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Infructescence size has a larger effect than light environment on the abundance of different arthropod feeding guilds dwelling on the infructescences of a terrestrial bromeliad in a xerophytic forest

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ABSTRACT

Bromeliads are a conspicuous feature of many Neotropical xerophytic forests. *Bromelia serra* is an understory bromeliad living in xerophytic forests of the Humid Chaco, which shows high phenotypic plasticity when exposed to different environmental conditions. Its infructescences carry many fleshy fruits that are colonized by arthropods from different feeding guilds. We used structural equation modeling and redundancy analysis to evaluate the influences of light environment, plant size, and infructescence size on the abundance of five different feeding guilds of arthropods dwelling on the infructescences ('fruit-secretion feeders,' 'infructescence-detritus feeders,' 'predators,' 'pulp feeders' or 'seed feeders'). Plant size was negatively associated with canopy openness, whereas infructescence size was positively associated with plant size. The abundance of all feeding guilds, except fruit-secretion feeders, were positively associated with infructescence size.

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Bromeliads; feeding guilds; infructescence size; light environment; phenotypic plasticity

Introduction

Habitat conditions are known to have a direct effect on fruit selection by animals by affecting their behaviors. Several studies have analyzed the influences of habitat on fruit foraging by vertebrates (Piper 1986; Jordano 2000) and fruit colonization by arthropods (Quilici & Rousse 2012; Migani et al. 2014). However, habitat may also have an indirect effect on fruit selection by affecting plant growth and therefore fruit production and fruit size (Schupp & Fuentes 1995). Large fruit and infructescences are known to attract higher numbers of mammals (Debussche & Isenmann 1989), birds (Snow 1971; Thébaud & Debussche 1992; Valido et al. 2011), and invertebrates (Sivinski 1991; Wang et al. 2009; Migani et al. 2014) than smaller ones.

Plant species of Neotropical forests are characterized by a large diversity of fleshy fruits, encompassing a wide range of forms, sizes, and arrangements, i.e. single fruits or infructescences (Wheelwright et al. 1984; Almeida-Neto et al. 2008). A conspicuous feature of many of these Neotropical forests is the presence of terrestrial bromeliads growing in the understory (Brokaw 1983; Scarano et al. 1999; Barberis et al.

2014). Many of these understory bromeliad species produce large infructescences with fleshy fruits (Smith & Downs 1979), which are consumed by vertebrate species (Janzen & Martin 1982; Almeida Jácomo et al. 2004; Keuroghlian et al. 2009), and used by many arthropod species (Gutiérrez Ochoa et al. 1993; Frank & Lounibos 2009).

Some of these bromeliads are known to be highly variable in shape when exposed to different light environments (Lee et al. 1989; Mantuano & Martinelli 2007; Cavallero et al. 2009). Bromeliad plants growing in the shade are taller and have larger diameters, whereas plants growing in the sun have more leaves, and larger sheath mass fraction (Lee et al. 1989; Cárcamo et al. 2006; Cavallero et al. 2009). On the other hand, the size of the reproductive structures is associated with plant size, and it has been demonstrated for several wild and cultivated bromeliad species that plants with more leaves, longer leaves, and larger diameters produced infructescences with more and heavier fruits (Overbeek 1946; Zotz et al. 2005; Scrok & Varassin 2011; Fassinou Hotegni et al. 2015). Therefore, larger infructescences are expected for bromeliads growing in the shade.

The xerophytic forests of the Southern Chaco (northern Argentina) are characterized by a high spatial heterogeneity, with dense woody patches in convex areas and open grassy patches in depressed areas (Lewis 1991; Barberis et al. 1998). Beside higher light intensity, the open areas have also higher temperatures and lower humidity than areas with dense vegetation (Cavallero et al. 2009). The understory of the *Schinopsis balansae* (Anacardiaceae) forests is colonized by dense populations of two terrestrial bromeliad species: *Aechmea distichantha* Lem. and *Bromelia serra* Griseb. (Barberis et al. 2002, 2014). *Bromelia serra* plants show high phenotypic plasticity: individuals growing in the sun have fewer leaves, smaller diameter, and smaller infructescences than those growing in the shaded understory (Cárcamo et al. 2006). Its infructescences can bear several dozens of fruits (Smith & Downs 1979), which are foraged by several bird and mammal species (Parera 2002) and consumed by several indigenous peoples of the Gran Chaco (Scarpa 2009). The infructescences are colonized by numerous arthropods from different feeding guilds (e.g. ‘fruit-secretion feeders,’ ‘infructescence-detritus feeders,’ ‘predators,’ ‘pulp feeders’ or ‘seed feeders’), but to our knowledge there is no study describing the abundance, diversity or species composition of arthropods dwelling on them.

The abundance of arthropods dwelling on the infructescences of *B. serra* plants could be associated with (1) the light environment where the plants grows, as well as with (2) the size of the infructescences. However, to our knowledge no study has yet assessed whether feeding guilds differ in their response to these factors. Therefore, in this paper, we first described the arthropods associated with the infructescence of *B. serra*. Then, we used structural equation modeling (Pugesek et al. 2003; Grace et al. 2010) to evaluate the direct and indirect influences of these factors on the abundance of different feeding guilds of arthropods dwelling on the infructescences of *B. serra* plants growing in the understory of a *S. balansae*-dominated forest in Argentina. Finally, we used redundancy analysis to examine the correlations between the abundance of different feeding guilds and descriptors of infructescence size and light environment.

Material and methods

Study site

The study was conducted in a 400 ha stand of a *S. balansae*-forest (‘quebrachal’; Lewis et al. 1997) located at Las Gamas, Santa Fe, Argentina (Estación Experimental Tito Livio Coppa, 29°28’S, 60°28’W, 58 m asl). The climate is humid

temperate to warm, with a mean annual temperature of about 20°C, and a mean annual precipitation of about 1,000 mm. Rainfall is concentrated in summer (December–March), and a dry season of variable length occurs in winter (June–August). The forest is located on a mosaic of soils with low hydraulic conductivity and high sodium content (Barberis et al. 1998). The soil surface has a noticeable microrelief comprising elevation differences of up to 50 cm over distances of a few meters (Barberis et al. 1998).

Bromelia serra occurs as terrestrial understory plant on relatively elevated patches (Lewis 1991; Barberis et al. 2002). This bromeliad may propagate both sexually and asexually (Smith & Downs 1979; Bianchi et al. 2000; Klekailo et al. 2012), but asexual reproduction is more common in these forests (Benzing 2000; I.M. Barberis, pers. obs.). The axis of the inflorescence is reduced and the flowers are arranged close together (Fernandes Monteiro et al. 2015), thus the infructescence has a globose shape (about 10–14 cm long by 7–10 cm in diameter) (Caffini et al. 1988), which bears dozens of yellow tricarpeal berries of about 4 × 2.5 cm size (Nájera 1974; Caffini et al. 1988), that carry up to 55 reddish-brown seeds (Barberis et al. unpublished data), often lenticular or discoid (5 mm long × 7 mm high × 3 mm wide) (Amat 1988). A gum is often recorded in the infructescences (Nájera 1974), which is mainly composed of neutral sugars (galactose, xylose, and arabinose) and acid oligosaccharides (xylose-galacturonic acid) (Caffini et al. 1976). Even though there are many gum cavities in the outer area of the ovarian mesophyll, gummosis is restricted to the fruit stage (Bernardello et al. 1991), and the gum is produced by schizolysogenic structures (Nájera 1974). In the last state of ripening, *B. serra* fruits have high content of water, soluble sugars and volatile substances that may be attractive to fruit-feeding animals, as has been reported for other bromeliads (Takeoka et al. 1989; Parada et al. 1996; Cardoso et al. 2010).

