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ORIGINAL PAPER

Determinants of tree species preference for foraging by insectivorous birds in a novel *Prosopis–Leucaena* woodland in Puerto Rico: the role of foliage palatability

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Abstract The foliage palatability hypothesis predicts that avian insectivores will preferentially forage in tree species with the greatest abundance of their arthropod prey, which in turn are associated with the tree's foliage nutrition and palatability. We tested this hypothesis in a novel *Prosopis–Leucaena* woodland in Puerto Rico by determining foraging preferences of five insectivorous bird species for six tree species (five alien, one native) and relating preferences to foliage arthropod biomass and leaf chemistry. The most frequently preferred tree species for foraging were the alien *Prosopis juliflora* (preferred by five bird species) and *Pithecellobium dulce* (preferred by four bird species). Both species had high foliage arthropod biomass, high N content, low lignin/N ratios, and low hemicellulose content. Compounds, previously known to affect herbivore responses to *Albizia lebbeck* and *Leucaena leucocephala*, may explain low arthropod biomass despite high N content in *Albizia* and avoidance of *Leucaena* by four bird species despite its high arthropod biomass. The native *Bucida buceras* had tough leaves with low N content, low arthropod biomass, and only one bird species showed a weak preference for foraging in it. Biomass of predaceous arthropods showed strong negative correlations with the ratios of lignin/N and hemicellulose/N. Some alien tree species had highly palatable foliage with high arthropod biomass and hence were preferred for foraging by avian insectivores as predicted by the foliage palatability hypothesis. High foliage palatability of some alien tree species may weaken the effect of enemy release in some novel plant communities.

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Introduction

Insectivorous birds may show species-specific preferences for foraging in particular tree species often based on the abundance of their preferred arthropod prey. Such tree species preferences have the potential to influence the composition of insectivorous bird communities (Airola and Barrett 1985; Gabbe et al. 2002) especially in wooded communities with few tree species where the dominant tree species may play a substantial role in determining the insectivorous bird species present (Greenberg and Bichier 2005). The existence of foraging preference for certain tree species in insectivorous birds has been well documented in north-temperate forests (Holmes and Robinson 1981; Gabbe et al. 2002; Park 2005; Strode 2009), but rarely studied in tropical or subtropical forests (Greenberg et al. 1997; Greenberg and Bichier 2005), in part due to the high tree species richness characteristic of most of these forests. However, not all tropical or subtropical forests have high tree species richness, such as the oak-acacia woodlands of Mesoamerica where Greenberg and Bichier (2005) took advantage of low tree species richness to study the determinants of avian tree species preferences. Similar woodlands with low tree species richness occur in overgrown or abandoned pastures on seasonally dry tropical or subtropical sites in which various N-fixing leguminous trees predominate. These legume-dominated woodlands are widespread throughout the seasonally dry portions of Caribbean islands (Beard 1949; Loveless and Asprey 1957; Kennaway and Helmer 2007; Helmer et al. 2008), where many of the dominant tree species in the genera *Acacia*, *Haematoxylum*, *Prosopis*, *Pithecellobium*, and *Leucaena* have been introduced. On Puerto Rico and nearby Culebra and Vieques, the alien *Prosopis juliflora* and *Leucaena leucocephala* often predominate in open or dense drought-deciduous woodlands covering more than 18,882 ha (Kennaway and Helmer 2007). Our study takes advantage of the low tree species richness of these *Prosopis–Leucaena* woodlands on Puerto Rico to study some of the determinants of tree species preferences of five insectivorous bird species.

Plant communities such as the *Prosopis–Leucaena* woodlands represent novel communities, which on Puerto Rico and surrounding islands have a mix of native and naturalized alien tree species and often occur on abandoned agricultural lands (Lugo and Helmer 2004; Lugo 2004). These naturalized alien tree species are dominant floristic elements in these new forests where they facilitate the establishment of other alien tree species as well as native and endemic species on degraded lands (Lugo 2004; Lugo et al. 2012). The alien tree species in these novel *Prosopis–Leucaena* woodlands are expected to have lower arthropod abundance than native species as predicted by the enemy release hypothesis. This hypothesis proposes that when a plant species is transferred outside its geographic range it leaves behind its specialized pests and once freed of its homeland pests the alien will have a competitive advantage over native species in human-disturbed habitats (Crawley 1997; Maron and Vilà 2001; Keane and Crawley 2002). Support for the hypothesis is accumulating (Liu and Stiling 2006), but some recent findings conflict with predictions (Fork 2010; Hartley et al. 2010). Although it is unknown if the alien tree species in the *Prosopis–Leucaena* woodlands have foliage with low arthropod abundance as predicted by enemy release, previous studies indicate that some insectivorous birds can be abundant in these woodlands (Staicer 1992; Baltz 2000).

The foliage of various tree species often differs in chemical, morphological, and nutritional traits that affect the abundance of herbivorous insects (Schädler et al. 2003; Silva and

Vasconcelos 2011), which in turn, may affect avian insectivore tree species preferences. Few studies, however, have examined the foliage characteristics that contribute to the arthropod abundance found on the avian insectivores' preferred tree species (Murakami 1998; Sipura 1999; Greenberg and Bichier 2005). The relation between avian insectivore tree species preferences and the nutritional and palatability traits of leaves of the preferred tree species may be explained by the foliage palatability hypothesis (Greenberg and Bichier 2005). This hypothesis posits that insectivorous birds select tree species characterized by foliage with the highest nutritional content and palatability for their preferred arthropod prey relative to the foliage of other tree species with lower nutrition and palatability.

The preference of herbivorous insects for foliage of certain plants is often linked to structural (e.g., toughness) and chemical traits of leaves (Peeters 2002; Cornelissen and Stiling 2008). Leaf toughness resulting from high concentrations of lignin, hemicellulose, and fiber provides an important physical defense against herbivorous insects (Coley and Barone 1996; Peeters et al. 2007). Highly fibrous and lignified leaves may be difficult for some herbivorous insects to ingest and digest thereby reducing feeding rates, which when coupled with low nutritional quality can decrease insect survival and growth rates (Choong 1996; Clissold et al. 2006, 2009). In addition, herbivorous insects often select plants with leaves that are high in nutrients such as nitrogen (McNeill and Southwood 1978). For example, performance indices in some herbivorous insects have been found to increase with leaf nitrogen and water content (Slansky and Scriber 1985). In addition, herbivorous insects may avoid leaves with secondary compounds such as condensed tannins and cyanogenic glycosides (Murakami 1998; Sipura 1999; Mundim et al. 2009).

