation (Weaver and Schwagerl 2009). During 1991–2005, March and October were the months with the lowest and highest average rainfall (37.6 and 128.4 mm, respectively; Fig. 1a). Mean annual air temperature during this study was 26.4°C, ranging from 24.7 in January to 27.9°C in July. Vegetation is dominated mostly by nonnative leguminous trees and shows an open canopy (mean cover 34.9%; Baltz 2000). Dominant tree species include *P. juliflora*, *Pithecellobium dulce*, (Roxburgh) Benth, *L. leucocephala*, *Albizia lebbbeck*, *Tamarindus indica* L., *Parkinsonia aculeata* L., and *Bucida buceras* L. Benth (Staicer 1991).

Field work in the Tinaja tract was conducted along the north border of the lower portion of the tract. This site encompasses 106 ha with elevations between 20 and 290 m. During 1991–2005, the average annual rainfall near here was 1,058 mm (Weaver and Schwagerl 2009), based on a climate station located approximately 2 km to the northeast of the study site (Fig. 1b). Mean annual air temperature near the study area for 1971–2000 was 25.3°C, ranging from 23.2 in January to 26.8°C in July (Weaver and Schwagerl 2009). Vegetation is heterogeneous and similar in structure and composition to that found within the Cabo Rojo refuge. Dominant tree species include *Pi. dulce*, *L. leucocephala*, *A. lebbbeck*, *Hymenaea coubaril*, and *P. juliflora* (Weaver and China 2003).

Selection of Tree Species. To select the most common tree species for arthropod sampling we sampled trees on the study sites in December 2009 using the point-center quarter method (Cottam and Curtis 1956). For this method, the area around the randomly chosen sampling point was divided into four 90° quarters. In each of the four quarters, the distance was measured from the sampling point to the closest tree. The diameter at breast height (DBH) of the selected tree was measured and converted to basal area and was recorded along with the tree's species identity. In this study, 13 transects each 100 m in length, separated by 50 m and distributed along two survey trails, were randomly selected to estimate tree species composition. In each transect, the DBH was recorded for individuals with >2.5 cm.

On the basis of measurements of trees along the transects, we calculated relative dominance ([basal area per species/total basal area of all tree species] × 100), relative frequency ([individuals per tree species/total of individual samples per species] × 100), and relative density ([number of individuals per tree species sampled/mean basal area of all individuals sampled of all tree species] × 100). These relative measures were used in calculating an Importance Value Index (IVI) for each sampled tree species as devised by Holmes and Robinson (1981). The IVI provides a relative index of the proportional representation of the foliage among tree species in the woodlands and was calculated as: IVI = relative dominance + relative density + relative frequency. We selected the six tree species with the highest IVIs scores for this study (Table 1); additional tree species found on the transects and their IVIs are listed in Beltrán and Wunderle (2013).

Arthropod Sampling. From May 2007 to July 2010, the first author (W.B.) sampled foliage arthropods monthly in the Cabo Rojo refuge to evaluate abundance on the six dominant tree species (Table 1). W.B. also surveyed arthropods monthly at La Tinaja tract from August 2009

to July 2010, sampling individuals of the four dominant tree species (*P. juliflora*, *Pi. dulce*, *L. leucocephala*, and *A. lebeck*). In both study sites, arthropods were sampled once each month during sunny days from 0700 to 1130 hours. At each arthropod sampling point determined haphazardly, an accessible branch was collected from each of five individuals of each tree species. Trees were selected haphazardly for sampling with the constraint that the foliage sample had to be sufficiently small to allow enclosure within the sampling bag (see below), with minimal disturbance. An attempt was made to sample different individuals of the same species each month; however, ~10% of the trees were sampled more than once. In total, 30 and 20 branch-clip samples per month were collected for the Cabo Rojo refuge and La Tinaja tract, respectively.

In each study site, arthropods were sampled using a branch-clipping, technique devised by Schowalter et al. (1981) as modified by Johnson (2000b). This technique is well suited to describe arthropod communities on tree foliage (Schowalter 1994), although “active” or quick flying insect taxa such as large Diptera, Hymenoptera, and Odonata may be poorly sampled (Johnson 2000b). The technique involved use of a cloth bag (45 by 90 cm) spread inside an insect sweep net, which was placed around the end of a branch in the subcanopy (up to 6 m with aid of extension poles). Foliage at the end of a branch was carefully surrounded by the open end of the bag and quickly enclosed by pulling a drawstring around the bag opening, enclosing the branch and a sample of foliage. Next, the enclosed branch was cut using a telescoping tree pruner. Once cut free, the closed sample bag with foliage sample was lowered to ground level where the bag and its enclosed foliage sample were weighed to the nearest 2 g with a Pesola spring scale. The weight of the enclosed foliage and associated branches and twigs was obtained by subtracting the bag weight from the total weight. After the bag with enclosed foliage sample was weighed, the bag was shaken to dislodge arthropods prior to opening the bag. Once opened, the bag and the foliage contents were carefully inspected and all arthropods were captured with forceps or aspirator.

All captured arthropods from each branch clip sample were preserved in 70% ethanol and sorted in the laboratory using a dissecting scope of 0.8–3.5× magnification. Arthropods were counted and identified to order (or family for ants, i.e., Formicidae) and their body length measured to the nearest 1 mm with a ruler.

Data Analyses. Arthropod abundance (number of individuals per gram of branch clip) was transformed ($\ln Y + 0.001$) to meet assumptions of normality (Sokal and Rohlf 1995). All data were tested for normality by inspecting a normal probability plot, and homogeneity of variances were verified with a Levene *F* test (Sokal and Rohlf 1995). A two-way analysis of variance was performed to determine whether the total monthly arthropod abundance varied between tree species and year. Tukey’s Kramer post hoc multiple comparison tests were used to determine the significance of results (Sokal and Rohlf 1995). Several *t*-tests were performed to determine if the total monthly abundance of arthropods varied between localities and if the average length of predominant taxa differed between periods. In all analyses, a probability of type I error $P < 0.05$ was considered significant. Bonferroni sequential

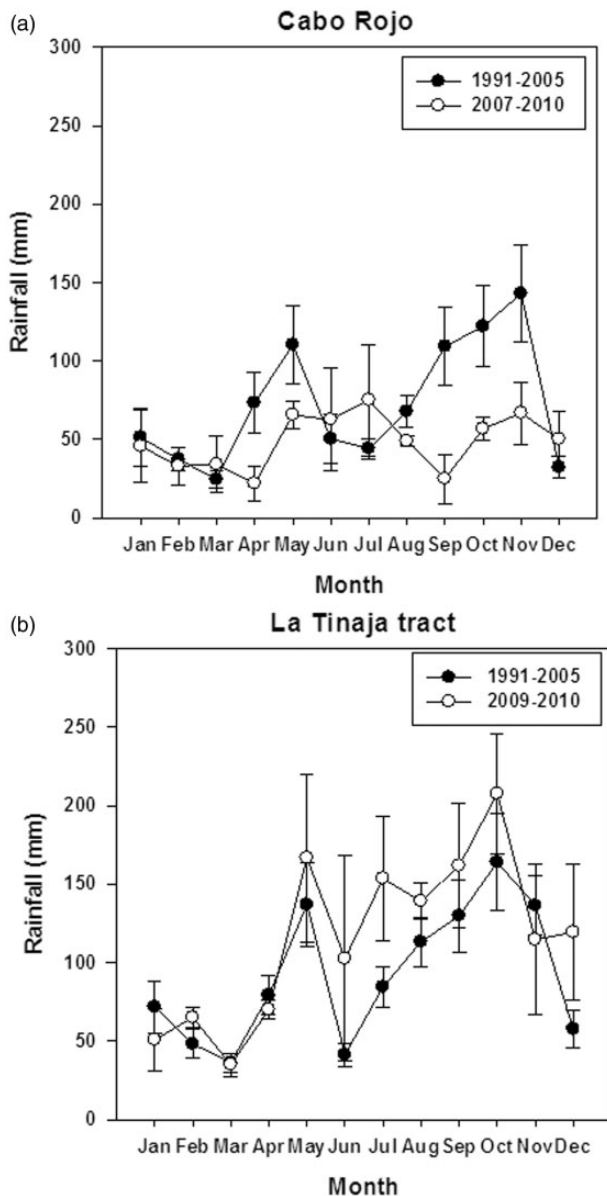


Fig. 1. (a) Monthly rainfall (mean \pm SE) during 1991–2005 and 2007–2010 periods at the Cabo Rojo National Wildlife Refuge. (b) Monthly rainfall during 1991–2005 and 2009–2010 periods at La Tinaja tract of Cartagena Lagoon Wildlife Refuge in southwestern Puerto Rico. Rainfall for 1991–2005 period is from Weaver and Schwagerl (2009).

