



Contrasting Relationship of True Weevils (Curculionidae) and Woody Plants Diversity in Semi-arid Landscape Units

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Keywords

Herbivory, interaction, Neotropics, phytophysiology, plant–insect

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Edited by Christian S Torres – UFRPE

Received 20 March 2020 and accepted 4 August 2020

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Abstract

In general, insect herbivore diversity is positively correlated to plant diversity since plant assemblages structure different microhabitats and provide food resources for such insects. Although poorly studied, insect herbivores in tropical dry forests are positively affected by tree species richness and the structural architecture of vegetation. In this study, we analyzed whether true weevil and woody plants present similar patterns of diversity across different landscape units in a Neotropical tropical dry forests located in Brazil, and if there is a correlation among their assemblages. We used Hill numbers according to species richness and the inverse of Simpson to compare the taxonomic diversity of true weevils and plants in nine landscape units located at the São Francisco river basin in the states of Sergipe and Alagoas, north-eastern Brazil. All trees and shrubs with diameter at breast height (1.3 m) \geq 5 cm were sampled, and true weevils were collected using a modified Malaise trap. We used co-correspondence analysis to test if plants and true weevil species tend to co-occur. A total of 538 true weevils from 60 species was collected, and a total of 1419 plants belonging to 49 species was recorded. There is no general pattern of co-occurrence and diversity among true weevils and plants, indicating that the plant community is not structuring true weevil assemblage in the Caatinga. However, there was positive relationship between *Sibinia* sp4 and Fabaceae–Mimosoideae. These results suggest true weevil–plant relationships in the Caatinga differ from that of more mesic ecosystems. Therefore, we observed that the mechanisms that regulate herbivore–plant diversity relationships do not always follow a positive relationship, as observed in previous studies.

Introduction

Plant diversity is expected to be positively related to insect herbivore diversity (Haddad *et al* 2009), with theoretical and empirical studies supporting this pattern (Haddad *et al* 2009, Ebeling *et al* 2017a). The Resource Specialization Hypothesis, for example, suggests a diverse plant community may provide a greater diversity of food resources, thus resulting in

diverse herbivorous communities (Hutchinson 1959, Ebeling *et al* 2017b). Furthermore, the increase in heterogeneity of the structural architecture of vegetation may also provide more microhabitats, positively affecting herbivorous diversity (Denno & Roderick 1991, Joern & Laws 2013). Habitats with a wide microhabitat availability may benefit from specific environmental conditions that may be absent in habitats with low heterogeneity.

Tropical dry forests (TDFs) comprise approximately 40% of the tropical forests of the world (Brown & Lugo 1982). Like other ecosystems, herbivore insects in TDFs are positively affected by tree species richness and the structural architecture of vegetation (Cuevas-Reyes *et al* 2004, Leal *et al* 2016, Silva *et al* 2016). Likewise, herbivore insects present specific adaptations to inhabit dry environments (Cuevas-Reyes *et al* 2004, Leal *et al* 2016, Silva *et al* 2016, Silva *et al* 2017). For example, Cuevas-Reyes *et al* (2004) found herbivore insects preferred to occupy drier areas of a TDF in Mexico. A similar pattern occurs in TDFs of Brazil, with high activity of herbivores in more xeric environments, proving that soil and vegetation composition may affect herbivore distribution (Silva *et al* 2016, Silva *et al* 2017). However, most TDFs are still poorly studied when compared to tropical rainforests and savannas (Silva *et al* 2018). With more studies analyzing the relationship between plant–insect diversities in TDFs, a wider perspective may be obtained regarding such interactive networks. Therefore, it is possible to reinforce the trends that have been already observed in the scarce studies conducted in TDFs, or to present contrasting ecological responses regarding plant–insect relationships in this biome.

Among the TDFs, the Brazilian Caatinga is the largest, comprising a wide variety of ecosystems (Andrade-Lima 1981, Silva *et al* 2018). The Caatinga is a mosaic of TDFs, comprising plants with a discontinuous canopy that is variable in height and density, thus resulting in heterogeneous habitats (Velloso *et al* 2002, Santos *et al* 2012). The plant community of the Caatinga mainly includes species from Fabaceae, Euphorbiaceae, and Myrtaceae (Rodal & Nascimento 2006, Barbosa *et al* 2007). Studies regarding the interaction between plants and herbivorous insects in the Caatinga are still incipient, focusing mainly on monospecific interactions with plants (Silva *et al* 2009, Sousa-Souto *et al* 2018) and gall-inducing insects (Santos *et al* 2011 Brito *et al* 2018).