Data acquisition

In April 2011, we selected and georegioned 48 *B. serra* plants with infructescences mainly composed of ripe (i.e. yellow) fruits, which had mostly not been preyed upon by mammals or birds. To calculate canopy openness, we took a hemispherical photograph above each plant, which was analyzed with the software Gap Light Analyzer (ver. 2.0; Frazer et al. 1999). All arthropods present on the infructescences were collected and placed in flasks with alcohol (95%). For each plant, we measured its diameter and the length of the longest leaf. The infructescences were removed, labeled, placed

in individual plastic-bags to avoid any arthropods escaping, and taken to the lab. For each infructescence we measured its perimeter, and extracted and counted its fruits. As there were differences in the ripening state of the fruits within the infructescence, they were classified as ‘fresh,’ which could be either ripe (i.e. yellow and soft) or unripe (i.e. green and hard), or ‘rotten.’ We randomly selected five fruits per infructescence and counted the seed number per fruit. All arthropods found inside the plastic bags were collected. The fruits were opened with a knife and carefully inspected for the presence of adult or immature stages of arthropods. The arthropods were removed, identified to morphospecies level, and assigned to the following feeding guilds: ‘fruit-secretion feeder,’ ‘infructescence-detritus feeder,’ ‘predator,’ ‘pulp feeder’ and ‘seed feeder,’ based on personal observations, as well as on previous classifications (Silvius & Fragoso 2002; Civrtecka et al. 2014). Specimens were deposited in the entomological collection of the Universidad Nacional de Rosario (FCA-UNR).

Data analysis

For each feeding guild, we fitted a structural equation model to the data to analyze apparent direct and indirect influences of light environment, plant size, and infructescence size on the abundance of arthropods. In the model, these apparent influences were estimated as path coefficients (i.e. standardized partial regression coefficients) and represented by arrows in a path diagram connecting the included variables. Direct influences are estimated by the standardized coefficients associated with each arrow linking two variables in a path diagram, whereas when one intermediary variable exists between two other variables indirect influences are estimated as the product of the intermediate standardized coefficients (Pugesek et al. 2003).

Light environment entered in our structural equation model as the apparent influence of canopy openness on the arthropod abundance in the bromeliad infructescence. This influence could be either ‘direct’ (i.e. through associated environmental properties) or mediated by its effects on plant size which is known to control infructescence size (Overbeek 1946; Zotz et al. 2005; Scrok & Varassin 2011; Fassinou Hotegni et al. 2015). The analysis of structural equation models needs several replicates for each relationship between variables that is added to the model. As we only have 48 plants, we had to choose a proxy variable for ‘plant size’ and another proxy variable for ‘infructescence size.’ As plant diameter was highly correlated with length of the longest leaf ($r = 0.734$; $p < 0.001$), we used the latter as a measure of plant size

because plant diameter is sometimes affected by the presence of other plants (IM Barberis, pers. obs.). Likewise, as infructescence perimeter was highly correlated with number of fruits ($r = 0.854$, $p < 0.001$) we used the former as a proxy for infructescence size, because within each infructescence there are large variations in fruit size and thus the number of fruits is sometimes not representative of the infructescence size (IM Barberis, pers. obs.).

We assessed model goodness of fit with a χ^2 test comparing the variance–covariance structure implied by the model with the variance–covariance structure of the data (Pugesek et al. 2003). We further evaluated the proposed model using four other fit measures, which balance objective-simplicity and goodness of fit, the minimum discrepancy (i.e. χ^2) divided by its degrees of freedom (CMIN/DF), the root mean square error of approximation (RMSEA), the standardized root mean residual (SRMR), and the Bollen’s incremental fit index (IFI). CMIND/DF is a measure of discrepancy between the model and the data; values higher than 2 represent an inadequate fit (Arbuckle 2013). RMSEA is a measure of the degree of misspecification per model degree of freedom, adjusted for sample size (Lam & Maguire 2012). For each model, we calculated the p value for testing the null hypothesis that the population RMSEA is no greater than 0.05, indicating a close fit of the model in relation to the degrees of freedom (Arbuckle 2013). SRMR is a goodness-of-fit measurement able to discriminate good from bad models, even though it does not take into account the parsimony of the model; good models have a cutoff value lower than 0.08 (Gallart et al. 2005). IFI is a relative measure that compare the proposed model with the independent model; values close to 1 indicate a very good fit (Arbuckle 2013). We used the path coefficients to partition the estimated overall influence of each variable into direct and indirect components. We evaluated the spatial independence of errors in the estimated arthropod abundance by means of Mantel tests of the correlations between spatial distances and differences between residuals within each feeding guild (Quinn & Keough 2002).

We examined the correlations between the abundances of arthropods in different feeding guilds dwelling in the infructescences, with plant size, infructescence size, percent of fresh fruits (i.e. infructescence quality), and light environment using redundancy analysis. As the variables were measured in different units the tests were based on a correlation matrix (Quinn & Keough 2002).

The structural equation modeling was performed using the LAVAAN package (version 0.5–19) in R (Rosseel 2012). The Mantel tests and the Redundancy Analysis were carried out with PC-Ord (Version 6.0; McCune & Mefford 2011).

Results

We collected 2050 individuals from 32 morphospecies belonging to 20 families of 11 orders (Hymenoptera, Blattodea, Coleoptera, Diptera, Psocoptera, Homoptera, Lepidoptera, Araneae, Pseudoscorpiones, Hemiptera

and Collembola) (Table 1). Coleoptera was the richest order with 13 morphospecies from six families, whereas Hymenoptera was the most abundant order with three ant species (Table 1). We recorded 11 morphospecies of predators, nine morphospecies of infructescence-detritus

Table 1. Stage, individual abundance and frequency of occurrence for the morphospecies of different feeding guilds recorded on the infructescences of *Bromelia serra* plants from a xerophytic forest (n = 48 infructescences).