Table 1. Abundance and size characteristics of the six tree species sampled for foliage arthropods in novel *Prosopis*–*Leucaena* woodlands in southwestern Puerto Rico

Tree species	IVI	Relative dominance	Relative density	Relative frequency	Mean canopy height (m)	Mean DBH (cm)	<i>N</i> along transect
<i>P. juliflora</i>	25.8	45.2	5.8	16.0	12.9	33.5	59
<i>L. leucocephala</i>	20.8	6.8	16.4	45.5	6.0	7.9	151
<i>B. buceras</i>	9.2	13.5	1.2	3.3	12.4	19.6	12
<i>T. indica</i>	7.5	13.6	0.9	2.4	13.6	41.8	9
<i>Pi. dulce</i>	7.3	5.7	2.5	6.9	13.6	18.4	22
<i>A. lebeck</i>	6.7	2.2	1.5	4.2	6.6	13.8	14

N refers to the number of individual trees sampled along randomly placed transects. IVI was calculated based on relative dominance, relative density, and relative frequency of the tree species as described under Materials and Methods.

adjustment (Rice 1989) was applied to individual *P* values for multiple *t*-tests to prevent inflation of experiment wise error rate.

Forward stepwise linear regressions, with alpha to enter and to remove both set at 0.10, were used to examine the relationship between abundance (dependent variable) for the predominant taxa and climate variables (predictor variables) collected at the Cabo Rojo refuge headquarters. Three variables were selected as possible predictors: average maximum temperature (°C), average relative humidity (%), and average monthly rainfall (mm) from the preceding weeks, run separately for 2, 3, and 4 wk.

A circular analysis (Zar 1999) was conducted to verify the existence of seasonality in the most abundant taxa. The monthly abundance of each taxa were converted into polar coordinates, and these were used to calculate a mean vector, which is a measure of concentration (*r*), and whose value varies from 0 (i.e., individuals dispersed evenly across the year) to 1 (i.e., all individuals of a taxa were sampled in a single month). The circular standard deviation (*S*_c) was also calculated. The value *r* quantifies the degree of temporal variation in abundance of each taxa during each year of the study but does not provide information on the type of seasonality with respect to rainfall. To determine this information, for predominant taxa we calculated the proportion of individuals recorded during the six wettest months of the year and used this as an index of each taxa's wet period preference (WPP after Hamer et al. 2005). Because rainfall showed year-to-year variation, the six wettest months of each year were selected on the basis of rainfall data collected during the study. The wettest months or driest months in a year were not necessarily contiguous, and therefore we designate the six wettest months as the wet period and the six driest months as the dry period. Rayleigh tests (Zar 1999) were used to determine whether the temporal distributions in abundance of each taxa in each year were random or clustered. Most statistical tests were conducted using STATISTICA (Statsoft 2000), but multiple regressions were conducted with SYSTAT v. 10.2 (SYSTAT 2002) and two-factor analysis of variances were run with SPSS (1990).

Results

Tree Species Monitored. On the basis of the rankings of their IVI scores (Table 1), we selected the top six tree species for study, including five naturalized alien leguminous species: *L. leucocephala* (L.) de Wit; *P. juliflora*; *Pi. dulce*; *A. lebbeck*, and *T. indica* and the native *Bucida bucidias* in the Combretaceae. A molecular phylogeny by Sulaiman et al. (2003) placed *L. leucocephala* and *P. juliflora* in the tribe Mimoseae in the family Mimosoideae and *T. indica* in the tribe Detarieae in the Caesalpinioideae. Both *A. lebbeck* and *Pi. dulce* were not included in the phylogeny but are traditionally placed in the Fabaceae. For simplicity, we henceforth refer only to the genus name for each species.

The six tree species showed considerable variation in the different measures of abundance and size (Table 1). For example, *Prosopis* had the highest IVI score due to high relative dominance (second highest DBH) and moderately high relative frequency. In contrast, *Leucaena* had the second highest IVI score and the lowest mean canopy height and DBH but the highest relative frequency. The remaining four tree species had IVI scores that were less than half the values of those of *Prosopis* and *Leucaena*. The native *Bucida* had moderate stature and DBH but had relatively low density on the study sites. The *Tamarindus* had the highest mean DBH and was one of the tallest trees, but it was relatively rare and as a result had the lowest values for relative density and frequency. The average *Pithecellobium* canopy was as tall as the high canopy of *Tamarindus* but had a much smaller DBH and was not as rare. The *Albizia* was of relatively low stature (second lowest canopy height), and small DBH (second lowest) and combined with moderately low abundance had the lowest IVI score.

Arthropod Samples. In total, 26,459 arthropods belonging to 17 taxa (i.e., 16 orders, including Hymenoptera exclusive of ants, and ants separately) were captured in 1,410 foliage clip samples, which totaled

608.4 kg collected over 39 mo from the 6 tree species. The most abundant taxa included Coleoptera (33.9%), Araneae (22.7%), Formicidae (20.7%), Orthoptera (9.7%), Lepidoptera larvae (5.0%), Homoptera (4.8%), and Hemiptera (1.0%). Together, these taxa represented 97.8% of all individuals collected. The remaining 2.2% of individuals were from the orders Isoptera, Neuroptera, Blattodea, Hymenoptera (nonformicid), Mantodea, Diptera, Pseudoscorpionida, Collembola, Psocoptera, Phasmida, and Thysanoptera, which were pooled in the category "other arthropods" for analyses. Neither overall arthropod abundance nor abundance of individual taxa differed between localities (*t* test, *P* > 0.05), so arthropod abundance samples were pooled for analyses.

Annual abundance patterns within specific taxa were highly variable among the 3 yr and were rarely consistent in terms of the month of peak abundance (Figs. 2 and 3). For example, Orthoptera displayed an erratic distribution over the first 2 yr but showed abundance peaks in different months; however, in the third year, it showed well-defined seasonality with a population peak in May (Fig. 2). In contrast, Homoptera displayed a distinct annual peak in abundance each year, although timing of the peak varied among June, October, and May for the three respective years (Fig. 2). The remaining taxa showed low seasonality, with irregular or inconsistent abundance distributions throughout the 3 yr (Figs. 2 and 3).

Annual abundance patterns (i.e., random vs. clustered) for most taxa were not significantly different from random, and most taxa had abundance patterns that remained consistent in each of the 3 yr (Table 2). Only Homoptera, consistently showed significant clustered abundance patterns in each of the years (see *r* values in Table 2; Rayleigh test *Z* = 3.68, *Z* = 3.55, *Z* = 6.95; *P* < 0.05 for the 3 yr, respectively). Clustering was suggested in Lepidoptera annual abundance only in the first 2 yr (see *r* values in Table 1), but the concentration values were not significant in either year (Rayleigh test *Z* = 2.31; *Z* = 2.59; *P* < 0.10 but > 0.05). Similarly, Hemiptera in the third year also showed a suggestive pattern of clustering (*r* = 0.468), but it was not significant (*Z* = 2.63, *P* < 0.10 but > 0.05). In contrast, Orthoptera in the third year showed a significant clustered abundance pattern (*Z* = 6.46, *P* < 0.05; Fig. 2; Table 2). The remaining taxa were not significantly seasonal (clumped), showing patterns consistent with random distributions over each of the 3 yr (range *r* = 0.059–0.343, Rayleigh tests *P* > 0.05; Fig. 3; Table 2).