True weevils (Coleoptera: Curculionidae) are a diverse herbivorous group, comprising ca. 51,000 species, with its higher species richness being recorded mainly in the tropics (Oberprieler *et al* 2014). Among ecological studies comprising Coleoptera diversity in tropical ecosystems, true weevils feature as one of the most diverse herbivorous (Iannuzzi *et al* 2003, Guedes *et al* 2019, Macedo-Reis *et al* 2019, Márquez *et al* 2019). True weevils feed on various plant organs, such as seeds, roots, leaves, and pollen, overcoming the structural and chemical defenses of plants (Anderson 1993, Oberprieler *et al* 2007). Most of them are diet specialists, and true weevil diversity is highly dependent on plant diversity and composition (Stoner & Joern 2004, Brown & Hyman 1986). Furthermore, habitat structure, which is related to plant community structure, also affects true weevil distribution

(Chown 1989, Suominen *et al* 2003, Meurer *et al* 2013). In Pantanal, a Neotropical wetland ecosystem, true weevils were more diverse in forested habitats that recorded high litter volume, and this trend related to the higher food availability under forested habitats (Meurer *et al* 2013).

In dry environments, there are true weevil species highly adapted and are well succeeded under harsh environmental conditions. For example, some species of the Curculioninae present a wide niche breadth and feed on arid-adapted plants, as the species of the genus *Opuntia* Mill. (Cactaceae) (Anderson 1993). On the other hand, species are strongly influenced by the blooming flower density (Stoner & Joern 2004). Based on the Resource Specialization Hypothesis (Hutchinson 1959, Ebeling *et al* 2017b), the true weevil community will respond to different physiognomies of the Caatinga. We can expect a positive relationship between diversity of both, vegetation and true weevil. Considering this scenario of relationship, in this study, we aimed to investigate the diversity patterns to both, true weevil and plant species across different landscape units within the region of the Caatinga TDF. Thus, we analyzed whether true weevil and woody plants present similar patterns of diversity across different landscape units. Besides, we tested whether true weevil and plant diversities are correlated within the Caatinga. This approach may provide the basis for a better understanding of plant–insect relationships in dry ecosystems, which have fauna and flora strongly adapted to water scarcity (Haim & Izhaki 1995, Silva *et al* 2017, Silva *et al* 2018). The evolution between plant and insects is asymmetric, with insects usually following plant evolution; thus, understanding the relationship between herbivorous insects and their hosts entails knowledge in ecological interactions between such taxa (Jermy 1984, Strauss & Zangerl 2002). The data provided in this study will give basis for the understanding of insect population establishment and dynamics in dry ecosystems.

Material and Methods

Study area

The study was conducted in conserved habitats at the São Francisco river basin (09°30′–10°00′S and 37°30′–38°00′W) in the states of Sergipe and Alagoas, north-eastern Brazil. The predominant soils of the region are Litolics, Cambisols, Podzolic, Eutrophic, Noncalic Brown, and Planosols. According to the Köppen climate classification, the climate is defined as hot semi-arid (BSh) (Peel *et al* 2006). Annual precipitation and mean annual temperature range from 500 to 600 mm and 25 to 27°C, respectively. This ecoregion of Caatinga is named “Depressão Sertaneja Meridional” (Southern Sertean Depression) and its vegetation mostly

comprises shrubs and trees, with Malpighiaceae, Bignoniaceae, and Euphorbiaceae being some of the common families of the flora in this region (Velloso *et al* 2002).