Morphospecies	Stage	Abundance	Frequency (%)
Fruit-secretion feeder			
Hymenoptera			
Formicidae			
Myrmicinae sp. 738	Imagines	486	14.6
<i>Camponotus</i> cf. sp. 944	Imagines	341	14.6
<i>Camponotus</i> sp. 736	Imagines	131	12.5
Infructescence-detritus feeder			
Blattodea			
Blattellidae			
<i>Ischnoptera</i> sp. 705	Imagines	4	8.3
Collembola			
Entomobryidae sp. 401	Imagines	13	12.5
Coleoptera			
Silvanidae sp. 5651	Imagines	74	41.7
Tenebrionidae sp. 5652	Imagines	4	6.3
Tenebrionidae sp. 5653	Imagines	116	66.7
Dermestidae cf sp. 5663	Larvae	3	4.2
Curculionidae sp. 900	Imagines	1	2.1
Psocoptera			
Psocidae sp. 5660	Nymph-imagines	86	18.8
Psocidae sp. 5661	Imagines	8	6.3
Predator			
Araneae			
Lycosidae sp. 871	Imagines	11	18.8
Spider sp. 5659	Imagines	1	2.1
Araneidae sp. 769	Imagines	4	6.3
Salticidae sp. 942	Imagines	5	8.3
Salticidae sp. 722	Imagines	3	4.2
Salticidae sp. 746	Imagines	2	4.2
Pseudoscorpionida			
Pseudoscorpionida sp. 5023	Imagines	64	41.7
Coleoptera			
Staphylinidae sp. 5662	Imagines	21	18.8
Staphylinidae sp. 709	Imagines	1	2.1
Staphylinidae sp. 744	Imagines	1	2.1
Hemiptera			
Reduviidae sp. 902	Imagines	1	2.1
Pulp feeder			
Coleoptera			
Nitidulidae			
<i>Neopocadius loretoensis</i> Bruch, 1938 cf.	Imagines	483	85.4
Nitidulidae cf. sp. 747	Imagines	2	4.2
Nitidulidae sp. 5654	Imagines	12	20.8
Curculionidae			
Dryophthorinae sp. 5656	Imagines	5	8.3
<i>Sphenophorus levis</i> Vaurie, 1987 cf.	Imagines	9	14.6
Diptera			
Stratiomyidae			
<i>Hermetia</i> sp. 5657	Larvae	56	6.3
Homoptera			
Diaspididae			
<i>Diaspis bromeliae</i> Kerner, 1778	Imagines	18	2.1
Lepidoptera			
Pyrilidae			
<i>Aglossa caprealis</i> Hübner, 1908	Larvae	6	6.3
Seed feeder			
Diptera			
Anthomyiidae sp. 5658	Larvae	78	35.4

feeders, eight morphospecies of pulp feeders, three morphospecies of fruit-secretion feeders, and one morphospecies of seed feeder (Table 1).

Fruit-secretion feeders were the most abundant (46.7%), followed by pulp feeders (28.8%), infructescence-detritus feeders (15.1%), predators (5.6%), and seed feeders (3.8%). Pulp feeders, infructescence-detritus feeders, and predators were found in almost all infructescences (92%, 83%, and 73%, respectively), whereas seed feeders and fruit-secretion feeders were recorded in fewer bromeliad infructescences (35% and 29%, respectively).

The sampled bromeliads were widely spread in the study site (median pairwise distance = 550.2 m;

range = 0–1463 m). They were distributed in clumps where the closest plants are separated by just few meters (Figure 1). These plants were located in places that varied widely in canopy openness, and showed large variation in plant size (i.e. plant diameter and length of the longest leaf), as well as in the size of their reproductive structures (i.e. infructescence perimeter, number of fruits per infructescences) (Figure 1).

The estimated correlation coefficients between variables included in our structural equation model were not high, but were statistically significant in 11 out of 18 cases (Table 2). The structural equation models fitted well the data of all feeding guilds (Table 3). All models had CMIN/DF values lower than 2, showed an

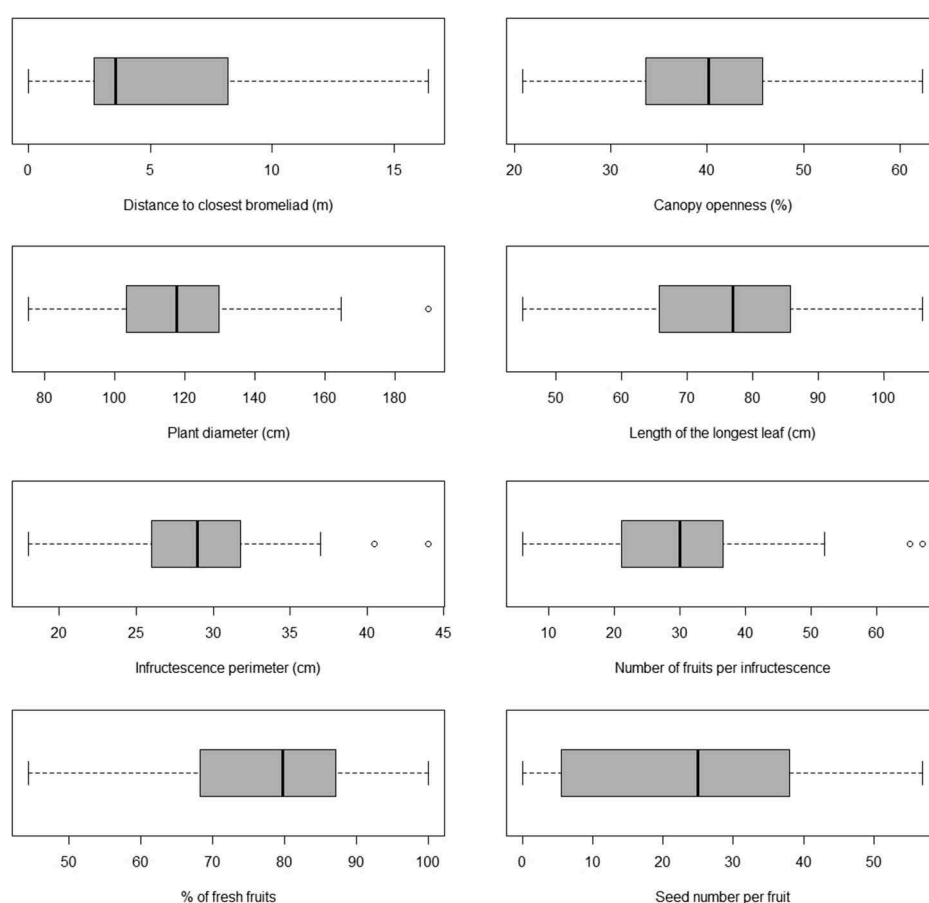


Figure 1. Boxplots of the main characteristics of the bromeliad plants and their infructescences. Each boxplot includes the 25th percentile, the median, and the 75th percentile. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles.

Table 2. Correlation coefficients between the variables included in the structural equation models. Bold values denote statistically significant correlations. Feeding guild codes: FSF (fruit-secretion feeder), IDF (infructescence-detritus feeder), PRE (predator), PuF (pulp feeder), and SeF (seed feeder).

	Length longest leaf	Infruct. perimeter	FsF	IDF	Pre	PuF	SeF
Canopy openness	-0.307	-0.217	-0.044	-0.177	-0.05	-0.270	-0.303
Length of the longest leaf		0.526	0.267	0.394	0.430	0.462	0.337
Infructescence perimeter			0.072	0.634	0.494	0.619	0.425

Table 3. Goodness of fit of the structural equation models for different feeding guilds P* is the *p* value for testing the null hypothesis that the population RMSEA is no greater than 0.05.