Arthropod Abundance and Climate Variables. Although annual rainfall at Cabo Rojo was highly seasonal in all 3 yr, the timing of occurrence of wet periods varied among years (Fig. 2), as did the total amount of rainfall per year (495.1, 713.2, and 826.3 mm for the three respective years). Despite marked rainfall seasonality in each year, some taxa showed substantial yearly abundance variation relative to wet and dry periods among the 3 yr (Figs. 2 and 3; Table 2). For instance, Formicidae and Orthoptera were least consistent among years in their abundance in wet and dry periods as quantified with the WPP (Table 2). Ants were more abundant during the drier months (dry period November and March–July) than the wetter months (wet period August–October and December–February) of the first year (WPP = 0.29). Likewise, during the second year, ants showed slightly higher abundance during the dry period (November–December and March–June) than the wet period (August–October, January, February, and July; WPP = 0.44). In contrast, ants in the third year had slightly higher abundance during the wet period (August, September, January, February, April, and May; WPP = 0.62).

The mean abundances of Araneae, Orthoptera, Coleoptera, Lepidoptera larvae, and total arthropods varied with one or several climatic variables measured prior to sampling (rainfall, maximum temperature, and relative humidity) over different durations (2, 3, and 4 wk) as demonstrated in weak significant relationships by forward stepwise multiple regressions (Table 3). For example, a positive relationship was found between monthly Araneae abundance, and the combined average rainfall and maximum temperature for the 4 wk preceding the sampling

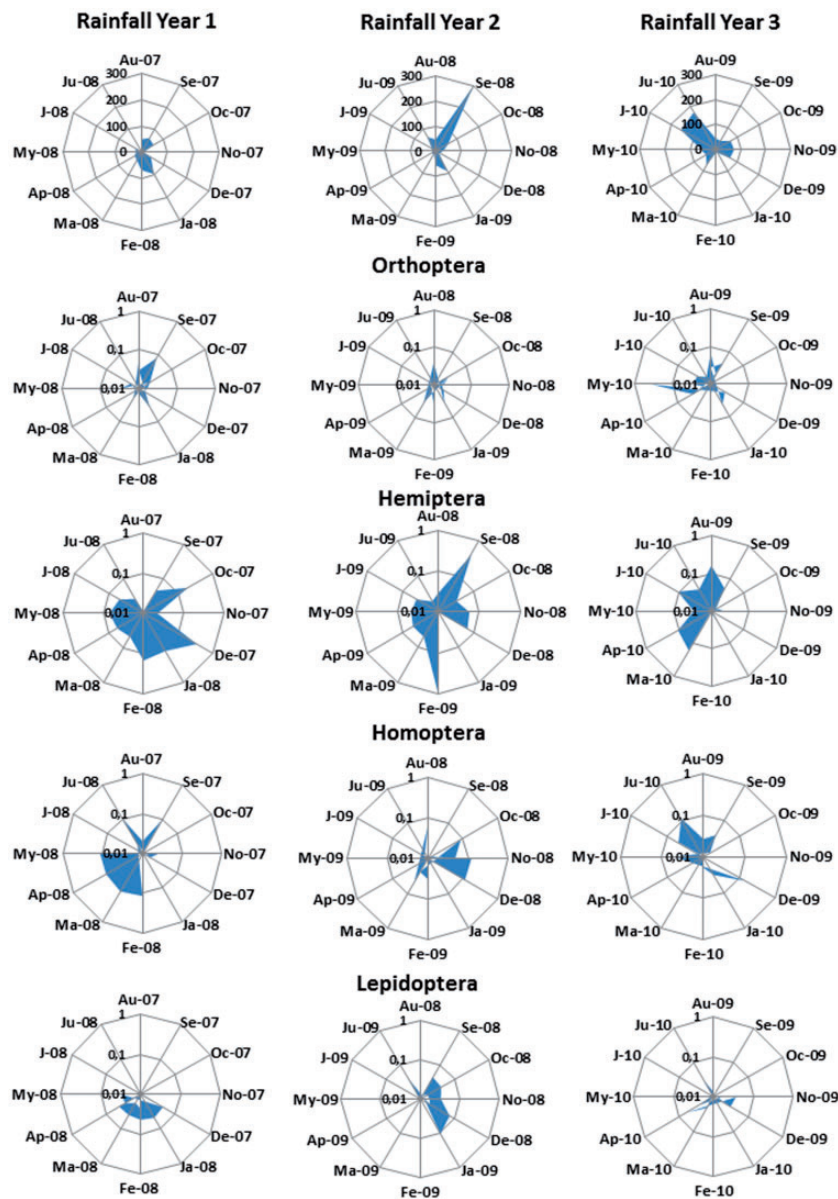


Fig. 2. Circular graphs of total monthly rainfall (mm per month) and abundance (log individuals per gram branch clip) of Orthoptera, Hemiptera, Homoptera, and Lepidoptera larvae collected by branch clipping from six tree species monthly for year 1 (August 2007–July 2008), year 2 (August 2008–July 2009), and year 3 (August 2009–July 2010), in a novel *Prosopis–Leucaena* woodlands in southwestern Puerto Rico. See text for names of the six tree species sampled and the branch clipping sampling method.

date. Maximum temperature, either in prior 2, 3, or 4 wk, had a significant positive effect on Orthoptera. For Coleoptera, both rainfall (positive) and maximum temperature (negative) together from the prior 4 wk had a significant effect. Lepidoptera larvae abundance showed a relationship with combined average maximum temperature (negative) and monthly average relative humidity (positive) for the 4 preceding weeks.

Arthropod Abundance Variation. The mean overall (i.e., all) arthropod abundance varied significantly among years ($F_{1, 3} = 8.16$, $P = 0.031$; Fig. 3) and among tree species ($F_{1, 5} = 12.94$; $P < 0.001$; Fig. 4), and there was no significant year by tree species interaction ($F_{1, 15} = 1.12$, $P = 0.248$). Mean total arthropod abundance in *Albizia*, *Tamarindus*, and *Bucida* was significantly (Tukey's test HSD, $P < 0.05$) less than in *Prosopis*, *Pithecellobium*, and *Leucaena*; however, no significant differences were found between *Albizia* and *Tamarindus* (Tukey's test HSD, $P > 0.05$).

Seasonal variation in wet and dry periods' abundance was found in only a few arthropod taxa in *Tamarindus*, *Bucida*, and *Pithecellobium* but not in *Albizia*, *Prosopis*, and *Leucaena* (Fig. 5). For example, significantly higher dry than wet period abundance was found in Lepidoptera larvae in *Tamarindus* (paired t -test = -3.45 , $df = 16$, $P < 0.001$) and Orthoptera in *Bucida* (paired t -test = 3.27 , $df = 16$, $P = 0.004$). In contrast, significantly higher abundance in wet than dry period was found for Coleoptera and Hemiptera in *Pithecellobium* (paired t -test, Coleoptera, $t = -2.45$, $df = 22$, $P = 0.022$; Hemiptera, $t = 0.045$, $df = 22$, $P = 0.045$).

Arthropod Size Variation. When body length of all arthropods was categorized into three size ranges (1–5, 6–10, and > 10 mm), circular analyses by month indicated that the abundance of arthropods in each of these size classes had low seasonality scores, with random distributions in all three sizes classes over the 3-yr period (year 1, range $r = 0.106$ – 0.295 ; year 2, range $r = 0.09$ – 0.223 , and year 3, range