Plant and true weevil surveys

Surveys were performed monthly between March 2000 and February 2001, within nine landscape units simultaneously, which differed among them according to the topography, soil depth and type, and water availability (Guerra 1972, IBGE 2007) (Table 1). In the Caatinga, such environmental parameters may influence the community structure of plants (Silva *et al* 2003), beetles (Iannuzzi *et al* 2003), and ants (Leal 2003). The habitats analyzed in this study reflect the most representative environments of the Caatinga domain (see Silva *et al* 2003). In each landscape, we surveyed plants across six randomly distributed plots (10 × 100 m), which were not spatially correlated (Silva *et al* 2003). All trees and shrubs with diameter at breast height (1.3 m) ≥ 5 cm were sampled in each plot and identified following the Angiosperm Phylogeny Group (APG3) system. In the same plots where plants were surveyed, the true weevils were collected using modified Malaise traps, being installed one trap in each plot. Malaise is a passive trap based on flight interception, commonly used as the standard method for sampling flying insects (Sheikh *et al* 2016) and this method samples a vast assortment of beetle taxa, including Curculionidae which is one of the dominant families (Iannuzzi *et al* 2003, Skvarla and Dowling 2017, Guedes *et al* 2019). The traps were mounted at clearings and natural trails, avoiding to install them near specific plant species. As sampling was performed throughout the year, we could not use each plot as a replicate, owing to effects of seasonality over insects of the Caatinga (Vasconcellos *et al* 2010). Therefore, we had only one replicate for each landscape unit, and thus, we considered the absolute number of individuals in each landscape unit for diversity measures and statistical analyses. The true weevils were identified with the assistance of the specialist Dr. Germano Rosado Neto (Federal

University of Paraná – UFPR). The voucher specimens are deposited at Entomology Collection of Federal University of Pernambuco (UFPE) and plants voucher are at UFP Herbarium (Recife, Pernambuco, Brazil).

Data analyses

We assessed sampling efficiency of true weevil and plant species in the studied landscape units of the Caatinga using the estimators of species richness Jackknife 1, Jackknife 2, Chao 1, and Chao 2. The estimators were performed based on the number of samples (i.e., number of landscape units). These analyses were performed using Estimates version 9.1.0 (Colwell 2013).

For each landscape unit, we calculated the Hill numbers with $q = 0$ and $q = 2$, which can be interpreted as richness and the Simpson's index of diversity, respectively (Chao *et al* 2014). Hill numbers not only obey the replication principle but also have equivalents in the most used indexes, such as Simpson's inverse and Shannon (Chao *et al* 2014). We compared the richness and Simpson's diversity index of true weevils and plants among the landscape units with extrapolation curves based on individual sampling with iNEXT in R version 3.2.0 (Hsieh *et al* 2016, R Core Team 2018). We considered the extrapolation until the total abundance of true weevils and plants in each landscape unit, i.e., 110 and 280, respectively. We also performed ranking abundance figures to understand the abundance patterns of plant and true weevil species in each landscape unit.

We tested if the abundance, estimated richness, and estimated Simpson's index between true weevils and plants were related among the landscape units with Pearson's correlation analysis. All diversity measures were normally distributed (Shapiro test, $P > 0.05$). Correlation analysis was performed in R version 3.2.0 (Hsieh *et al* 2016, R Core Team 2018). To test if abundance of *Sibinia* sp4 and *Pappista* sp. was affected by abundance of plant species (Fabaceae–Mimosoideae and Euphorbiaceae, respectively), we conducted generalized linear models with correction for overdispersion of Poisson

Table 1 The nine landscape units in the studied area and their soil and topography features.

Abbreviation	Description	Soil depth	Soil type	Soil water availability	Terrain
FlSanB	Flat sandy board	Deep	Sandy	Low	Flat
RiSanB	Riparian sandy board	Deep	Sandy	High	Flat
ErForW	Erosive formation from water	Shallow	Vary	High	Inclined
CoMouR	Counterfort mountain range	Vary	Vary	Vary	Rough
ScMouR	Scarp mountain range	Vary	Vary	Vary	Rough
CaOutS	Canyons without soils	Shallow	Not applicable	Low	Inclined
CaWitS	Canyons with soils	Deep	Vary	Low	Inclined
RiClab	Riparian clayey board	Deep	Clayey	High	Flat
FlClab	Flat clayey board	Deep	Clayey	Low	Flat

distribution (Crawley 2013). Analyses were performed in R version 3.2.0 (R Core Team 2018). This relationship was previously suggested by Clark (1979), as these true weevil species preferentially use the bark and trunk resources of the species from these plant families. These true weevil species were chosen by the large number of specimens sampled and by the well-documented and specific relationship with hosts of both genera (Clark 1978).