In this study we tested the predictions of the foliage palatability hypothesis in relation to the use of five naturalized alien tree species and one native tree species by five insectivorous bird species in a novel *Prosopis–Leucaena* woodlands on Puerto Rico. Our study's inclusion of alien tree species enabled us to examine the interaction of the foliage palatability hypothesis with the enemy release hypothesis when foliage of the alien species was highly nutritious and palatable. We first quantified foraging use of the six tree species in relation to their availability by each of the five bird species to determine whether foraging use indicated preference, avoidance, or use equivalent to a tree species' availability. Once a bird species' preference for or avoidance of each tree species was established, we compared its foraging use to the biomass of foliage arthropods available on each tree species to test the hypothesis that foraging birds were selecting tree species based on the biomass of foliage arthropods. We then related the biomass of arthropods on the foliage of each tree species to measures of nutrition (nitrogen) and palatability, (hemicellulose and lignin content) from leaves of each tree species. This latter comparison was made to test the hypothesis that foliage arthropods were most abundant on alien or native tree species with the most nutritious and palatable leaves as predicted by the foliage palatability hypothesis. High nutrition content (i.e., high N content) and palatability (i.e., low hemicellulose and lignin content) were expected to weaken the effect of enemy release on foliage arthropods in the alien tree species.

Methods

Study area

This study was conducted in the northern half of the Cabo Rojo National Wildlife Refuge (17°59′N, 67°10′W) located 6 km southeast of the town of Boquerón in southwestern Puerto Rico. Here the 8.0 ha study site was situated in the subtropical dry forest life zone

(Ewel and Whitmore 1973) and located on low plains covered in secondary dry woodlands, which receive a mean annual rainfall of 930 mm (Weaver and Schwagerl 2009). The vegetation is mostly dominated by nonnative leguminous trees, which grow separately or in clumps (Staicer 1992). The dominant tree species in the refuge include *P. juliflora*, *Pithecellobium dulce*, *Leucaena leucocephala*, *Albizia lebbeck*, *Tamarindus indica*, *Parkinsonia aculeata*, *Meliccocus bujugatus*, and *Bucida buceras*.

Sampling

Vegetation was sampled in December 2009 using the point-center method (Cottam and Curtis 1956) in which 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 recorded along with the tree's species identity. Tree species composition was determined in 13 transects each 100 m long, separated by 50 m and distributed along two survey trails. In each transect, individual trees with >2.5 cm DBH were recorded. Tree frequency and density were used for calculations of the Importance Value Index (IVI) for each dominant tree species (Holmes and Robinson 1981; Gabbe et al. 2002). The IVI is an indirect measure, which Holmes and Robinson (1981), Gabbe et al. (2002) argue provides a useful relative index of the proportional representation of foliage among different tree species in a forest community. This parameter was calculated as follows: IVI = relative dominance + relative density + relative frequency.

To establish whether the foraging birds were using certain tree species disproportionately or simply in relation to availability, we compared expected foraging frequencies with observed foraging frequencies for each tree species as per Holmes and Robinson (1981), Gabbe et al. (2002). The observed frequencies were obtained from the observations of each bird species while foraging on arthropods (fruit and nectar foraging were excluded). The expected insectivore foraging frequencies were calculated by multiplying IVIs by the total number of arthropod foraging observations for each bird species.

Avian foraging observations were made on three resident species, including two tyranids (*Myarchus antillarum*, Puerto Rican Flycatcher, PRFL; *Elaenia dominica*, Caribbean Elaenia, CAEL) and a parulid (*Setophaga adelaidae*, Adelaide's Warbler, ADWA) and two Nearctic-Neotropical migrant parulids (*S. americana*, Northern Parula, NOPA; and *S. discolor*, Prairie Warbler, PRAW). Observations were made from September 2007 to December 2010 for ADWA, and from January to April 2009 and September to December 2010 for PRFL, CAEL, NOPA, and PRAW. Although some of the species fed on fruit or nectar our analyses included only observations in which the foragers were consuming arthropods. If a bird was initially encountered as it was consuming fruit or nectar in a tree the subsequent arthropod foraging maneuver in the same tree was excluded from our analyses. Analyses were restricted to observations from September to April, to cover the period when migrants were present. Foraging behavior was recorded by WB using 8 × 30 binoculars between 06:30 and 11:00 and 16:00 and 18:00 h. Observations were made by walking slowly along trails within the study site to reduce the likelihood of bias from repeated observation of the same individuals. Whenever a bird was found, it was followed for at least 15 s before recording the first foraging maneuver to avoid bias toward the more conspicuous feeding techniques. To reduce autocorrelation, only a single foraging maneuver (directed at arthropod prey) was recorded per individual per day (Wagner 1981).

This was accomplished by restricting foraging observations of a bird species on a specific trail to either morning or afternoon of the same day.

To quantify tree species preferences for foraging by each bird species, we used a tree preference index as devised by Holmes and Robinson (1981) and more recently used by Gabbe et al. (2002). The preference index was obtained for each insectivore by summing the absolute values of the differences (positives or negatives) between the tree IVI and bird foraging frequencies for each of six dominant tree species. The higher the value, the more specialized the insectivore is in its use of a particular tree species.

To estimate the relative abundance of birds, we used samples of birds captured in mist nets from March 2007 to December 2010. The abundance index for each species was estimated as the number of individuals captured per 100 net-hours from September to April for each year. Birds were captured using seven to ten mist-nets (2.6 m × 12 m, 30 mm-mesh). Nets were set up from 7:30 until 12:00 h for three consecutive days each week, and placed in different areas located in the interior or edges of patches of secondary vegetation.

We selected the six most dominant tree species based on their IVI scores (Table 1) for studies of foliage arthropod biomass and leaf chemistry. Arthropod biomass (biomass per g of foliage) for each of six tree species was determined by sampling foliage arthropods monthly from May 2007 to July 2010 using the branch clipping technique developed by Johnson (2000). This technique involved placement of a cloth bag 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 draw string around the bag opening. Next, the enclosed branch was cut using a tree pruner. The closed bag with the foliage sample was lowered to ground level where the foliage sample and bag were weighed to the nearest 2 g with a Pesola spring scale. The bag weight was subtracted from the total weight to obtain the weight of the foliage sample. Once weighed, the bag was shaken to dislodge arthropods prior to opening the bag. Once opened, the bag and foliage contents were carefully inspected and all arthropods were captured with forceps or aspirator.