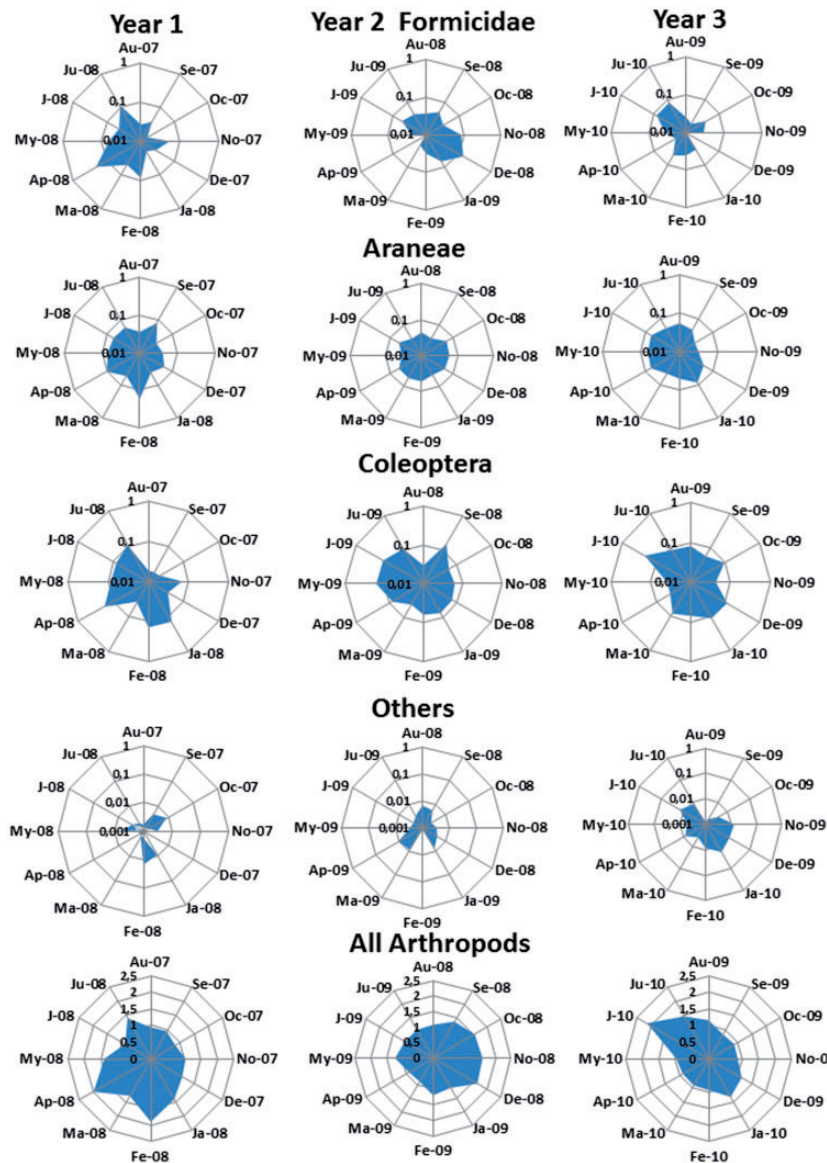


Fig. 3. Circular graphs of total monthly rainfall (mm per month) and abundance (log individuals per gram branch clip) of Araneae, Formicidae, Coleoptera, others taxa, and all arthropods (individuals per gram branch clip) collected per branch clipping from six tree species monthly for year 1 (August 2007–July 2008), year 2 (August 2008–July 2009), and year 3 (August 2009–July 2010), in a novel *Prosopis–Leucaena* woodlands in southwestern Puerto Rico. See text for names of the six tree species sampled and the branch clipping sampling method.

$r = 0.067–0.216$; Rayleigh tests $P > 0.05$). However, the average length of Formicidae, Araneae, Coleoptera, and Lepidoptera was each significantly greater in wet than dry season (paired t -tests, $P < 0.05$; Table 4). In contrast, Homoptera showed a higher average length in dry than wet season (paired t -test = -2.12 , $df = 67$, $P = 0.037$). The remaining taxa showed no significant differences in length between wet and dry periods (Table 4).

Discussion

The weak seasonal patterns of abundance exhibited by almost all arthropod taxa in this study likely resulted from the low predictability in rainfall patterns recorded over the 3 yr. Abundance of most taxa did not exhibit predictable annual patterns but instead showed annual abundance peaks in few taxa, which did not coincide among years. However, we cannot eliminate the possibility that the absence of predictable seasonality of arthropod abundance may have occurred because arthropods were grouped according to taxonomic orders (or

family), and analyses of seasonality performed at high taxonomic levels can sometimes mask differences in seasonal patterns of arthropod abundance within lower taxonomic levels or ecological groups (Grimbacher and Stork 2009). Nevertheless, the lack of consistent seasonal patterns in rainfall and arthropod abundance in this study is similar to those reported in other tropical or subtropical studies (Anu et al. 2009, Grimbacher and Stork 2009, Kishimoto-Yamada et al. 2010). In contrast, areas with well-defined wet and dry seasons show distinct arthropod seasonality (Wolda 1988), especially in semiarid and dry habitats, where arthropod abundance usually decreases during the dry season (Tanaka and Tanaka 1982, Silva et al. 2011).

In this study, only abundance of Homoptera and Orthoptera showed significant clustered distributions over the year, with periods of scarcity, which varied among years. The relatively low abundance of these taxa during certain times of year may be due to local migration to other suitable host plants that probably offered alternatives food resources (Janzen and Schoener 1968, Delinger 1980). For example, we found

Table 2. Measure of concentration (r), circular standard deviation (S_0), distribution and the wet-season preference index (WSPI) for monthly abundance of major arthropod taxa, and total arthropods captured by branch clipping on six tree species for year 1 (August 2007–July 2008), year 2 (August 2008–July 2009), and year 3 (August 2009–July 2010) in a novel *Prosopis–Leucaena* woodlands in southwestern Puerto Rico

Taxa	Year 1				Year 2				Year 3			
	r	S_0	Distribution	WSPI	R	S_0	Distribution	WSPI	r	S_0	Distribution	WSPI
Formicidae	0.342	83.900	Random	0.29	0.306	88.181	Random	0.44	0.222	99.329	Random	0.62
Araneae	0.183	105.597	Random	0.52	0.001	207.706	Random	0.47	0.123	117.297	Random	0.43
Orthoptera	0.307	88.029	Random	0.8	0.280	91.429	Random	0.73	0.734	45.059	Clustered*	0.05
Coleoptera	0.180	106.107	Random	0.45	0.189	104.659	Random	0.46	0.059	136.316	Random	0.61
Hemiptera	0.269	78.499	Random	0.67	0.343	83.790	Random	0.53	0.468	70.606	Random	0.61
Homoptera	0.524	92.807	Clustered*	0.22	0.544	63.211	Clustered*	0.5	0.761	42.346	Clustered**	0.11
Lepidoptera	0.439	73.507	Random	0.44	0.465	70.931	Random	0.57	0.095	124.317	Random	0.64
Others	0.246	95.954	Random	0.71	0.140	113.699	Random	0.45	0.199	102.796	Random	0.56
All arthropods	0.154	110.748	Random	0.47	0.118	118.392	Random	0.5	0.098	123.493	Random	0.55

* $P < 0.05$

** $P < 0.001$.

The term "Others" under taxa refers to combined rare insect orders as explained under Results. Significance levels are indicated with an asterisk and values shown at bottom of the table are based on Rayleigh tests as explained under Materials and Methods.

Table 3. Forward stepwise multiple regression parameters for monthly average abundance (Y) in foliage clipping samples from six tree species for each of four Arthropod taxa and total arthropods and the climatic variables: average rainfall (Rain, mm), average maximum temperature (Temp °F), and average relative humidity (Humi, %) in a novel *Prosopis–Leucaena* woodlands in southwestern Puerto Rico over 3 yr

Taxa	Regression equation	R adj ²	F	P
Araneae	$Y = 0.06 \text{ Rain}4w^* + 1.96 \text{ Temp}4w^{**}$	0.21	6.17	0.005
Orthoptera	$Y = 9.84 \text{ Temp}4w^*$	0.12	3.57	0.024
	$Y = 10.21 \text{ Temp}3w^*$	0.10	5.43	0.025
	$Y = 10.87 \text{ Temp}2w^*$	0.10	5.39	0.026
Coleoptera	$Y = 0.47 \text{ Rain}4w^* - 0.32 \text{ Temp}4w^*$	0.19	5.73	0.007
Lepidoptera (larvae)	$Y = -1.81 \text{ Temp}4w + 0.99 \text{ Humi}4w^*$	0.15	4.27	0.022
	$Y = 0.87 \text{ Humi}2w^*$	0.09	4.72	0.036
All arthropods	$Y = 0.072 \text{ Rain}2w^*$	0.13	3.83	0.031

* $P < 0.05$.

** $P < 0.01$.

Climatic variables were collected for two (2w), three (3w), and four (4w) weeks prior to sampling. See Materials and Methods for description of foliage clipping method and names of six tree species sampled as well as the years sampled.