To visualize and interpret true weevil and plant assemblage structure, we performed Nonmetric Multidimensional Scaling (NMDS) with Bray–Curtis distance, which considers species abundance. To test if the dissimilarity on species assemblage differ between plants and weevils, we performed Mantel test (Legendre & Legendre 2012). To test if plants and true weevil species tend to co-occur, we performed a co-correspondence analysis (CoCa). CoCa is an ordination method to test if two species compositions from the same sampled sites are related. In this method, the “leave-one-out” cross-validation method is implemented; i.e., partial least squares regression models are calculated for the number of sites, wherein with each iteration, a different site is left out. We used the asymmetric predictive methods, in which the species composition is predicted in each run and is compared to the actual data. Owing to its mathematical properties, any value of cross-validation above zero indicates that the prediction is better than by chance. In addition, we tested if the differences between models are by chance using the randomization test. The true weevil abundance was log-transformed to decrease the skewness of the abundance distribution. For detailed explanation about the CoCa, see ter Braak & Schaffers (2004). We used the package “cocorresp” in R (Simpson 2009) to perform CoCa.

Results

We recorded 538 true weevils belonging to 60 species and 1419 plants belonging to 49 species (Supplementary material). The mean abundance of true weevils was 59.77 ± 23.88 and that of plants was 159.62 ± 55.81 per landscape unit. According to Chao 1 and Chao 2, true weevil inventory completeness was 46.30% and 40.59%, respectively; according to Jackknife 1 and Jackknife 2, true weevil inventory completeness was 64.35% and 50.72%, respectively. Plant inventory completeness was 87.17% and 79.27%, according to Chao 1 and Chao 2, respectively; according to Jackknife 1 and Jackknife 2, plant inventory completeness was 79.27% and 70.91%, respectively. The landscape units FIClaB, FISanB, and ErForW had the highest true weevil abundance, whereas FIClaB, ScMourR, and FIClaB had the highest plant abundance (Table 2). The RiClaB had the highest true weevil estimated species richness, while CoMouR had the highest plant estimated species richness (Table 2). True weevils had, on average, $14.89 (\pm 3.62)$ species per landscape unit, whereas

plants had an average of $15.55 (\pm 4.06)$ species per landscape unit. The average Simpson’s diversity of true weevils per landscape unit was 5.34 ± 2.71 , whereas for plants, it was 4.14 ± 2.5 . The landscape units with the highest estimated Simpson’s diversity were CaWitS for true weevils and CaOutS for plants (Table 2). According to the Simpson’s diversity index, CaWitS, RiSanB, and RiClaB had a statistically higher true weevil diversity than the other landscape units. For plant species, CaOutS was statistically the most diverse landscape unit, based on the Simpson’s diversity index (Table 2).

Three true weevil species presented a high abundance in the study ($> 10\%$ of the total true weevil abundance): *Sibinia* sp4 (33% of total true weevil abundance), *Naupactus* sp3 (11%), and *Pappista* sp. (11%). More than half of the true weevil species were singletons. *Sibinia* sp4 was the dominant true weevil species in five of the studied landscape units (RiSanB, ErForW, CaOutS, CaWitS, and FIClaB, see Fig 1A). *Naupactus* sp3 was the dominant true weevil species in FISanB and CoMouR while *Pappista* sp. was dominant in ScMourR. Both *Pappista* sp. and *Chalcodermus* sp7 were the dominant true weevils in RiClaB (Fig 1A). *Poincianella pyramidalis* (Tul.) L. P. Queiroz was the most abundant plant species in the studied area, with 3735 individuals (ca. 45% of the total plants recorded) followed by *Aspidosperma pyriformis* Mart. & Zucc, with 740 individuals (approximately 8%) (Fig 1B). Only eight plant species were singletons (Fig 1B). *Poincianella pyramidalis* was the most abundant species in all landscape units except ErForW, in which the dominant species was a *Bauhinia* sp. (Fig 1B).

The abundance of true weevils and plants was not statistically related ($r = -0.17$; $P = 0.65$). Similarly, estimated richness ($r = -0.31$; $P = 0.42$) and estimated Simpson diversity ($r = -0.25$; $P = 0.51$) were not related. In addition, there was no significant relationship between *Pappista* sp. and Euphorbiaceae plant species ($F_{8,7} = 0.09$, $P = 0.77$; Table 3) and between Mimosoidea and *Sibinia* sp1 ($F_{8,7} = 2.3$, $P = 0.17$; Table 3), *Sibinia* sp2 ($F_{8,7} = 0.01$, $P = 0.9$; Table 3), and *Sibinia* sp3 ($F_{8,7} = 0.18$, $P = 0.68$; Table 3). However, there was a significant positive relationship between *Sibinia* sp4 and the abundance of Fabaceae–Mimosoideae plant species ($F_{8,7} = 7.65$, $P = 0.02$; Table 3). According to NMDS and Mantel test, the dissimilarity in species composition among landscape units was also different between true weevils and plants (Fig 2; $r = -0.26$; $P = 0.96$). Only one axis of predictive CoCa cross-validation was positive, indicating that all the predictions were lower than by random. The permutation test confirmed the cross-validation result; i.e., all axes, except one, were nonsignificant (Table 4).