All captured arthropods were placed in plastic vials and preserved in 70 % ethanol and taken to a lab where they were sorted and counted using a dissecting scope of 0.8–3.5× magnification. Each arthropod was classified to order or family and measured to the nearest 1 mm with a plastic ruler. Five branch clip samples (one branch sample per individual) were collected for each tree species during each monthly sampling session. The lengths of the arthropods were converted to biomass using taxa-specific length-mass regressions for Jamaican foliage arthropods (Johnson and Strong 2000). Arthropod biomass (mg) per g of foliage clipping is reported for total arthropods and separately for herbivorous and predaceous arthropods, as well as separately for Araneae, Coleoptera, and Lepidoptera larvae. The latter three orders were the most important taxa found in regurgitation samples obtained from each of the five bird species (Beltrán Salazar 2012). Although the branch clipping method provides an inadequate sample of fast flying insects such as Dipterans (Johnson 2000), we believe it provides an accurate measure of abundance of the arthropod prey consumed by the insectivorous birds in this study.

For biomass calculations the herbivorous arthropod taxa included the orders Homoptera (families Flatidae and Membracidae), Hemiptera, Lepidoptera larvae, and Orthoptera (families Tettigonidae and Acrididae), and Coleoptera (families Elateridae, Chrysomelidae, Cerambycidae, and Curculionidae). Taxa classified as predacious arthropods included Hymenoptera (family Formicidae) and Araneae and the Coleoptera family Coccinelidae.

Table 1 Tree species composition and Importance Value Index (IVI) along vegetation transects in a novel *Prosopis–Leucaena* woodlands, southwestern Puerto Rico

Plant species	IVI (%)	N
Prosopis juliflora	25.81	59
Leucaena leucocephala	20.79	151
Bucida buceras	9.20	12
Tamarindus indica	7.51	9
Pithecellobium dulce	7.25	22
Albizia lebbeck	6.67	14
Pilosocereus royenni	6.34	21
Guaicum officinale	3.87	11
Adelia rincilla	1.98	5
Bourreria succulenta	1.79	3
Guazuma ulmifolia	1.64	5
Zizyphus reticulata	1.33	3
Cordia alliodora	1.06	2
Tabebuia heterophylla	0.86	1
Sweetenia mahagoni	0.84	3
Piscidia carthagenensis	0.79	2
Parkinsonia aculeata	0.61	1
Melicoccus bijugatus	0.58	1
Lantana involucrata	0.58	1
Colubrina arborescens	0.5	5

IVI calculated based on relative dominance, relative density, and relative frequency of plant species as described in the methods

N number of individual plants

Leaf chemistry

Foliage samples for chemical analysis were collected from terminal leaves on lower branches from each of the six tree species in February and July 2010. For each sample, 25 fresh leaves were removed from five individuals of each tree species, and placed in sealed plastic bags on ice in insulated containers. Then, on the day of collection, leaves were transferred to the laboratory, where each leaf was weighed with a microbalance (Model AB104-S/SCT Mettler, Toledo, Greifensee, Switzerland). Petioles were removed from all leaves sampled before determination of fresh mass. In addition, total leaf area of 11 leaves from each tree species was measured with an automatic leaf-area meter (Model 3100 Li-Cor, St. Lincoln, NE). Leaves were dried at 60 °C for 72 h and leaf water content was calculated as the difference between dry mass and fresh mass. Leaf toughness was measured in the field within 30 min of collection with a penetrometer (Model 509-1000, Chatillon Instruments, New York, NY), which registered the pressure required to punch a rod 3.1 mm in diameter through the leaf lamina. We placed each leaf between two sheets of plexiglass that had several drilled holes to accommodate the penetrometer tip and held the leaf lamina in place. The penetrometer tip was then pressed against the leaf lamina until it broke through the lamina, and the mass (g) required to produce the breakthrough pressure was recorded from the indicator on the penetrometer. We took one or two measurements from 11 leaves in each sample, depending on leaf size. Leaf toughness measurements were restricted to the three tree species with leaves or leaflets of adequate size to fit in the penetrometer. Dry leaves of each tree species were ground into a fine powder using a ball mill grinder (Model MM200, Retsch Inc., Newton, PA), and percent dry mass foliar carbon and nitrogen was determined by microcombustion with a nitrogen-carbon analyzer (Model

Tru Spec CN, Leco Corp., St. Joseph, VA). In addition, another 20-g sample of ground leaves from each tree species was used to measure foliar concentration of hemicellulose (H) and lignin (L) at the UC Davis Analytical Lab, University of California. Analyses of fiber (neutral detergent fiber [NDF] and acid detergent fiber [ADF]) were conducted following the official methods 973.18 and 2002–2004 of analysis of AOAC (AOAC International 1997, 2006). H was calculated as NDF minus ADF.

Statistical analyses

Tree species preference of each bird species was evaluated by comparing differences between observed and expected frequencies of foraging observations with chi squared goodness of fit tests. A multivariate analysis of variance (MANOVA) was used to test for significant differences in the major arthropod taxa among tree species. One-way analyses of variance (ANOVA) were conducted to reveal differences in arthropod biomass among tree species by herbivorous, predaceous, and total arthropods. In addition, leaf chemical traits (N, C/N ratio, L, L/N ratio, H, H/N ratio) and toughness were compared among tree species using one-way ANOVAs. Because we ran numerous one-way ANOVAs we used Bonferroni adjusted P values to control for inflation of experiment-wise error rate (Rice 1989). When ANOVAs indicated statistical differences, Tukey–Kramer post hoc tests were used to determine where differences occurred in pairwise comparisons. Spearman correlations were used to characterize relations between foliage arthropod biomass with leaf chemical constituents for the six tree species and P values for these correlations were adjusted with sequential Bonferroni corrections (Holm 1979). A Spearman correlation was also used to characterize the relation between biomass of herbaceous and predaceous arthropods on the foliage of a tree species. All tests were performed using STATISTICA v. 5.1 (Statsoft 2000). Biomass data used for ANOVAs were transformed using log $(X + 0.001)$ to meet assumptions of normality (Sokal and Rohlf 1995). In all statistical tests, a P value of ≤ 0.05 was accepted as significant, but larger values are shown for descriptive purposes. All P values shown for one-way ANOVAs and Spearman correlations have been adjusted with the Bonferroni correction.