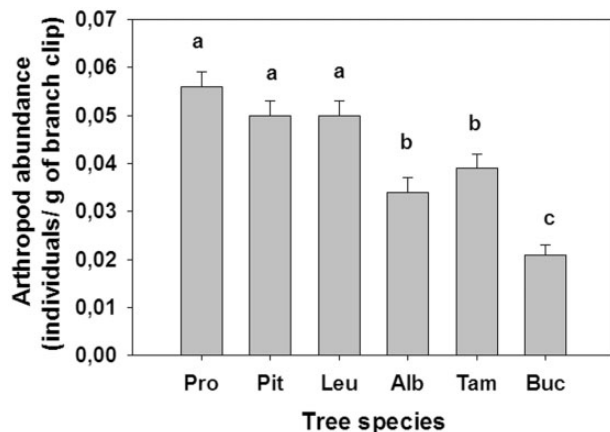


Fig. 4. Mean (\pm SE) total arthropods in foliage clipping samples from six tree species, in a novel *Prosopis–Leucaena* woodlands in southwestern Puerto Rico. Tree species include *P. juliflora* (Pro), *Pi. dulce* (Pit), *L. leucocephala* (Leu), *A. lebeck* (Alb), *T. indica* (Tam), and *B. buceras* (Bu). Letters indicates significant differences among tree species (Tukey's HSD, $P < 0.05$). See Materials and Methods for description of the foliage clipping sampling method.

large aggregations of Homoptera on *Lantana involucreta* (L.) (Verbenaceae), particularly during dry periods when *Lantana* shrubs may have served as a refuge when other plants presumably offered low food resources (W. Beltrán, unpublished observation). Studies in other dry tropical forests show that many taxa exhibit significant temporal aggregation over the course of a year, with high arthropod abundance in the early rainy season or in the transition from late dry season to early rainy season (Pinheiro et al. 2002, Silva et al. 2011).

In our study, mean abundance of Araneae, Orthoptera, Coleoptera, Lepidoptera larvae, and total arthropods were weakly related to one or more of the climatic variables measured prior to sampling (i.e., rainfall, maximum temperature, and relative humidity). Several factors may contribute to these patterns. First, if the populations of adult arthropods and Lepidoptera larvae are responding directly to climatic variables, our results suggest that the relationships with climate variables are not simply linear, and therefore, temporal changes in abundance are not directly related to any specific climatic variable. Second, arthropod abundance in this study might also display threshold and nonlinear type responses to climatic variables as demonstrated by others (Tauber and Tauber 1976, Chown and Gaston 1999). Third, the weak relationships found between arthropod abundance and climate variables might be explained by the large number of species involved and the multiple direct and indirect ways in which climate could independently drive population changes in each species (Kowk and Corlett 2002).

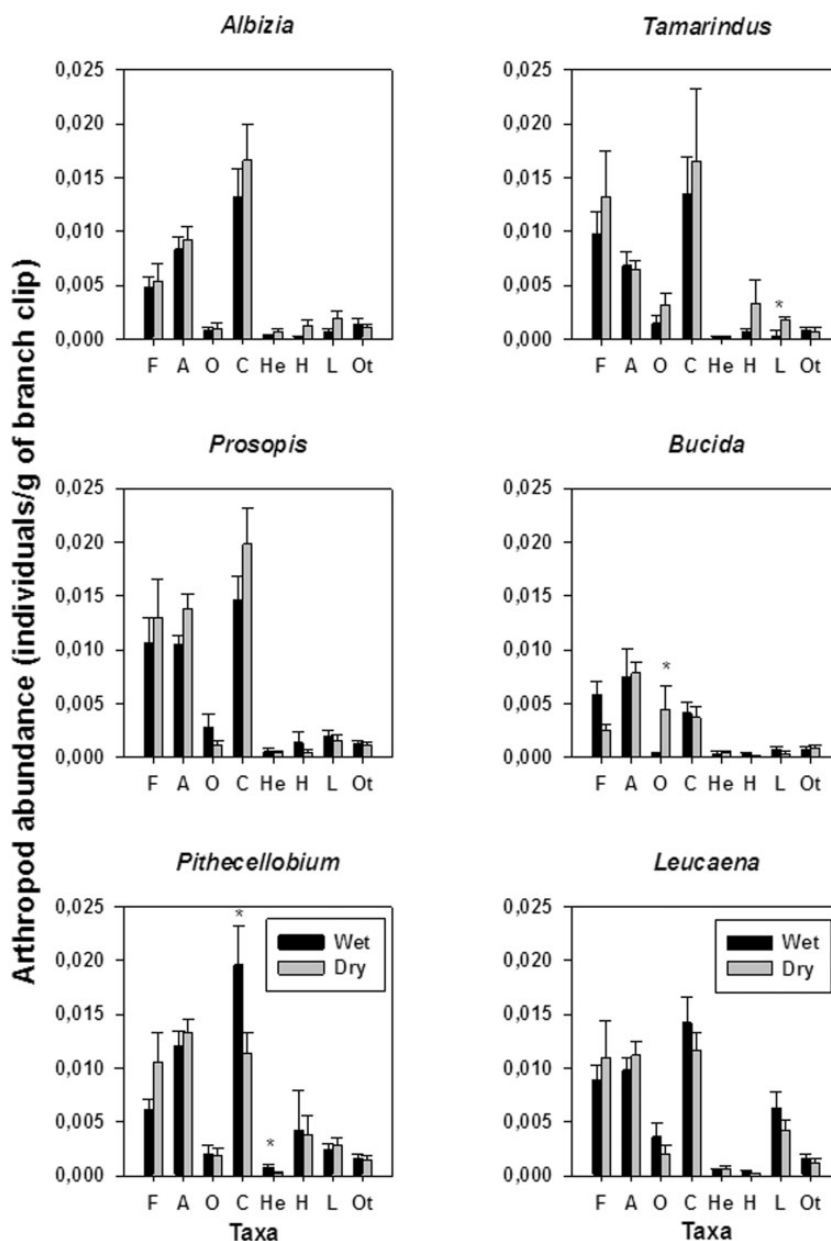


Fig. 5. Abundance of arthropods (mean \pm SE) sampled by branch clipping from six tree species during wet and dry periods plotted by major taxa, in a novel *Prosopis*–*Leucaena* woodlands in southwestern Puerto Rico. Abbreviations for taxa include: F, Formicidae; A, Araneae; O, Orthoptera; C, Coleoptera; He, Hemiptera; H, Homoptera; L, Lepidoptera; and Ot, Others taxa. Wet and dry periods were defined on the basis of the wettest and driest half of each year of sampling, respectively. See text for names of the six tree species sampled and the branch clipping sampling method.

Abundance of Formicidae, Homoptera, Hemiptera, and other taxa in our study did not show a direct response to the climate variables, suggesting that other abiotic or biotic factors (e.g., chemical cues, food availability, and predators) not measured here could explain the abundance patterns of these taxa. Both climatic factors and chemical cues in plants have also been suggested as important factors, which drive insect seasonality in some tropical areas (Wolda 1989, Didham and Springate 2003). Chemical changes in host plants might serve as triggers to break diapause in some tropical herbivorous insects (Tanaka et al. 1987). In addition, leaf volatile chemicals can attract some species such as rolled-leaf beetle species (Chrysomelidae, *Cephaloleia* spp.; García-Robledo and Horvitz 2009).

In southwestern Puerto Rico, the wet season is characterized by an increase in rainfall, primary productivity, vegetation cover, arthropod

abundance, and a decline in ambient temperatures (Lugo et al. 1978, Lister 1981). In our study, a marked increase in production of young leaves and flowers was observed in all tree species during the early rainy season for each year. Consequently, the branch clip samples in the early rainy season usually contained higher herbivore abundance (mainly caterpillars) and predators (ants and spiders) than samples collected in late dry season. Various studies have shown that an increase in rainfall in the early rainy season triggers production of young leaves, fruits, and flowers in many tropical plants (e.g., van Schaik et al. 1993, Williams et al. 1997), which in turn stimulates an increase in herbivore abundance (Richards and Coley 2007, Connahs et al. 2011, but see Sloan et al. 2007).