Feeding guild	χ^2 (CMIN)	DF	P	CMIN/DF	RMSEA	P*	SRMR	IFI	Squared Multiple Correlations
Fruit-secretion feeder	3.87	2	0.144	1.935	0.140	0.178	0.073	0.92	0.060
Infructescence-detritus feeder	0.55	2	0.757	0.278	0.000	0.781	0.027	1.03	0.401
Predator	3.40	2	0.183	1.701	0.121	0.219	0.061	0.96	0.250
Pulp feeder	1.64	2	0.439	0.823	0.000	0.481	0.040	1.01	0.397
Seed feeder	0.68	2	0.710	0.343	0.000	0.738	0.030	1.04	0.220

Table 4. Mantel test correlations (*r*) between spatial distances and differences between residuals within each feeding guild. Bold values denote statistically significant correlations.

Feeding guild	R	<i>p</i>
Fruit-secretion feeders	-0.108	0.0290
Infructescence-detritus feeders	-0.041	0.3635
Predators	-0.037	0.4172
Pulp feeders	0.067	0.1546
Seed feeders	0.005	0.9196

adequate RMSEA (< 0.05), SRMR values lower than 0.08, and IFI values close to 1 for all feeding guilds (Table 3). The models explained more than 20% of the variance of the abundance of each feeding guild, except for the fruit-secretion feeders (Table 3). According to the Mantel tests, correlations between distance and differences between the path analysis residuals were not significant for any feeding guild, except for the fruit-secretion feeders (Table 4).

According to the estimated path coefficients, bromeliad size decreased significantly with canopy openness, and infructescence size increased significantly with the increase in bromeliad size (Figure 2). The abundance of arthropod individuals increased significantly with infructescence size, but was not significantly affected by light environment (Figure 2). The only exception was the guild of the fruit-secretion feeders whose abundance was not affected by the infructescence size (Figure 2). Overall, the estimated negative indirect associations were not significant but reinforced the apparent negative direct influences of the characteristics of the light environment on the abundance of most feeding guilds (Table 5). However, the total effect of light was significant only on the abundance of the pulp feeders and seed feeders, while it was not significant for fruit-secretion feeders and infructescences-detritus feeder. In contrast, predators showed contrasting effects (i.e. positive direct effect and negative indirect effect; Table 5).

Axes 1 and 2 of the RDA (Figure 3) accounted for 28.3% of the total species variance and 29.6% of the species–environment relationship. Eigenvalues for axes 1 and 2 were 1.32 and 0.08 respectively, and the species–environment correlations were 0.77 for axis 1 and 0.28 for axis 2. There was a highly significant value ($p < 0.001$), only for the first axis and its species–environment correlation. Axis 1 displayed a gradient

of bromeliad habitat conditions. There was a gradient of plant size and infructescence size from high (left side of the scatterplot) to low (right), and a gradient of light environment ranging from low (left) to high (right). Axis 2 was positively associated with percentage of fresh fruits and with light environment. The abundances of pulp feeders and infructescence-detritus feeders were positively associated with bromeliad infructescence size, and negatively associated with light environment (Figure 3). The abundances of fruit-secretion feeders and predators were positively associated with light environment and with the percentage of fresh fruits, whereas the abundance of seed feeders showed the opposite pattern (Figure 3).

Discussion

Feeding guild account

Our results showed an abundant and diverse arthropod fauna living on the infructescences of *B. serra* plants. Predators were the most diverse feeding guild, while fruit-secretion feeders were the most abundant. Similar results have been reported for other bromeliad species (Gutiérrez Ochoa et al. 1993; Montero et al. 2010).

Pulp feeders are highly constant species, and by their abundance, the larvae of *Nepocadius loretoensis* (Nitidulidae) stood out, which are known to feed on fleshy fruits of bromeliads when they enter a state of fermentation and decomposition (Viana & Williner 1978). Similar pattern showed *Hermetia* larvae (Stratiomyidae), which are voracious consumers of organic matter (Diener et al. 2009). We found few weevils dwelling in some infructescences. Even though some weevil species are known to eat bromeliad leaves

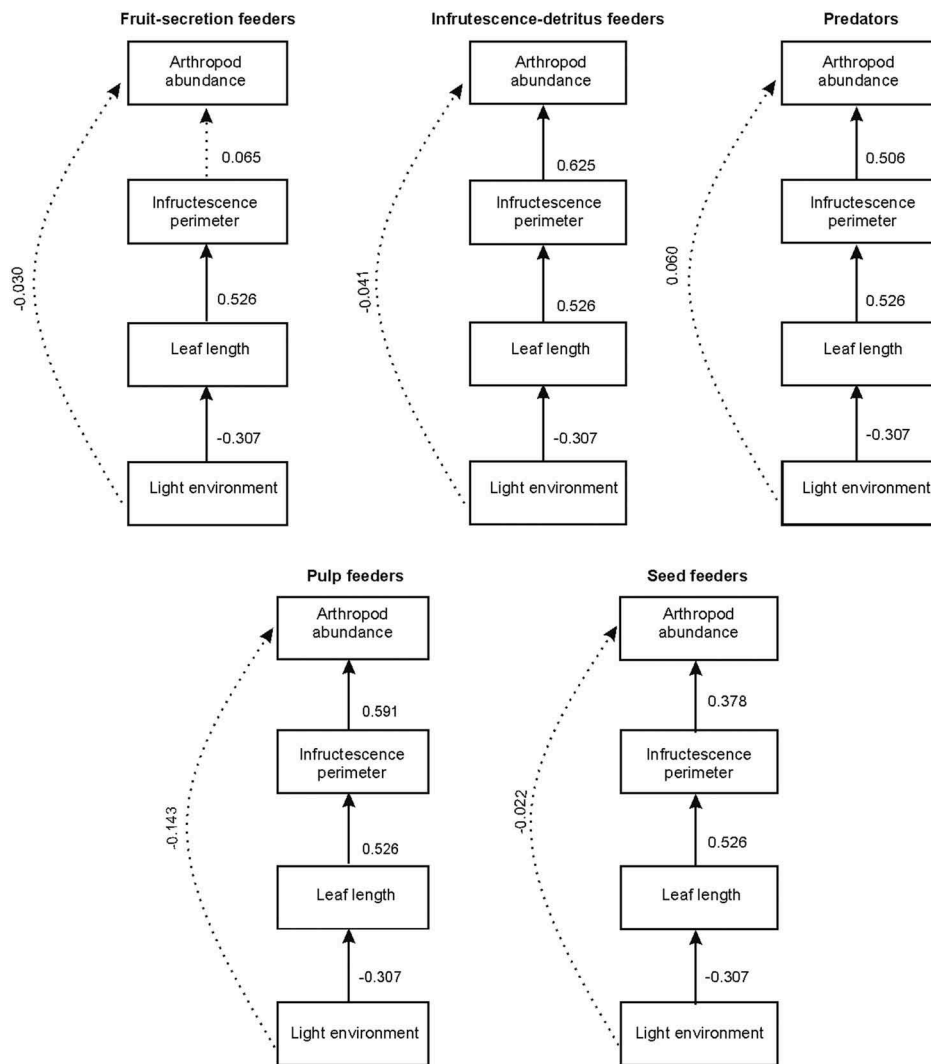


Figure 2. Results of the structural equation models for each feeding guild. Standardized path coefficients (i.e. direct effects) are shown in the figure. Paths that were not significant ($p > 0.05$) are indicated by dotted arrows. Different fit measures of these models are shown in Table 5.