Results

A total of 323 trees and shrubs belonging to 20 plant species were sampled along 13 transects through the study area (Table 1). The six most dominant tree species based on relative IVIs were selected for study and included one native species (*B. buceras*) and five naturalized alien species (*P. juliflora*, *Leucaena leucocephala*, *Tamarindus indica*, *P. dulce*, and *A. lebbeck*). For simplicity, we henceforth refer only to the genus name of each of these species.

Mist net capture rates for the winter period (September–April) from September 2007 to December 2010 indicated that ADWA was the most abundant bird species (2.31 captures/100 net h) followed by PRFL (1.79 captures/100 net h), CAEL (1.44 captures/net h), PRAW (1.33 captures/100 net h), and NOPA (0.89 captures/100 net h).

Observations pooled for the five bird species when foraging on arthropods showed that *Prosopis* and *Pithecellobium* were used as foraging substrates in higher proportion than their availability based on the IVI, whereas the other four tree species were used in equivalent or lower proportions than their importance values (Fig. 1). Comparisons between observed and expected frequencies of tree use indicated that all bird species were

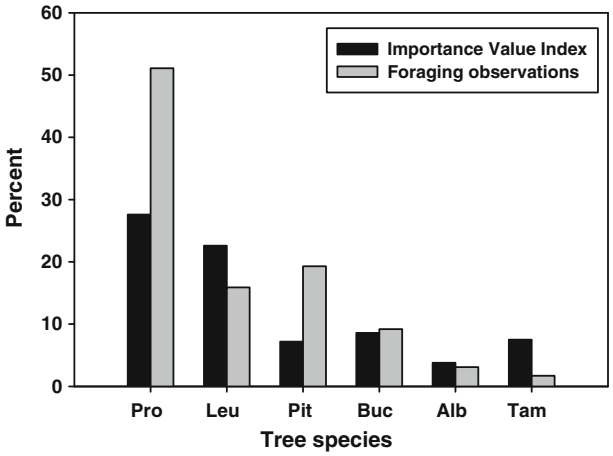

Fig. 1 Percentage of total foraging observations and importance value index (IVI) for six tree species based on 13 vegetation transects in a novel *Prosopis–Leucaena* woodlands, southwestern Puerto Rico. Foraging was observed from September through April and the percentage calculation based on 1,630 observations from five bird species, including Adelaide's Warbler, Caribbean Elaenia, Northern Parula, Prairie Warbler, and Puerto Rican Flycatcher. IVI values were based on 20 tree species and the index includes the sum of densities, frequencies of occurrence, and basal areas for individuals of each tree species. Tree species codes are Pro, *Prosopis juliflora*; Pit, *Pithecellobium dulce*; Tam, *Tamarindus indica*; Leu, *Leucaena leucocephala*; Buc, *Bucida buceras* and Alb, *Albizia lebbeck*

selective in their foraging substrates (Table 2), although the degree of selectivity as measured by the preference index was variable (range 35.9 for PRAW to 72.6 for PRFL).

Only *Prosopis* was strongly preferred (i.e., tree preference for positive values >5 % and aversion for negative values >5 %; Gabbe et al. 2002) by all bird species as a foraging substrate (Fig. 2). Next in importance was *Pithecellobium*, which was strongly or moderately (i.e., ADWA) preferred as a foraging substrate by all species except the CAEL, which foraged in it only in a proportion equivalent to its availability. The *Leucaena* was avoided by four species and PRAW was indifferent to its use (i.e., foraged in it in proportion to its availability). *Bucida* was used by four species in proportions similar to its availability and only NOPA showed a weak preference for it. The *Albizia* was used by all bird species in proportions similar to its availability, whereas *Tamarindus* was consistently avoided by all bird species.

Mean biomass for all arthropods varied significantly among tree species (One-way ANOVA, $F_{1,5} = 13.81$, $P < 0.0001$). The highest mean arthropod biomass values were found on *Prosopis*, *Pithecellobium*, and *Leucaena*, all of which differed significantly from the lower mean biomass found on *Albizia, Bucida*, and *Tamarindus* (Fig. 3a). Mean biomass of herbivorous and predaceous arthropods both varied significantly among the tree species (One-way ANOVAs: $F_{1,5} = 10.13$ and $F_{1,5} = 6.19$, both $P < 0.01$, respectively). Herbivorous arthropods showed higher mean biomass on *Prosopis*, *Leucaena*, and *Bucida* than on the other tree species (Fig. 3b). Predaceous arthropods showed higher mean biomass on *Prosopis*, *Pithecellobium*, and *Leucaena* than on the remaining tree species (Fig. 3c).

The distribution of three major arthropod orders differed among the tree species as evidenced by significant differences in biomass on foliage of the six tree species (MANOVA, Wilk's lambda $F_{3,15} = 17.45$, $P < 0.01$). Both *Prosopis* and *Pithecellobium* had

Table 2 Preference index (PI) for five bird species foraging on arthropods from September to April in six tree species in a novel *Prosopis–Leucaena* woodland, in southwestern Puerto Rico

Species	PI	χ^2	*P* value	N
Puerto Rican Flycatcher	72.6	124.8	<0.0001	180
Caribbean Elaenia	52.2	64.3	<0.0001	125
Adelaide's Warbler	63.5	361.3	<0.0001	610
Prairie Warbler	35.9	35.2	<0.0001	75
Northern Parula	68	91.1	<0.0001	73

The PI is based on the sum of the absolute values of the percent deviations of observed values from the importance value index (IVI) for all species. This value represents the foraging selectivity of each bird species. Results of chi squared goodness-of-fit test and significance level are shown for comparisons of observed and expected foraging frequencies of use for six tree species. Expected frequencies were calculated by multiplying IVIs by the total number of observations for each bird species