In our study, some arthropod taxa such as Lepidoptera larvae, Orthoptera, Coleoptera, and Hemiptera showed significant seasonal

Table 4. Average length (mm) of major and other arthropod taxa captured by branch clipping for wet and dry season, in a novel *Prosopis–Leucaena* woodlands in southwestern Puerto Rico

	Wet season			Dry season		
	Mean	SE	N	Mean	SE	N
Formicidae	2.43	0.01	1611	2.26	0.01**	1770
Araneae	3.34	0.05	1461	2.97	0.04**	2022
Orthoptera	6.43	0.31	140	6.31	0.36	150
Coleoptera	3.15	0.03	3299	2.71	0.03**	2387
Hemiptera	5.36	0.54	103	6.06	0.59	81
Homoptera	4.43	0.23	113	5.11	0.23*	108
Lepidoptera	11.66	0.33	507	6.53	0.28**	310
Other	4.45	0.41	188	4.11	0.36	208

Category of "other" Arthropods refers to rare orders as described under Results. Wet and dry seasons were defined on the basis of the wettest and driest half of each year of sampling, respectively. Asterisk behind each taxa name refer to significance levels (* $P < 0.05$, ** $P < 0.001$) for difference in body length between wet and dry seasons.

(i.e., wet vs. dry) variation in abundance but each only on a single tree species. Our inability to detect seasonal variation in abundance for specific arthropod taxa on more tree species may have been due to large variance in arthropod abundance among branch clip samples (see Fig. 5), small sample size, and low arthropod abundance (Schowalter and Ganio 2003). When results were pooled across tree species, different seasonal patterns in arthropod abundance were evident among most taxa examined in this study. Some groups such as Araneae and Homoptera showed higher abundance in the dry periods, whereas others groups such as Lepidoptera larvae, Coleoptera, and Hemiptera were more abundant in the wet periods. Thus, higher rainfall amounts do not always promote an increase in arthropod abundance in all taxa, as others have demonstrated previously (Nyeko et al. 2002, Hilt et al. 2007). For example, in agroforestry stands, Nyeko et al. (2002) found that chewing insects tend to be more abundant in the wet season, whereas sucking insects were more abundant in the dry season.

Total arthropod abundance differed significantly among tree species, as expected from previous studies (Schowalter 1994, Schowalter and Ganio 1999) including our own studies of these same tree species (Beltrán and Wunderle 2013). As we showed previously with measures of arthropod biomass, *Prosopis*, *Pithecellobium*, and *Leucaena* each displayed higher total arthropod biomass than the other tree species. We found that these species had relatively high N content, low lignin/N ratios, and low hemicellulose content consistent with expectations that herbivorous arthropods preferred leaves high in nutrition (i.e., high N), and highly palatable (i.e., low lignin relative to N, low hemicellulose). The lowest arthropod abundance in this study occurred on the native *Bucida*, which has tough leaves with very low N content. Although more arthropods occurred on *Tamarindus* than *Bucida*, it also had very low N content and high hemicellulose content. *Albizia*, which had arthropod abundance equivalent to abundance on *Tamarindus*, had high N content, but some of the N is contributed by substances known to have insecticidal properties. Thus, given our previous findings, we believe that leaf chemistry traits likely explain a substantial proportion of the variation in arthropod abundance among the six tree species. Similarity of leaf chemical traits, however, may occur because many of the tree species are closely related, especially the alien species in the Mimosoideae (*Prosopis*, *Leucaena*) and Fabaceae (*Albizia*, *Pithecellobium*).

We found significant seasonal changes in the arthropod size distribution for all arthropod taxa, except Orthoptera, Hemiptera, and the combined minor taxa. The Formicidae, Araneae, Coleoptera, and larvae of Lepidoptera were all significantly larger in the wet than dry period. This larger wet than dry season size is consistent with expectations of greater food availability (e.g., new foliage) in the wet period, allowing larval instars to grow bigger than in the dry period when their food is

scarcer (Alcock et al. 2005). In contrast, Homoptera were significantly larger in the dry than the wet period. The smaller Homoptera size in the wet period was probably due to a higher abundance of nymphs (W. Beltrán, unpublished data). This is consistent with findings of Erwin and Scott (1980), who found that coleopterans tend to be smaller in the dry than wet periods. However, it is possible that other factors also contributed to seasonal changes in arthropod body size, including temperature, water availability, and predation pressure (Berger et al. 2006, Chown and Gaston 2010). For instance, higher temperatures and lower water availability during the dry period may lead to increased energy expenditure and water loss in different larval instars affecting body length, which in turn affects adult size (Warren et al. 2006). High temperatures typical of the dry period may be particularly costly for larger individuals, because larger individuals can generate internal temperatures above ambient temperature, affecting their metabolic rates (Carroll and Quiring 1993). The occurrence of smaller adult individuals during the dry period may also be an adaptive response to escape predation and therefore favored under high predation pressure (Berger et al. 2006).

We previously compared biomass of foliage arthropods from the novel *Prosopis–Leucaena* woodlands with biomass values from similarly sampled native dry forests and found that our novel woodland foliage arthropod biomass values were slightly lower than the lowest biomass values found in some native dry forests (Beltrán and Wunderle 2013). However, comparison of abundance of foliage arthropods (i.e., individuals per gram of branch clip) rather than biomass indicates that our abundance values from the novel *Prosopis–Leucaena* woodlands were higher than the range of abundance values found previously in native dry forests. For example, we found an average of 0.47 individuals per gram of branch clip, which was slightly higher than the foliage arthropod abundance range (0.28–0.40 individuals per gram branch clip) on native leguminous trees in northwestern Nicaraguan dry forest, where dry season rainfall was similar to that of Cabo Rojo (Greenberg and Bichier 2005). Also, mean arthropod abundance in several native successional forests in Yucatan, Mexico (range: 0.10–0.13 individuals per gram branch clip; Smith and Robertson 2008) was lower than abundance found in our novel *Prosopis–Leucaena* woodlands. Although there were some differences among dry forest sites in foliage arthropod abundance, as might be expected to due to differences in tree species composition, severity of dry seasons, and successional stages of the compared sites, we believe the novel *Prosopis–Leucaena* woodlands, despite the predominance of alien tree species, appear to have comparable levels of foliage arthropod abundance as found in similar tropical dry forests with native tree species. Moreover, the patterns of arthropod seasonality documented in these novel woodlands share similarities with temporal abundance patterns documented in native dry forests elsewhere. Nonetheless, future studies of foliage arthropod abundance and seasonality should compare the novel *Prosopis–Leucaena* woodlands with native dry forest on Puerto Rico to provide a more rigorous comparison of native and novel communities.

Annual rainfall during our study at Cabo Rojo (2007–2010) was on average lower than the mean value for the earlier 1991–2005 period and showed less predictable seasonality than previously reported by Weaver and Schwagerl (2009). Recently, a similar trend of decreasing annual rainfall and increasing variability in rainfall seasonality has been documented in a Jamaican dry forest (Studds and Marra 2007, 2011) along with decreasing rainfall in The Bahamas (Martin and Weech 2001) and Luquillo Mountains of Puerto Rico (Heartsill-Scalley et al. 2007). These patterns of decreasing and more variable annual rainfall are consistent with climate change predictions for the Caribbean basin (Neelin et al. 2006) and predictions of greater overall environmental variability (Easterling et al. 2000). The consequences of this increased rainfall variability during our study were evident in findings that indicated that the annual abundance of arthropods, either for individual taxa or total arthropods, was highly variable among years and showed no consistent annual seasonality. We expect that the loss of

consistent rainfall seasonality in dry tropical forests and woodlands will have substantial effects on seasonality of arthropods and their predators.