Table 5. Direct and indirect standardized effects (path coefficients) of light on the abundance of each feeding guild. The direct effects of light are the same as shown for each feeding guild in Figure 2. The indirect effects are estimated as the product of the intermediate direct effects. Bold values denote significant effects.

Feeding guild	Direct effects (d)	Indirect effects (i)	Total effects (e = d + i)
Fruit-secretion feeder	-0.030	-0.011	-0.041
Infructescence–detritus feeder	-0.041	-0.101	-0.142
Predator	0.060	-0.082	-0.022
Pulp feeder	-0.143	-0.095	-0.239
Seed feeder	-0.222	-0.061	-0.283

and stem, some may mine and feed on fruits (Frank 1999). Finally, we also found a low abundance of Lepidoptera larvae feeding on the infructescence, and we did not record the presence of Lycaenidae larvae

which are common among other bromeliads (Robbins 2010; Schmid et al. 2010a; Arellano et al. 2015).

Infructescence–detritus feeders exploit the resins, waxes and sugar-rich substances secreted by ripe fruits of *B. serra*. Tenebrionidae, which generally live on the forest floor (Montero et al. 2011) and feed upon plant matter and detritus (Flores & Debandi 2004), have also been recorded in bromeliads in other forests (Gutiérrez Ochoa et al. 1993; Bermúdez-Monge & Barrios 2011). Psocoptera species feed upon a diverse range of food (Muzón & Viegas 2008), and have been recorded in other bromeliads (Frank & Lounibos 2009). Finally, we also detected Silvanidae, some of which are known to feed on dead leaves of Musaceae or Heliconiaceae, and others feed on honeydew produced by Pseudococcidae (Böving 1921; Barber 1928).

Two feeding guilds were recorded in fewer bromeliad plants. Seed feeders (Anthomyiidae) showed low

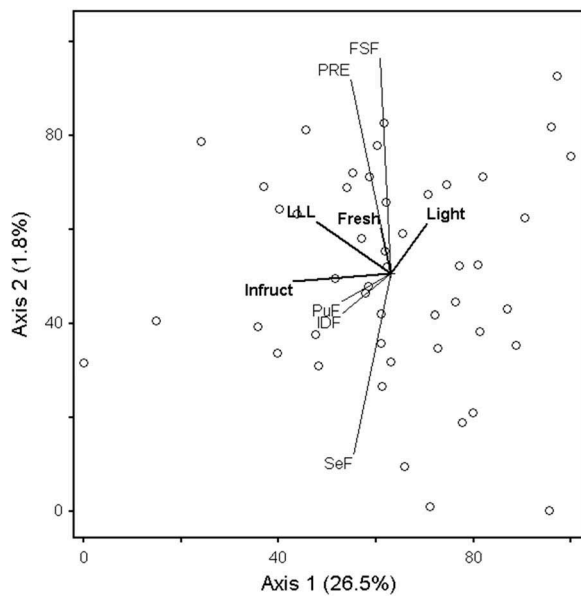


Figure 3. Redundancy analysis (RDA) biplots. Distribution of bromeliad plants, environmental variables and feeding guilds in the ordination space. Circles are used to indicate the bromeliad plants. Environmental variables are represented as vectors (thick lines); directions show the gradients. The lengths of vectors represent the strengths of the variables in the ordination space. Feeding guilds are represented as vectors (thin lines). Environmental variables: LLL (length of the longest leaf), Light (canopy openness), Infruct (infructescence perimeter), and Fresh (percentage of fresh fruits). Feeding guild codes: FSF (fruit-secretion feeder), IDF (infructescence-detritus feeder), PRE (predator), PuF (pulp feeder), and SeF (seed feeder).

abundance, whereas fruit-secretion feeders were recorded in large numbers. The latter are composed of three opportunistic and omnivorous ant species. When some of these ants discover an abundant source of food, such as bromeliad infructescences, many members of the colony congregate to feed on this food resource (Pizo & Oliveira 2000). A similar pattern has been observed for ants that visit the inflorescences of many bromeliad species (Benzing 2000; Schmid et al. 2010b, 2014). In general, the Camponotinae are opportunistic and omnivorous species with regard to diet and generalist with regard to nesting (Silvestre et al. 2003; Gonçalves et al. 2016). Their food range can be very variable and sometimes they feed on sugary secretions of plants (Jaffe & Sanchez 1984; Montero et al. 2011). Ants have been reported previously on *B. serra* fruit, and associated with the presence of gum in their infructescences (Caffini et al. 1976). This gum does not seem to be a natural trap, as has been reported for sticky exudate (mucilage) secreted by the inflorescences of other bromeliad species (*Vriesea bituminosa* Wawra; Monteiro & Macedo 2014). Presence of ants on bromeliad infructescences may also be related to their

nesting behavior (Montero GA, personal observation). If so, architectural and morphological differences between *B. serra* infructescences can be determinant factors on nesting site selection, but this needs further research.

Epigeal predators are abundant in these chaquenan xerophytic forests (Montero et al. 2011). In the infructescences of *B. serra* we recorded a low abundance, but constant and diverse group of generalistic predators, mainly composed of spiders, pseudoscorpions and Staphylinidae. Pseudoscorpions were the most abundant predators, and like in other environments they probably fed upon Psocidae and Entomobryidae (Ceballos 2011). We detected six spider species living on the infructescences of *B. serra*. Spiders are common inhabitants of different bromeliad species (Romero & Vasconcellos-Neto 2004), and are the main epigeal predators living in the foliage of *Aechmea distichantha* (Montero et al. 2010), a facultatively epiphytic bromeliad that also lives in the understory of these Chaco dry forests (Barberis et al. 2014). Finally, the Staphylinidae are common generalist predators that live in the foliage and inflorescences of bromeliads (García-Jarquín 2008; Montero et al. 2010; Bermúdez-Monge & Barrios 2011; Hornung-Leoni et al. 2011; Albertoni et al. 2016).

Direct and indirect effects of light on arthropod abundance

Size of *B. serra* plants decreased significantly with canopy openness. A similar pattern has been observed for several other bromeliad species (Lee et al. 1989; Mantuano & Martinelli 2007; Cavallero et al. 2009). In turn, infructescence size increased with plant size, which has also been recorded for other bromeliads (Overbeek 1946; Zotz et al. 2005; Scrok & Varassin 2011; Fassinou Hotegni et al. 2015). Therefore, as predicted our results showed that infructescence size of *B. serra* was negatively correlated with light environment.