N the number of foraging observations for each species

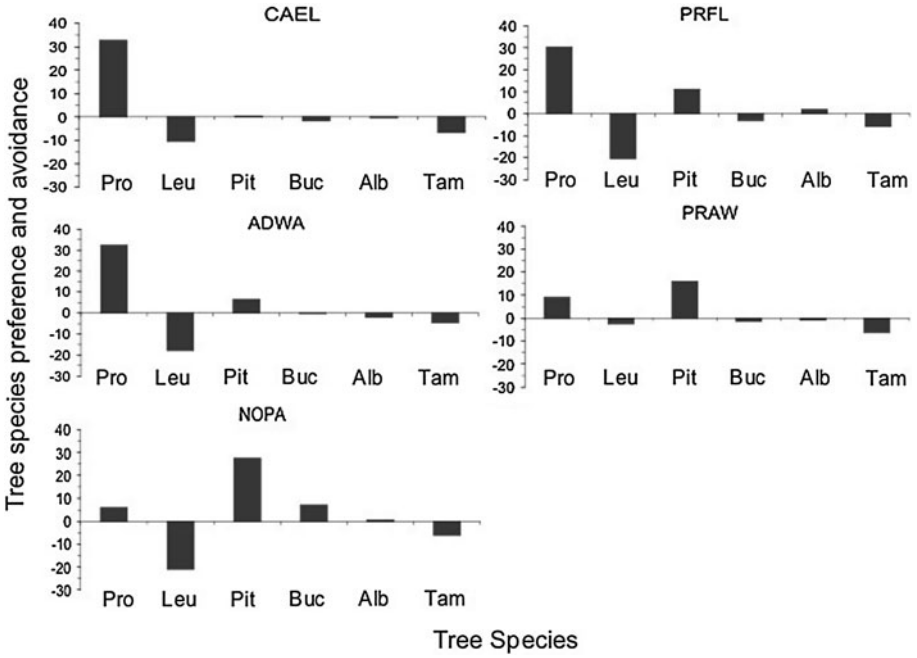

Fig. 2 Preferential use of six dominant tree species by five insectivorous bird species foraging in a novel *Prosopis–Leucaena* woodlands in southwestern Puerto Rico during September–April from 2007 to 2010. *Bars* indicate the differences (positive or negative) between the frequencies observed of birds foraging on foliage of specified tree species (coded) and the occurrence frequencies of each tree species (importance values). Bird species codes refer to Adelaide's Warbler (ADWA), Caribbean Elaenia (CAEL), Northern Parula (NOPA), Prairie Warbler (PRAW), and Puerto Rican Flycatcher (PRFL). Tree species codes are Pro, *Prosopis juliflora*; Pit, *Pithecellobium dulce*; Tam, *Tamarindus indica*; Leu, *Leucaena leucocephala*; Buc, *Bucida buceras* and Alb, *Albizia lebbeck*

significantly higher Araneae and Coleoptera mean biomass values than the other tree species (ANOVA, $F_{1,5} = 7.77$ and $F_{1,5} = 20.58$, respectively; $P < 0.01$, Fig. 4). *Leucaena* had significantly higher biomass of Lepidoptera larvae than the other tree species

(ANOVA, $F_{1,5} = 1614.64$, $P < 0.01$; Fig. 4). *Bucida*, *Leucaena* and *Albizia* showed similar and intermediate Araneae biomass values, which were significantly higher than found on *Pithecellobium.* Both *Leucaena* and *Albizia* had intermediate levels of Coleoptera

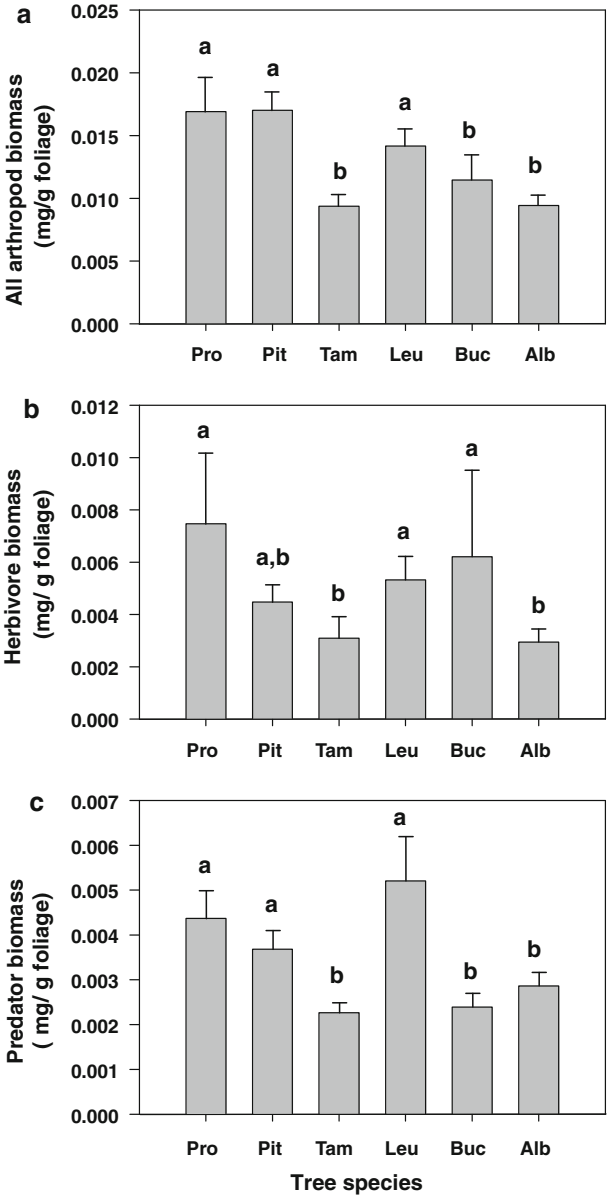

Fig. 3 Mean (±SE) arthropod biomass (mg/g foliage) for **a** total arthropods, **b** herbivorous arthropods, and **c** predaceous arthropods found on six tree species during September–April from 2007 to 2010 in a novel *Prosopis–Leucaena* woodland in southwestern Puerto Rico. Tree species codes are Pro, *Prosopis juliflora*; Pit, *Pithecellobium dulce*; Tam, *Tamarindus indica*; Leu, *Leucaena leucocephala*; Buc, *Bucida buceras* and Alb, *Albizia lebbeck*. *Different letters above* each *bar* denote means that are statistically different ($P < 0.05$)

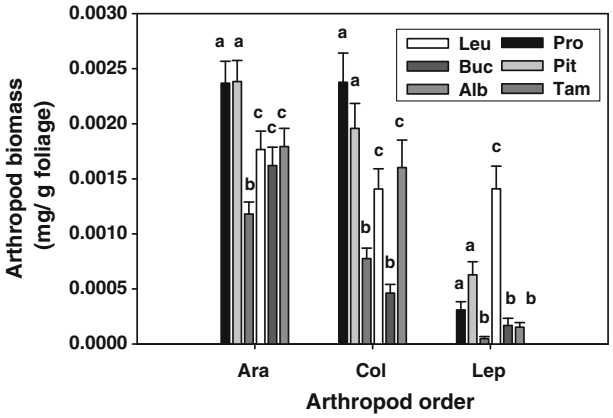

Fig. 4 Mean (±SE) Araneae (Ara), Coleoptera (Col), and Lepidoptera larvae (Lep) biomass (mg/g branch clip) found on six tree species in September–April from 2007 to 2010 in a novel *Prosopis–Leucaena* woodland in southwestern Puerto Rico. *Different letters above* each *bar* denote means that are statistically different ($P < 0.05$). Tree species codes are Pro *Prosopis juliflora*, Pit *Pithecellobium dulce*, Tam *Tamarindus indica*, Leu *Leucaena leucocephala*, Buc *Bucida buceras* and Alb *Albizia lebbeck*

biomass, which were significantly higher than found on *Bucida* and *Tamarindus. Prosopis* and *Pithecellobium* had intermediate levels of Lepidoptera biomass, which were significantly greater than found on *Tamarindus*, *Bucida*, and *Albizia.*