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References Cited

- Alcock, J., L. W. Simmons, and M. Beveridge. 2005.** Seasonal change in offspring sex in size in Dawson's burrowing bees (*Amegilla dawsonii*) (Hymenoptera: Anthophorini). *Ecol. Entomol.* 30: 247–254.
- Amorim, F. W., R. S. de Avila, Jr., A. J. A. de Camargo, A. L. Viera, and P. E. Oliveira. 2009.** A hawkmoth crossroads? Species richness, seasonality and biogeographical affinities of Sphingidae in a Brazilian Cerrado. *J. Biogeogr.* 36: 662–674.
- Anu, A., T. K. Sabu, and P. J. Vineesh. 2009.** Seasonality of litter insects and relationship with rainfall in a wet evergreen forest in south Western Ghats. *J. Insect Sci.* 9: 46.
- Baltz, M. E. 2000.** The nonbreeding season ecology of Neotropical migratory birds in the dry zone of Puerto Rico. Ph.D. dissertation, University of Missouri, Columbia, MO.
- Banerjee, B. 1981.** An analysis of the effect of latitude, age, and area on the number of arthropods pest species of tea. *J. Appl. Ecol.* 18: 339–342.
- Basset, Y. 1996.** Local communities of arboreal herbivores in Papua New Guinea: predictors of insect variables. *Ecology* 77: 1906–1919.
- Beard, J. S. 1949.** The natural vegetation of the Windward and Leeward Island. Oxford Forestry Memoirs, Oxford, UK.
- Beltrán, W., and J. M. Wunderle. 2013.** Determinants of tree species preference for foraging by insectivorous birds in a novel *Prosopis–Leucanea* woodland in Puerto Rico: the role of foliage palatability. *Biodiver. Conserv.* 22: 2071–2089.
- Beltrán Salazar, J. W. 2012.** Tritrophic interactions in subtropical novel dry woodlands: differential use of tree species by foraging birds and their arthropod prey. Ph.D. Dissertation, University of Puerto Rico, Río Piedras.
- Berger, D., R. Walter, and K. Gottard. 2006.** What keeps insects small? Size dependent predation on two species of butterfly larvae. *Evol. Ecol.* 20: 575–589.
- Blackburn, T. M., and K. J. Gaston. 1994.** Animal body size distribution: patterns, mechanisms and implications. *Trends Ecol. Evol.* 9: 471–474.
- Carroll, A. L., and D. T. Quiring. 1993.** Interactions between size and temperature influence fecundity and longevity of a tortricid moth, *Zeiraphera canadensis*. *Oecologia* 93: 233–241.
- Chown, S. L., and K. J. Gaston. 1999.** Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. *Biol. Rev.* 74: 87–120.
- Chown, S. L., and K. J. Gaston. 2010.** Body size variation in insects: a macroecological perspective. *Biol. Rev.* 25: 139–169.
- Chown, S. L., and J. Klok. 2003.** Water-balance characteristics respond to changes in body size in sub-Antarctic weevils. *Physiol. Biochem. Zool.* 76: 634–643.
- Connahs, H., A. Aiello, S. van Bael, and G. Rodríguez-Castañeda. 2011.** Caterpillar abundance and parasitism in a seasonally dry versus wet tropical forest of Panama. *J. Trop. Ecol.* 27: 51–58.
- Cottam, G., and J. T. Curtis. 1956.** The use of distance measures in phytosociological sampling. *Ecology* 37: 451–460.
- Crawley, M. J. 1997.** Plant ecology. Blackwell Science, Oxford, UK.
- De Castro, F. S., A. B. Gontijo, P. T. A. Castro, and S. P. Ribeiro. 2012.** Annual and seasonal changes in the structure of litter-dwelling ant assemblages (Hymenoptera: Formicidae) in Atlantic semideciduous forests. *Psyche* 2012: 12.
- Delinger, D. L. 1980.** Seasonal and annual variation in insect abundance in the Nairobi National Park, Kenya. *Biotropica* 12: 100–106.
- Didham, R. K., and N. Springate. 2003.** Determinants of temporal variation in community structure, pp. 28–39. *In* Y. Basset, V. Novotny, S. E. Miller, and R. L. Kitching (eds.), *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy*. Cambridge University Press, Cambridge, United Kingdom.
- Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000.** Climate extremes: observations, modeling, and impacts. *Science* 289: 2068–2074.
- Erwin, T. L., and J. C. Scott. 1980.** Seasonal and size patterns, trophic structure, and richness of Coleoptera in the tropical arboreal ecosystems: the fauna of the tree *Luehea seemannii* in the canal zone of Panama. *Coleopt. Bull.* 34: 305–322.
- Fork, S. K. 2010.** Arthropod assemblages in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Environ. Entomol.* 39: 753–762.
- García-Robledo, C., and C. C. Horvitz. 2009.** Host plants scents attract rolled-leaf beetles to Neotropical gingers in a Central American tropical rain forest. *Entomol. Exp. Appl.* 131: 115–120.
- Greenberg, R., and P. Bichier. 2005.** Determinants of tree species preference of birds in oak-acacia woodlands of Central America. *J. Trop. Ecol.* 21: 57–66.
- Grimbacher, P. S., and N. E. Stork. 2009.** Seasonality of a diverse beetle assemblage inhabiting lowland tropical rain forest in Australia. *Biotropica* 41: 328–337.
- Hamer, K. C., J. K. Hill, N. Mustaffa, S. Benedick, T. N. Sherratt, V. K. Chey, and M. Maryati. 2005.** Temporal variation in abundance and diversity of butterflies in Bornean rain forests: opposite impacts of logging recorded in different seasons. *J. Trop. Ecol.* 21: 417–421.
- Hartley, M. K., W. E. Rogers, and E. Siemann. 2010.** Comparison of arthropod assemblages on an invasive and native trees: abundance, diversity and damage. *Arthropod Plant Interact.* 4: 237–245.
- Heartsill-Scalley, T., F. N. Scatena, C. Estrada, W. H. McDowell, and A. E. Lugo. 2007.** Disturbance and long-term patterns of rainfall and throughfall nutrient fluxes in a subtropical wet forest in Puerto Rico. *J. Hydrol.* 333: 472–485.
- Helmer, E. H., T. A. Kennaway, D. H. Pedreros, M. L. Clark, H. Marcano-Vega, L. L. Tieszen, T. R. Ruzycski, S. R. Schill, and C. M. S. Carrington. 2008.** Land cover and forest formation distribution for ST. Kitts, Nevis, St. Eustatius, Grenada and Barbados from decision tree classification of cloud-cleared satellite imagery. *Caribbean J. Sci.* 44: 175–198.
- Hilt, N., G. Brehm, and K. Fiedler. 2007.** Temporal dynamics of rich moth ensembles in the montane forest zone in Southern Ecuador. *Biotropica* 39: 94–104.
- Holmes, R. T., and S. K. Robinson. 1981.** Tree species preferences by foraging insectivorous birds in a northern hardwoods forest. *Oecologia* 48: 31–35.
- Jahn, A. E., D. J. Levey, A. M. Mamani, M. Saldias, A. Alcoba, M. J. Ledezma, B. Florez, J. Q. Vidoz, and F. Hilarion. 2010.** Seasonal differences in rainfall, food availability, and the foraging behavior of Tropical Kingbirds in the southwestern Amazon. *J. Field Ornithol.* 81: 340–348.
- Janzen, D. H., and T. W. Schoener. 1968.** Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49: 96–110.
- Johnson, M. D. 2000a.** Effects of shade-tree species and crop structure on the winter arthropod and bird communities in a Jamaican shade coffee plantation. *Biotropica* 32: 133–145.
- Johnson, M. D. 2000b.** Evaluation of arthropod sampling technique for measuring food availability for forest insectivorous birds. *J. Field Ornithol.* 71: 88–109.
- Keane, R. M., and M. J. Crawley. 2002.** Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 17: 164–169.
- Kennaway, T., and E. H. Helmer. 2007.** The forest types and ages cleared for land development in Puerto Rico. *GISci Remote Sens.* 44: 356–382.
- Kishimoto-Yamada, K., T. Itioka, S. Sakai, and T. Ichie. 2010.** Seasonality in light-attracted chrysomelid populations in a Bornean rainforest. *Insect Conserv. Divers.* 3: 266–277.
- Kwok, H. K., and R. T. Corlett. 2002.** Seasonality of forest invertebrates in Hong Kong, South China. *J. Trop. Ecol.* 18: 637–644.
- Lister, B. C. 1981.** Seasonal niche relationships of rain forest anoles. *Ecology* 62: 1548–1560.