The abundance of most feeding guilds of arthropods present at *B. serra* fruits was affected by the size of the infructescence, given by the size of the plant. Larger infructescences provide higher rewards for fruit-eating insects, and larger habitats for insects dwelling inside these reproductive structures (Benzing 2000). The only exception was the fruit-secretion feeders, mainly composed by ant species whose abundance was not affected by the infructescence size. These ant species are known to congregate when they find an abundant and resource-rich food (Silvestre et al. 2003)

Light environment did not directly affect the abundances of invertebrates in all feeding guilds living on or inside *B. serra* fruits. However, most of these feeding

guilds seem to be negatively, but not significantly, affected by light. This is probably associated with higher temperature and lower humidity in open areas than in the understory of these xerophytic forests (Cavallero et al. 2009). Thus, infructescences of plants growing in open areas are likely to be more stressful habitats for arthropods living on them or inside their fruits, than those of plants living in the forest understory. This is more important in summer when fruit ripening occurs and therefore more stressful high temperatures are expected. In contrast to most feeding guilds, predators seemed to increase their abundance in these xeric open areas. This trend could be associated with the ability of pseudoscorpions, the most abundant predators, to live in these stressful environments (Ceballos & Rosso de Ferradás 2008).

However, light environment indirectly affected the abundances of pulp feeders and seed feeders by negatively affecting plant size. Therefore, these feeding guilds showed a lower number of arthropods in the infructescences of bromeliads growing in the light due to a combination of smaller infructescences and maybe a harsher environment. Interestingly, besides of infructescence size, it is known that light may change fruit quality in other bromeliad species (*Ananas comosus* (L.) Merr.) (Lin et al. 2015); therefore, this aspect needs further research in these feeding guilds.

Final comments

Our results showed that the infructescences of *B. serra* harbored an abundant and diverse set of arthropod species from different feeding guilds, and that the abundances of most feeding guilds are more related to infructescence size than to the light environment. Infructescences with higher percentage of rotten fruits had higher number of seed feeders and lower numbers of predators and infructescence-detritus feeders. Therefore, the potential number of arthropod species could be probably higher than recorded because the infructescences were harvested at a similar maturity stage, but there may be a succession of different groups of insects through the ripening process from immaturity to post-maturity stages, as has been observed in other plant species (García-Robledo et al. 2005). On the other hand, it should be considered that bromeliad density in the surroundings of the collected bromeliads may also affect the abundance of interacting organisms (García-Meneses & Ramsay 2012).

Our results emphasized the need to consider plant size, as well as the light environment where the plants grow, when evaluating the abundance of arthropods in bromeliad infructescences.

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References

- Albertoni FF, Steiner J, Zillikens A. 2016. The associated beetle fauna of *Hohenbergia augusta* and *Vriesea friburgensis* (Bromeliaceae) in southern Brazil. *J Nat Hist.* 50:2917–2939.
- Almeida Jácomo A, Silveira L, Diniz-Filho JAF. 2004. Niche separation between the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Dusicyon thous*) and the hoary fox (*Dusicyon vetulus*) in central Brazil. *J Zool.* 262:99–106.
- Almeida-Neto M, Campassi F, Galetti M, Jordano P, Oliveira-Filho A. 2008. Vertebrate dispersal syndromes along the Atlantic forest: broad-scale patterns and macroecological correlates. *Global Ecol Biogeogr.* 17:503–513.
- Amat AG. 1988. Identificación de las especies argentinas del género *Bromelia* L. (Bromeliaceae: Bromelioideae) mediante caracteres espermatológicos. *Acta Farmacéutica Bonaerense.* 7:25–32.
- Arbuckle J. 2013. AMOS 22. User's guide. Chicago: SmallWaters Corporation.
- Arellano GN, Vergara C, Bello S. 2015. Plagas entomológicas y otros artrópodos en el cultivo de la piña (*Ananas comosus* var. *comosus* (L.) Merr., Coppens & Leal) en Chanchamayo y Satipo, Departamento de Junín, Perú. *Ecología Aplicada.* 14:175–189.
- Barber HS. 1928. A new Bolivian silvanid beetle from the myrmecodomatia of *Cordia*. *Psyche.* 35:167–168.
- Barberis IM, Batista WB, Pire EF, Lewis JP, León RJC. 2002. Woody population distribution and environmental heterogeneity in a Chaco forest, Argentina. *J Veg Sci.* 13:607–614.