Significant differences in leaf nitrogen content and C/N ratios were found among the tree species (One-way ANOVAs, nitrogen $F_{1,5} = 10.73$; C/N ratio $F_{1,5} = 162.29$; both tests $P < 0.01$; Table 3). Percent nitrogen content was highest in *Leucaena*, *Prosopis*, and *Albizia* all of which had significantly higher percent nitrogen values than found in *Pithecellobium*, *Tamarindus*, and *Bucida.*

Both percent lignin and L/N ratios varied significantly among tree species (one-way ANOVA: $F_{1,5} = 164.15$, $P = 0.05$ and $F_{1,5} = 88.11$, $P < 0.01$; respectively). High percent lignin values were found in *Albizia*, *Prosopis*, and *Tamarindus* in contrast to low values in *Leucaena* and *Bucida.* The L/N ratio values ranged from lowest values in *Leucaena* to the highest values in *Tamarindus*, with intermediate values in the other species. Hemicellulose values and H/N ratios varied significantly among the tree species ($F_{1,5} = 604.4$ and $F_{1,5} = 81.89$, respectively; both $P < 0.01$). Both *Albizia* and *Tamarindus* had high hemicellulose content in contrast to the remaining species, which had uniformly lower values (Table 3). High hemicellulose/N ratio values were characteristic of *Tamarindus*, whereas low values were found in *Leucaena* and *Pithecellobium.*

Leaf water content and toughness varied significantly among tree species (One-way ANOVAs: $F_{1,5} = 8.51$ and $F_{1,2} = 51.07$, respectively; both $P < 0.01$; Table 3). Percent water content was highest in leaves of *Leucaena*. Leaf toughness was higher in *Bucida* (mean = 446.82 ± 15.47 SE) than in *Albizia* (mean = 257.25 ± 13.49 SE) and *Pithecellobium* (mean = 140.00 ± 18.39 SE).

We found correlations between various leaf constituents and the mean biomass of predaceous arthropods. For example, mean biomass of predaceous arthropods showed significant negative correlations with the lignin/N ratio (Spearman $r = -1.0$, $n = 6$, $P < 0.008$), hemicellulose/N ratio (Spearman $r = -0.94$, $n = 6$, $P < 0.01$) and C/N ratio (Spearman $r = -0.87$, $n = 6$, $P < 0.013$). No statistically significant correlations were

Table 3 Mean (±SE) chemical composition of leaves of six tree species sampled in a novel *Prosopis–Leucaena* woodlands in southwestern Puerto Rico

Tree species	Nitrogen	C/N ratio	Mean percent dry weight				
			Lignin	L/N ratio	Hemicellulose	H/N ratio	Water
Prosopis juliflora	3.76 ± 0.18a	13.27 ± 0.59d	12.85 ± 0.05b	2.91 ± 0.11c	9.81 ± 0.01a	2.12 ± 0.09a	56.53 ± 1.54c
Pithecellobium dulce	2.66 ± 0.09b	18.25 ± 0.68c	9.41 ± 0.03a,b	3.22 ± 0.23c	10.01 ± 0.02a	3.43 ± 0.25b	49.08 ± 1.09c
Tamarindus indica	1.78 ± 0.05b	27.48 ± 0.86b	14.41 ± 0.02b	7.71 ± 0.05d	16.41 ± 0.01b	8.78 ± 0.06c	60.76 ± 1.06b
Leucaena leucocephala	4.48 ± 0.14a	10.81 ± 0.33a	5.31 ± 0.05a	1.33 ± 0.16a	9.11 ± 0.11a	2.28 ± 0.27a	67.64 ± 2.76a
Albizia lebbeck	3.82 ± 0.16a	13.31 ± 0.41d	13.71 ± 0.04b	4.48 ± 0.13b	16.41 ± 0.05b	4.57 ± 0.13b	58.98 ± 1.39c
Bucida buceras	1.39 ± 0.04b	33.15 ± 1.02e	7.45 ± 0.25a,b	4.68 ± 0.26b	9.81 ± 0.11a	6.16 ± 0.19d	53.19 ± 1.01b

Three individuals were sampled per tree species. Different letters following the SE value denote means that are statistically different ($P < 0.05$)

found between mean biomass of herbaceous arthropods and various leaf constituents (strongest correlation was with hemicellulose, Spearman $r = -0.79$, $P > 0.05$).

Discussion

The five avian insectivores showed distinct tree species preferences for foraging with strong preferences for *Prosopis* evident in the pooled observations indicating birds foraged in it much more frequently than expected based on its availability (i.e., importance value) and all bird species individually showed moderate to strong preferences for foraging in its foliage. *Pithecellobium* was also used more frequently than expected, based on the pooled foraging observations, and all but CAEL showed moderate to strong preferences for foraging in its foliage. At the other extreme, *Tamarindus* was avoided, as evidenced by the pooled foraging observations indicating it was used less frequently than expected based on availability and all bird species avoided foraging in it. Similarly, pooled foraging observations indicated that foraging use of *Leucaena* was less than expected based on its availability. Four bird species avoided foraging in *Leucaena* and PRAW was indifferent to its use. Although some bird species showed either preference or avoidance of *Albizia* and *Bucida*, the responses to these tree species were generally weak and not much different than expected based on availability.

Tree species preferences for foraging by the five bird species were generally consistent with expectations that the most highly preferred tree species would have the highest biomass of arthropod prey and the least preferred or avoided species would have the lowest arthropod biomass. For instance, the highly preferred foraging substrates offered by *Prosopis* and *Pithecellobium* both hosted high total arthropod biomass. The high total arthropod biomass on foliage of *Prosopis* and *Pithecellobium* reflected high biomass of Araneae and Coleoptera, both of which are important constituents of the diet of the five insectivores as found in regurgitation samples (Beltrán Salazar 2012). Biomass of Lepidoptera larvae, however, was not especially high on these two tree species, despite expectations of higher biomass based on the larvae's prevalence in regurgitation samples from the five insectivores. At the other extreme, and as expected based on avoidance by all insectivorous bird species, *Tamarindus* had low total arthropod biomass reflecting the lowest biomass of any tree species for Araneae and low Coleoptera and Lepidoptera larvae biomass. The rarely or weakly preferred *Albizia* and *Bucida* both had low total arthropod biomass (equivalent to *Tamarindus*) and low to intermediate biomass values for each of the arthropod orders.