- Liu, H., and P. Stiling. 2006. Testing the enemy release hypothesis: a review and meta-analysis. *Biol. Invasions* 8: 1535–1545.
- Loveless, A. R., and G. F. Asprey. 1957. The dry evergreen formations of Jamaica: I. The limestone hills of the south coast. *J. Ecol.* 45: 799–822.
- Lugo, A. E. 2004. The outcome of alien tree invasions in Puerto Rico. *Front. Ecol. Environ.* 2: 265–273.
- Lugo, A. E., and E. Helmer. 2004. The outcome of alien tree invasions in Puerto Rico. *Front. Ecol. Environ.* 2: 265–273.
- Lugo, A. E., T. A. Carlo, and J. M. Wunderle. 2012. Natural mixing of species: novel plant-animal communities on Caribbean Islands. *Anim. Conserv.* 15: 233–241.
- Lugo, A. E., J. A., González, B., Cintrón, and K. Dugger. 1978. Structure, productivity and transpiration of a subtropical dry forest. *Biotropica* 10: 278–291.
- Maron, J. L., and M. Vilà. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypothesis. *Oikos* 95: 361–373.
- Martin, H. C., and P. S. Weech. 2001. Climate change in the Bahamas? Evidence in the meteorological records. *Bahamas J. Sci.* 5: 22–32.
- Neelin, J. D., M. Munnich, H. Su, J. E. Meyerson, and C. E. Holloway. 2006. Tropical drying trends in global warming models and observations. *Proc. Natl Acad. Sci. USA.* 103: 6110–6115.
- Nyeko, P., G. Edwards-Jones, and R. K. Day. 2002. Population dynamics of herbivorous insects and potential arthropod natural enemies on *Alnus* species in Kabale district, Uganda. *Agroforest. Syst.* 56: 213–228.
- Novotny, V., and Y. Basset. 1999. Body size and host plant specialization: a relationship from a community of herbivorous insects on *Ficus* from Papua New Guinea. *J. Trop. Ecol.* 15: 315–328.
- Pinheiro, F., R. Diniz, D. Coelho, and M. P. S. Bandeira. 2002. Seasonal pattern of insect abundance in the Brazilian cerrado. *Aust. Ecol.* 27: 132–136.
- Reagan, D. P., and R. B. Waide. 1996. The food web of a tropical rain forest. University of Chicago, Chicago, IL.
- Rice, W. R. 1989. Analyzing tables of statistical results. *Evolution* 43: 223–225.
- Richards, L. A., and P. D. Coley. 2007. Seasonal and habitat differences affect the impact of food and predation on herbivores: a comparison between gaps and the understory of a tropical forest. *Oikos* 116: 31–40.
- Schoener, T. W., and D. H. Janzen. 1968. Notes on environmental determinants of tropical versus temperate insect size patterns. *Am. Nat.* 102: 224–253.
- Schwalter, T. D. 1994. Invertebrate community structure and herbivory in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. *Biotropica* 26: 312–319.
- Schwalter, T. D., and L. Ganio. 1999. Invertebrate communities in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. *Ecol. Entomol.* 24: 191–201.
- Schwalter, T. D., and L. Ganio. 2003. Diel, seasonal and disturbance-induced variation in invertebrate assemblages, pp. 315–328. In Y. Basset, V. Novotny, S. E. Miller, and R. Kitching (eds.), *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy*. Cambridge University Press, Cambridge, United Kingdom.
- Schwalter, T. D., J. W., Webb, and D. A. Crossley, Jr. 1981. Community structure and nutrient content of canopy arthropod in clearcut and uncut forest ecosystems. *Ecology* 62: 1010–1019.
- Silva, N. A., M. R. Frizzas, and C. M. de Oliveria. 2011. Seasonality in insect abundance in the “Cerrado” of Goiás State, Brazil. *Rev. Bras. Entomol.* 55: 79–81.
- Sloan, S. A., J. K. Zimmerman, and A. M. Sabat. 2007. Phenology of *Plumeria alba* and its herbivores in a tropical dry forest. *Biotropica* 39: 195–201.
- Smith, A. L., and R. J. Robertson. 2008. Seasonal changes to arthropod abundance in successional forests of the Yucatan Peninsula with implications for overwintering forest birds. *Ornitol. Neotropical* 19: 81–95.
- Sokal, R. R., and E. J. Rohlf. 1995. *Biometry*. W. H. Freeman and Co., New York, NY.
- SPSS. 1990. The SPSS base system user’s guide. SPSS, Inc., Chicago, IL.
- Staicer, C. A. 1991. The role of male song in the socioecology of the tropical resident Adelaide’s Warbler (*Dendroica adelaidae*). Ph.D. dissertation, University of Massachusetts, Amherst, MA.
- Statsoft. 2000. STATISTICA for Windows software. Statsoft, Inc., Tulsa, OK.
- Sulaiman, S. F., A. Culham, and J. B. Harborne. 2003. Molecular phylogeny of Fabaceae based on RBCL sequence data: with special emphasis on the tribe Mimoseae (Mimosoideae). *Asian Pacific J. Mol. Biol. Technol.* 11: 9–35.
- Studds, C. E., and P. P. Marra. 2007. Linking fluctuations in rainfall to non-breeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. *Climate Res.* 35: 115–122.
- Studds, C. E., and P. P. Marra. 2011. Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. *Proc. R. Soc. Lond. Ser. B* 278: 3437–3443.
- SYSTAT. 2002. Statistics, version 10.2. SYSTAT Software Inc., Richmond, CA.
- Tanaka, L. K., and S. K. Tanaka. 1982. Rainfall and seasonal changes in arthropod abundance on a tropical oceanic island. *Biotropica* 14: 114–123.
- Tanaka, S., H. Wolda, and D. L. Delinger. 1987. Seasonality and its physiological regulation in three neotropical insect taxa from Barro Colorado Island, Panama. *Int. J. Trop. Insect Sci.* 8: 507–514.
- Tauber, M. J., and C. A. Tauber. 1976. Insect seasonality: diapause maintenance, termination, and postdiapause development. *Annu. Rev. Entomol.* 21: 81–107.
- Tovar-Sánchez, E., S. Cano-Santana, and K. Oyama. 2003. Canopy arthropod communities on Mexican oaks at sites with different disturbance regimes. *Biol. Conserv.* 115: 79–87.
- Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* 11: 1351–1363.
- van Schaik, S. P., J. W. Terborgh, and S. J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences of primary consumers. *Annu. Rev. Ecol. Syst.* 24: 353–377.
- Vasconcellos, A., R. Andreatze, A. M. Almeida, H. F. P. Araujo, E. S. Oliveira, and U. Oliveira. 2010. Seasonality of insects in the semi-arid Catinga of northeastern Brazil. *Rev. Bras. Entomol.* 54: 471–476.
- Wagner, T. 2001. Seasonal changes in the canopy arthropod fauna in *Rinorea beniensis* in Budongo Forest, Uganda. *Plant Ecol.* 153: 169–178.
- Wall, D. H., and J. C. Moore. 1999. Interactions underground-soil biodiversity, mutualism, and ecosystem processes. *Bioscience* 49: 109–117.
- Warren, M., M. A. McGeoch, S. W. Nicolson, and S. L. Chown. 2006. Body size pattern in *Drosophila* inhabiting a mesocosmos: interactive effects of spatial variation in temperature and abundance. *Oecologia* 149: 245–255.
- Weaver, P. L., and J. D. Chinea. 2003. Secondary subtropical dry forest at the La Tinaja tract of the Cartagena Lagoon National Wildlife Refuge, Puerto Rico. *Caribbean J. Sci.* 39: 273–285.
- Weaver, P. L., and J. J. Schwagerl. 2009. U.S. Fish and Wildlife Service refuges and other nearby reserves in southwestern Puerto Rico. International Institute of Tropical Forest Paper 40, U.S. Forest Service, San Juan, Puerto Rico.
- Williams, R. J., B. A. Myers, W. J. Muller, G. A. Duff, and D. Eamus. 1997. Leaf phenology of woody species in a North Australian tropical savanna. *Ecology* 78: 2542–2558.
- Wolda, H. 1988. Insect seasonality: why? *Annu. Rev. Ecol. Syst.* 19: 1–18.
- Wolda, H. 1989. Seasonal cues in tropical organisms. Rainfall? Not necessarily. *Oecologia* 80: 437–442.
- Zar, J. H. 1999. *Biostatistical analysis*, 4th ed. Prentice Hall, Upper Saddle River, NJ.

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