- Barberis IM, Pire EF, Lewis JP. 1998. Spatial heterogeneity and woody species distribution in a *Schinopsis balansae* (Anacardiaceae) forest of the Southern Chaco, Argentina. *Rev Biol Trop*. 46:515–524.
- Barberis IM, Torres PS, Batista WB, Magra G, Galetti L, Lewis JP. 2014. Two bromeliad species with contrasting functional traits partition the understory space in a Southamerican xerophytic forest: correlative evidence of environmental control and limited dispersal. *Plant Ecol*. 215:143–153.
- Benzing DH. 2000. Bromeliaceae. Profile of an adaptive radiation. Cambridge (UK): Cambridge University Press.
- Bermúdez-Monge J, Barrios H. 2011. Insectos asociados a *Vriesia sanguinolenta* Cogn. & Marchal (Bromeliaceae). *Scientia*. 21:7–32.
- Bernardello LM, Galetto L, Juliani HR. 1991. Floral nectar, nectary structure and pollinators in some Argentinean Bromeliaceae. *Ann Bot*. 67:401–411.
- Bianchi MB, Gibbs PE, Prado DE, Vesprini JL. 2000. Studies on the breeding systems of understorey species of a Chaco woodland in NE Argentina. *Flora*. 195:339–348.
- Böving AG. 1921. The larvae and pupae of the social beetles *Coccidotrophus socialis* (Schwarz and Barber) and *Eumausibius wheeleri* (Schwarz and Barber) with remarks on the taxonomy of the family Cucujidae. *Zoologica*. 3:197–213.
- Brokaw NVL. 1983. Groundlayer dominance and apparent inhibition of tree regeneration by *Aechmea magdalenae* (Bromeliaceae) in a tropical forest. *Tropical Ecol*. 24:194–200.
- Caffini N, Bongiorno De Pfrirter G, Buttazzoni De Cozzarin M. 1976. Posibilidades quimiotaxonomicas de los exudados gomosos producidos por las especies argentinas del genero *Bromelia* (Bromeliaceae). *Bol Soc Arg Bot*. 17:119–126.
- Caffini NO, Natalucci CL, Priolo NS, Buttazzoni MS. 1988. Proteasas de Bromeliaceae. IV. Aislamiento de una fitoproteasa sulfhidrúlica presente en frutos de *Bromelia serra* Griseb. *Acta Farmacéutica Bonaerense*. 7:9–14.
- Cárcamo JJ, Cárcamo JM, Albertengo J, Barberis I. 2006. Variaciones morfológicas de plantas de *Bromelia serra* crecidas al sol y la sombra. Page 64 in Resúmenes del VIII Congreso de la Sociedad de Biología de Rosario. Rosario: UNR Editora.
- Cardoso CAL, Ré-Poppi N, Coelho RG. 2010. Fruit oil of *Bromelia balansae*. *J Essent Oil Res*. 22:558–559.
- Cavallero L, López D, Barberis IM. 2009. Morphological variation of *Aechmea distichantha* (Bromeliaceae) in a Chaco forest: habitat and size-related effects. *Plant Biol*. 11:379–391.
- Ceballos A. 2011. Grupos menores: pseudoescorpiones. In: Viera C, editor. Arácnidos de Uruguay. Diversidad, comportamiento y ecología. Montevideo (Uruguay): Ediciones de la Banda Oriental. p. 91–100.
- Ceballos A, Rosso De Ferradás B. 2008. Pseudoscorpiones. In: Claps LE, Debandi G, Roig-Juñent S, editors. Mendoza; Argentina: biodiversidad de Artrópodos Argentinos. Vol. 2. Mendoza: Sociedad Entomológica Argentina. p. 105–116.
- Ctvrtecka R, Sam K, Brus E, Weiblen GD, Novotny V. 2014. Frugivorous weevils are too rare to cause Janzen-Connell effects in New Guinea lowland rain forest. *J Trop Ecol*. 30:521–535.
- Debussche M, Isenmann P. 1989. Fleishy fruit characters and the choices of bird and mammal seed dispersers in a Mediterranean region. *Oikos*. 56:327–338.
- Diener S, Zurbrugg C, Tocknera K. 2009. Conversion of organic material by black soldier fly larvae. Establishing optimal feeding rates. *Waste Manage Res*. 27:603–610.
- Fassinou Hotegni VN, Lommen WJM, Agbossou EK, Struik PC. 2015. Influence of weight and type of planting material on fruit quality and its heterogeneity in pineapple [*Ananas comosus* (L.) Merrill]. *Front Plant Sci*. 5:798.
- Fernandes Monteiro R, Mantovani A, Forzza RC. 2015. Morphological phylogenetic analysis of two early-diverging genera of Bromelioideae (Bromeliaceae). *Rodriguésia*. 66:505–521.
- Flores GE, Debandi GO. 2004. Tenebrionidae. In: Cordo HA, Lograzo G, Braun K, Di Iorio O, editors. Catálogo de insectos fitófagos de la Argentina y sus plantas asociadas. Buenos Aires (Argentina): SEA Ediciones. p. 197–201.
- Frank J. 1999. Bromeliad-eating weevils. *Selbyana*. 20:40–48.
- Frank JH, Lounibos LP. 2009. Insects and allies associated with bromeliads: a review. *Terr Arthropod Rev*. 1:125–153.
- Frazer GW, Canham CD, Lertzman KP. 1999. Gap light analyzer (GLA). Burnaby: Simon Fraser University and The Institute of Ecosystem Studies.
- Gallart GC, Saris Batista-Foguet JM, Saris WE. 2005. Temas avanzados en modelos de ecuaciones estructurales. Madrid: La Muralla.
- García-Jarquín MI. 2008. Macroartrópodos asociados a la bromelia *Tillandsia prodigiosa* (Lem.) Baker en dos localidades de Santa Catarina Ixtepeji, Oaxaca. Santa Cruz Xoxocotlán: Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional and Instituto Politécnico Nacional.
- García-Meneses PM, Ramsay PM. 2012. Pollinator response to within-patch spatial context determines reproductive output of a giant rosette plant. *Basic Appl Ecol*. 13:516–523.
- García-Robledo C, Quintero-Marín P, Mora-Kepfer F. 2005. Geographic variation and succession of arthropod communities in inflorescences and infructescences of *Xanthosoma* (Araceae). *Biotropica*. 37:650–656.
- Gonçalves AZ, Oliveira RS, Oliveira PS, Romero GQ, Schausberger P. 2016. Species-specific effects of ant inhabitants on bromeliad nutrition. *PLOS One*. 11:e0152113.
- Grace JB, Anderson TM, Olf H, Scheiner SM. 2010. On the specification of structural equation models for ecological systems. *Ecol Monogr*. 80:67–87.
- Gutiérrez Ochoa M, Camino Lavín M, Castrejon Ayala F, Jiménez Pérez A. 1993. Arthropods associated with *Bromelia hemisphaerica* (Bromeliales: Bromeliaceae) in Morelos, Mexico. *Florida Entomol*. 76:616–621.
- Hornung-Leoni CT, Márquez J, Bueno-Villegas J. 2011. Arthropods associated with *Tillandsia deppeana* (Bromeliaceae) from Hidalgo State, México, with three first state records of Coleoptera species. *Entomol News*. 122:469–476.
- Jaffe K, Sanchez C. 1984. On the nestmate-recognition system and territorial marking behaviour in the ant *Camponotus rufipes*. *Insectes Soc*. 31:302–315.
- Janzen DH, Martin PS. 1982. Neotropical anachronisms: the fruits the Gomphotheres ate. *Science*. 215:19–27.