Based on the foliage palatability hypothesis (Greenberg and Bichier 2005), we expected that the foliage of tree species with high biomass of herbivorous arthropods would be more nutritious (i.e., high N content; McNeill and Southwood 1978; Mattson 1980; White 1984) and palatable (i.e., low lignin and hemicellulose content) than foliage of tree species with low herbivore biomass, which would have low N content and high lignin and hemicellulose content. Support for these predictions came from samples of this suite of chemical constituents from leaves of two tree species at opposite extremes of the range of the foliage herbivore biomass values. At one extreme, the foliage of *Tamarindus* with low herbivore biomass was characterized by low N content, which was especially low relative to carbon (i.e., high C/N ratio). Moreover, lignin and hemicellulose content of *Tamarindus* leaves were among the highest of any sampled tree species and given its low N content, both the L/N and H/N ratio values were the highest of the six tree species. This indicates that *Tamarindus* leaves provide little nutrition in the form of N and are highly unpalatable. At

the other extreme, *Prosopis* with high herbivore biomass had foliage characterized by high N content and relatively low C/N ratio (only *Leucaena* was lower). Although lignin content of *Prosopis* leaves was among the highest values, the L/N ratio was low, reflecting the high nitrogen content. Furthermore, high N content in combination with low hemicellulose content also resulted in a low H/N ratio value, placing the H/N ratio for *Prosopis* leaves among the lowest of the six tree species. Thus the high herbivorous arthropod biomass on *Prosopis* leaves was associated with expected high N content and relatively high palatability.

Results of our comparisons of leaf chemistry with arthropod biomass were likely influenced by our use of biomass rather than population turnover as a measure of arthropod foliage use, especially for comparisons of herbivorous and predaceous arthropod biomass and their correlations with leaf chemistry. A potential problem with the use of arthropod biomass is that it is a measure of standing crop at the time of sampling and does not account for population turnover, which is usually higher in herbivores than predators and may result in an inverted trophic pyramid of biomass (i.e., higher biomass of predators than herbivores that nourish them; Odum 1971). Although we found no evidence for an inverted trophic pyramid of biomass, the correlation between herbivorous and predaceous arthropod biomass was weak and statistically nonsignificant (Spearman $r = 0.429$, $n = 6$, $P = 0.194$). This result indicates that the biomass of herbivorous arthropods explains only 19 % of the variation in the biomass of predaceous arthropods on the same tree species and thus results of correlations of biomass with leaf chemistry may not be congruent between herbivorous and predaceous arthropods. In addition, avian insectivores may have depressed arthropod biomass before foliage was sampled, a likely possibility given results of exclusion experiments conducted previously at our study site demonstrating that birds can depress foliage arthropod abundance in these woodlands (Baltz 2000). Thus biomass, as a measure of arthropod standing crop at the time of sampling, may not fully measure arthropod use of the foliage of the different tree species. Therefore, use of the biomass measure may have contributed to the lack of congruence between herbivorous and predaceous arthropod biomass in the results from correlations with leaf chemistry.

Despite expectations for a lack of concordance in correlation results from herbivorous and predaceous arthropod biomass with leaf chemistry, our results were consistent with expectations from the foliage palatability hypothesis. For example, the biomass of predaceous arthropods showed strong negative correlations with the ratios of L/N and H/N indicating that predaceous arthropod biomass was highest on tree species with foliage containing potentially high nutrient content (N) and high palatability (i.e., low lignin or hemicellulose). These relationships may reflect an abundance of herbivorous arthropod prey (responding directly to higher N and palatability) for the predaceous arthropods, but not evident in our measures of herbivore biomass.

Although the leaf palatability hypothesis was supported by the suite of measures including N, lignin, and hemicellulose and their ratios at the extremes of herbivorous arthropod biomass values typified by *Tamarindus* and *Prosopis*, the association of herbivore biomass with our measures of leaf chemistry was not as consistent in the other tree species. In addition, herbivore biomass was not correlated with N content or any of the individual ratios in which N was included (C/N, L/N, and H/N) in the leaves of the six tree species. This lack of association of arthropod herbivore biomass with our measured chemical constituents may have resulted from the presence of secondary plant compounds not measured in our study and/or with the limitations of using total N as a measure of nutrient availability for herbivorous arthropods. For instance, total N content may include nitrogen-based secondary compounds and insoluble proteins, which are of little nutritional

value to insects (Mattson 1980). Nor does total N indicate the quality of amino acids and proteins present in leaves (McNeill and Southwood 1978). This may apply to *Albizia* foliage, which had low biomass of herbivorous arthropods despite high N content. In *Albizia*, some of the N is contributed by non-protein amino acid albizzine and pipecolic acid, which have insecticidal properties (Shea and Romeo 1991; Romeo 1984). Thus these compounds together with high lignin and hemicellulose content may discourage herbivorous arthropod use of *Albizia* leaves.

Leucaena was notable in having foliage with high N content, low lignin and hemicellulose content, and the expected high herbivorous arthropod biomass, but nonetheless, was visited by avian insectivores less frequently than expected and avoided by four bird species. This avoidance or low foraging use was unexpected because *Leucaena* also had high total arthropod biomass, which was equivalent to *Prosopis* and *Pithecellobium*. *Leucaena* differed from the latter two tree species in having lower biomass values for Araneae and Coleoptera, but significantly higher biomass of *Lepidoptera* larvae of any of the tree species. In *Leucaena* foliage, the non-protein amino acid mimosine contributes to its high total N content, and together with appreciable amounts of condensed tannins can serve as a defense against insect herbivores and browsing ruminants (Hammond 1995; Bell 2003). Nevertheless, some herbivores are not deterred by these compounds such as the *Leucaena* psyllid, which can break down mimosine (Kamada et al. 1996). The high biomass of Lepidoptera larvae on *Leucaena*, suggests they too may be capable of breaking down the secondary compounds and/or have the ability to sequester the compounds, thereby potentially protecting the larva from insectivorous birds (Nishida 2003; Harvey et al. 2003). The avoidance of *Leucaena* for foraging by four insectivorous bird species suggests avoidance of prey with sequestered compounds.

We did not test the hypothesis that tree species preferences shown by the five insectivore species were due to differences in species-specific preferences for foraging substrates. Tree species differences in vegetation structure have been shown to affect insectivore foraging behavior and tree species preferences (e.g., Holmes and Robinson 1981; Parrish 1995a, b; Whelan 2001). Avian insectivores may primarily select tree species with structure (e.g., foliage structure, petiole length, and branching characteristics) appropriate to their specific behavior and morphology that facilitate foraging efficiency (Greenberg and Gradwohl 1980; Holmes and Robinson 1981; Robinson and Holmes 1982). Therefore, given trees with appropriate structure, an avian insectivore would secondarily select those tree species with the highest arthropod abundance. Therefore it is possible that *Leucaena*, despite its high arthropod biomass, is avoided by the four insectivore species because of inappropriate vegetation structure for efficient foraging. Although we did not measure vegetation structure we note that *Leucaena* has bipinnately compound leaves similar to those of the highly preferred *Prosopis*, suggesting that *Leucaena*'s leaf structure might not be an issue in avoidance by the four insectivore species. Future studies, however, are needed to quantify the role of vegetation structure in the tree species avoidance and preference shown by the insectivores in our study.

Our findings from the two thorny tree species in our study (*Prosopis* and *Pithecellobium*) are consistent with previous studies indicating that thorny mimosoid legumes have a high abundance of foliage arthropods and hence are preferentially utilized by insectivorous birds (Greig-Smith 1978; Greenberg et al. 1997). Plant mechanical defenses, such as thorns, while providing a defense against ruminants, may require a concomitant reduction in chemical defenses against herbivorous arthropods, as posited by the defense trade-off hypothesis (Greenberg et al. 1997). In other words, energy allocated to a plant's defenses may be limited during development and hence energy spent on mechanical defenses limits

the energy available for chemical defenses or vice versa. Support for the hypothesis comes from observations that spinescent plants (primarily mimosoid legumes) tend to be highly palatable in contrast to non-spiny plants that are unpalatable (Coe and Coe 1987; Owen-Smith and Cooper 1987; Cooper et al. 1988). Therefore, thorny tree species growing in dry woodlands may be dependent on high browser and grazer densities to compete with thornless trees, which may have better chemical defenses against herbivorous arthropods. This suggests that foliage of thorny woody legumes in the novel *Prosopis–Leucaena* woodlands is well defended against livestock, but poorly protected from herbivorous insects as found in our study. Thus these thorny leguminous trees were pre-adapted for defense against herbivory by domestic livestock when introduced to the Caribbean, which may contribute to their success as alien invasive species.

Although our study was not designed to test the enemy release hypothesis (Liu and Stiling 2006) some of our findings are relevant to the hypothesis, especially when compared with results obtained from native tree species in native forests. Based on this hypothesis, we expected that the alien tree species of the *Prosopis–Leucaena* woodlands "escaped" many of their species-specific arthropod pests when introduced to Puerto Rico. As communities dominated by alien tree species the *Prosopis–Leucaena* woodlands might be expected to have foliage with lower arthropod densities than found on foliage in native forests that have their full complement of species-specific arthropods, which have co-evolved with their native hosts. Unfortunately, arthropod biomass samples are unavailable from foliage of native trees in subtropical dry forest in Puerto Rico, which would allow comparisons with our samples. However, arthropod biomass samples from native trees in native subtropical dry forests elsewhere in the Caribbean may permit comparisons.

Arthropod biomass samples are available for comparison from seasonally dry limestone forests of native tree species on Jamaica (Johnson and Sherry 2001) and Eleuthera, The Bahamas (Wunderle et al. unpubl. data). At all locations, foliage arthropods were sampled using the same branch clip method during similar winter periods (3 November–24 March, Jamaica; 10 November–30 April, Eleuthera), but analyses from Jamaica excluded arthropods >10 mm (except Lepidoptera). Arthropod biomass samples from foliage of randomly sampled native trees in seasonally dry native forest ranged from a mean of 0.033 ± 0.005 SE mg/g clipping from Eleuthera to 0.052 ± 0.007 SE mg/g clipping on Jamaica. These mean values suggest that arthropod biomass on native dry forest tree species on Jamaica is higher, but only slightly higher on Eleuthera than found on the alien tree species (highest mean biomass of 0.017 ± 0.003 SE mg/g clipping from *Prosopis*) in the novel *Prosopis–Leucaena* woodlands.

Only one native tree species, *Bucida*, was available for comparison with the alien tree species in our woodlands and most insectivorous birds were indifferent to foraging in it with the exception of the NOPA, which showed a weak preference for it. The low overall avian use of *Bucida* foliage for foraging was consistent with its relatively low biomass of total arthropods, but the mean biomass of herbivorous arthropods on its foliage was among the highest mean biomass values (equivalent to *Prosopis*, *Pithecellobium*, and *Leucaena*). This relatively high herbivorous insect biomass was unexpected given the low N content of its leaves and our finding that *Bucida* leaves were the toughest of the three species tested. Nonetheless, the lignin and hemicellulose content of its leaves were among the lowest recorded, suggesting that the toughness of *Bucida* leaves resulted from an unmeasured fiber constituent, such as cutin. Perhaps, the arthropod herbivores on *Bucida* foliage have evolved mechanisms or behaviors that allow use of low N levels while bypassing or ameliorating deterrent effects of toughness on palatability and/or epiphyll on the leaf surface provides adequate resources for some herbivorous arthropods (Peeters 2002).

Whatever the underlying cause of the relatively high herbivorous arthropod biomass on *Bucida*, as a native tree species its herbivore biomass was not especially high in comparison to herbivore biomass on aliens *Prosopis*, *Pithecellobium*, and *Leucaena* as might be expected from the enemy release hypothesis.

Although future studies in these *Prosopis–Leucaena* woodlands are needed to test the enemy release hypothesis by comparing foliage arthropod abundance within a tree species in both its site of origin and introduction, it appears that the effects of enemy release on foliage arthropod abundance on alien trees were likely minimal. Avian insectivores showed preferences for foraging in some of the alien trees with high foliage arthropod biomass. Foliage arthropod biomass was related to measures of leaf nutrition and palatability suggesting that the foliage palatability hypothesis applies to the tree species preferences of avian insectivores foraging in alien and native tree species in this novel community.

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