- Jordano P. 2000. Fruits and frugivory. In: Fenner M, editor. Seeds: the ecology of regeneration in plant communities. Wallingford: CABI Publishing. p. 125–166.
- Keuroghlian A, Eaton DP, Desbiez ALJ. 2009. The response of a landscape species, white-lipped peccaries, to seasonal resource fluctuations in a tropical wetland, the Brazilian pantanal. *Int J Biodiver Conser.* 1:87–97.
- Klekailo GN, Tuesca DH, Barberis IM. 2012. Efectos de la temperatura, el ambiente lumínico y la escarificación sobre la germinación de semillas de *Bromelia serra* Griseb. (Bromeliaceae). *Rev Bras Sementes.* 34:605–612.
- Lam TY, Maguire A. 2012. Structural Equation Modeling: theory and applications in forest management. *Int J Forest Res.* 2012:16.
- Lee HSJ, Lüttge U, Medina E, Smith JAC, Cram WJ, Diaz M, Griffiths H, et al. 1989. Ecophysiology of xerophytic and halophytic vegetation of a coastal alluvial plain in northern Venezuela. III. *Bromelia humilis* Jacq., a terrestrial CAM bromeliad. *New Phytol.* 111:253–271.
- Lewis JP. 1991. Three levels of floristical variation in the forests of Chaco. *J Veg Sci.* 2:125–130.
- Lewis JP, Pire EF, Barberis IM. 1997. Structure, physiognomy and floristic composition of a *Schinopsis balansae* (Anacardiaceae) forest in the Southern Chaco, Argentina. *Rev Biol Trop.* 45:1013–1020c.
- Lin M-T, Chen AM, Lin T-S, Kuan C-S, Lee C-L, Yang W-J. 2015. Prevention of natural flowering in pineapple (*Ananas comosus*) by shading and urea application. *Hortic Environ Biotechnol.* 56:9–16.
- Mantuano DG, Martinelli G. 2007. Estrutura populacional e crescimento da bromélia clonal *Neoregelia cruenta* na restinga de Jurubatiba. *Rev Bras Biociências.* 5:876–878.
- McCune B, Mefford MJ. 2011. Multivariate analysis of ecological data. Gleneden Beach: MjM Software.
- Migani V, Ekési S, Hoffmeister TS. 2014. Physiology vs. environment: what drives oviposition decisions in mango fruit flies (*Bactrocera invadens* and *Ceratitidis cosyra*)? *J Appl Entomol.* 138:395–402.
- Monteiro RF, Macedo MV. 2014. First report on the diversity of insects trapped by a sticky exudate of the inflorescences of *Vriesea bituminosa* Wawra (Bromeliaceae: Tillandsioideae). *Arthropod Plant Interact.* 8:519–523.
- Montero G, Carnevale NJ, Magra G. 2011. Ensembles estacionales de artrópodos epigeos en un bosque de quebracho (*Schinopsis balansae*) en el Chaco Húmedo. *Rev Colomb Entomol.* 37:294–304.
- Montero G, Feruglio C, Barberis IM. 2010. The phytotelmata and foliage macrofauna assemblages of a bromeliad species in different habitats and seasons. *Insect Conserv Diver.* 3:92–102.
- Muzón J, Viegas A. 2008. Psocoptera. In: Claps LE, Debandi G, Roig-Juñent S, editors. Biodiversidad de Artrópodos Argentinos. Vol. II. Buenos Aires: SEA Ediciones. p. 185–188.
- Nájera M. 1974. Estructuras secretoras de las especies argentinas del género *Bromelia* (Bromeliaceae). *Bol Soc Arg Bot.* 15:384–392.
- Overbeek J. 1946. Control of flower formation and fruit size in the pineapple. *Bot Gaz.* 108:64–73.
- Parada F, Krajewski D, Duque C, Jäger E, Herderich M, Schreiber P. 1996. 1-O-β-D-Glucopyranosyl anthranilate from piñuela (*Bromelia plumieri*) fruit. *Phytochemistry.* 42:871–873.
- Parera A. 2002. Los mamíferos de la Argentina y la región austral de Sudamérica. Buenos Aires: El Ateneo.
- Piper JK. 1986. Effects of habitat and size of fruit display on removal of *Smilacina stellata* (Liliaceae) fruits. *Can J Bot.* 64:1050–1054.
- Pizo MA, Oliveira PS. 2000. The use of fruits and seeds by ants in the Atlantic Forest of Southeast Brazil. *Biotropica.* 32:851–861.
- Pugesek BH, Tomer A, Von Eye A, editors. 2003. Structural equation modeling. Applications in ecological and evolutionary biology. Cambridge: Cambridge University Press.
- Quilici S, Rousse P. 2012. Location of host and host habitat by fruit fly parasitoids. *Insects.* 3:1220–1235.
- Quinn GP, Keough MJ. 2002. Experimental design and data analysis for biologists. Cambridge: Cambridge University Press.
- Robbins RK. 2010. The ‘upside down’ systematics of hair-streak butterflies (Lycaenidae) that eat pineapple and other Bromeliaceae. *Stud Neotrop Fauna E.* 45:21–37.
- Romero GQ, Vasconcellos-Neto J. 2004. Spatial distribution patterns of jumping spiders associated with terrestrial bromeliads. *Biotropica.* 36:596–601.
- Rosseel Y. 2012. Lavaan: an R package for structural equation modeling. *J Stat Softw.* 48:1–36.
- Scarano FR, De Mattos EA, Franco AC, Herzog B, Ball E, Grams TEE, Mantovani A, Barreto S, Haag-Kerwer A, Lüttge U. 1999. Habitat segregation of C-3 and CAM *Nidularium* (Bromeliaceae) in response to different light regimes in the understory of a swamp forest in southeastern Brazil. *Flora.* 194:281–288.
- Scarpa GF. 2009. Wild food plants used by the indigenous peoples of the South American Gran Chaco: A general synopsis and intercultural comparison. *J Appl Bot Food Qual.* 83:90–101.
- Schmid S, Schmid VS, Kamke R, Steiner J, Zillikens A. 2010a. Association of three species of *Strymon* Hübner (Lycaenidae: Theclinae: Eumaeini) with bromeliads in southern Brazil. *J Res Lepidoptera.* 42:50–55.
- Schmid VS, Langner S, Steiner J, Zillikens A. 2014. Inflorescences of the bromeliad *Vriesea friburgensis* as nest sites and food resources for ants and other arthropods in Brazil. *Psyche: J Entomol.* 2014:1–9.
- Schmid VS, Schmid S, Steiner J, Zillikens A. 2010b. High diversity of ants foraging on extrafloral nectar of bromeliads in the Atlantic rainforest of southern Brazil. *Stud Neotrop Fauna E.* 45:39–53.
- Schupp EW, Fuentes M. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience.* 2:267–275.
- Srok GJ, Varassin IG. 2011. Reproductive biology and pollination of *Aechmea distichantha* Lem. (Bromeliaceae). *Acta Bot Bras.* 25:571–576.
- Silvestre R, Brandão CRF, Da Silva RR. 2003. Grupos funcionales de hormigas: el caso de los gremios del Cerrado. In: Fernández F, editor. Introducción a las hormigas de la región Neotropical. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt. p. 113–148.
- Silvius KM, Fragoso J. 2002. Pulp handling by vertebrate seed dispersers increases palm seed predation by bruchid beetles in the northern Amazon. *J Ecol.* 90:1024–1032.

- Sivinski J. 1991. The influence of host fruit morphology on parasitization rates in the Caribbean fruit fly, *Anastrepha suspensa*. *Entomophaga*. 36:447–454.
- Smith LB, Downs RJ. 1979. Bromeliaceae, subfamily Bromelioideae. *Flora Neotropica Monograph*. 14:1493–2142.
- Snow DW. 1971. Evolutionary aspects of fruit-eating by birds. *Ibis*. 113:194–202.
- Takeoka G, Buttery RG, Flath RA, Teranishi R, Wheeler E, Wieczorek R, Guentert M. 1989. Volatile constituents of pineapple (*Ananas comosus* [L.] Merr.). ACS Symposium Series-American Chemical Society; Washington DC; 1898 February 21. p. 223–237.
- Thébaud C, Debussche M. 1992. A field test of the effects of infructescence size on fruit removal by birds in *Viburnum tinus*. *Oikos*. 65:391–394.
- Valido A, Schaefer H, Jordano P. 2011. Colour, design and reward: phenotypic integration of fleshy fruit displays. *J Evol Biol*. 24:751–760.
- Viana MJ, Williner GJ. 1978. Evaluación de la fauna entomológica y aracnológica de las provincias centrales y cuyanas. *Acta Scient Serie Ent*. 11:1–77.
- Wang X-G, Johnson MW, Daane KM, Yokoyama VY. 2009. Larger olive fruit size reduces the efficiency of *Psytalia concolor*, as a parasitoid of the olive fruit fly. *Biol Control*. 49:45–51.
- Wheelwright NT, Haber WA, Murray KG, Guindon C. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican Lower Montane Forest. *Biotropica*. 16:173–192.
- Zotz G, Laube S, Schmidt G. 2005. Long-term population dynamics of the epiphytic bromeliad, *Werauhia sanguinolenta*. *Ecography*. 28:806–814.