Discussion

Although different landscape units can affect plant and true weevil diversities, both groups responded differently in this

Table 2 Abundance (and its percentage in relation to the total), richness, and its percentage in relation to the total, Simpson (1/D), and the estimated richness and Simpson for true weevils and plants in each landscape unit.

	RiSanB	FISanB	ErForW	CoMouR	ScMouR	CaOuts	CaWits	RiClaB	FiClaB	Total	Mean ± SD
True weevil											
Abundance (%)	35 (6%)	79 (14%)	70 (13%)	58 (10%)	46 (8%)	65 (12%)	48 (9%)	30 (5%)	107 (20%)	538	59.77 ± 23.88
Species richness (%)	9 (15%)	22 (36%)	13 (21%)	15 (23%)	14 (23%)	17 (28%)	16 (26%)	16 (26%)	12 (20%)	60	14.88 ± 3.62
Estimated richness (CI 95%)	26.48 (11.46 ± 133.38)	51.86 (28.22 ± 165.33)	21.87 (14.49 ± 65.55)	17.46 (15.39 ± 30.42)	49.22 (24.06 ± 137.23)	52.44 (24.56 ± 183.17)	21.87 (17.04 ± 48.98)	91.40 (42.32 ± 232.02)	13.11 (12.12 ± 21.94)		
Simpson	2.52	7.89	4.20	4.77	5.75	2.76	10.20	7.50	2.54	6.71	5.34 ± 2.71
Estimated Simpson (CI 95%)	2.63 (2.51 ± 3.82)	8.65 (7.89 ± 11.78)	4.39 (4.19 ± 5.84)	5.10 (4.76 ± 7.16)	6.43 (5.75 ± 9.01)	2.84 (2.76 ± 3.91)	12.67 (10.19 ± 16.54)	9.66 (7.50 ± 20.12)	2.57 (2.54 ± 3.24)		
Plants											
Abundance (%)	112 (8%)	169 (12%)	125 (8%)	142 (10%)	217 (15%)	77 (5%)	138 (9%)	258 (18%)	181 (12%)	1419	159.62 ± 55.81
Species richness (%)	13 (26%)	29 (51%)	13 (26%)	16 (32%)	13 (26%)	14 (28%)	13 (26%)	14 (28%)	19 (38%)	49	15.55 ± 4.06
Estimated richness (CI 95%)	21.92 (14.50 ± 65.82)	38.42 (27.88 ± 87.52)	14.11 (13.12 ± 22.95)	47.77 (20.80 ± 226.09)	15.24 (13.26 ± 31.96)	16.96 (14.34 ± 39.12)	15.23 (13.26 ± 31.91)	14.33 (14.02 ± 18.67)	26.95 (20.68 ± 56.64)		
Simpson	2.35	6.30	4.45	3.12	2.83	9.17	3.41	2.02	3.75	3.82	4.14 ± 2.25
Estimated Simpson (CI 95%)	2.38 (2.35 ± 2.98)	6.50 (6.29 ± 8.32)	4.57 (4.45 ± 5.48)	3.16 (3.11 ± 3.90)	2.84 (2.82 ± 3.40)	10.19 (9.10 ± 12.55)	3.46 (3.40 ± 4.35)	2.03 (2.02 ± 2.31)	3.81 (3.75 ± 4.56)		

The estimation was for 107 and 262 individuals of true weevils and plants, respectively, and are based on the most abundant landscape unit. Italic values indicate landscape unit with the highest value. RiSanB riparian sandy board, FISanB plane sandy board, ErForW ravine, CoMouR counterfort mountain range, ScMouR scarp mountain range, CaOuts canyon without soil, CaWits canyon with soil, RiClaB riparian clayey board, FiClaB plane clayey board.

study, resulting in no apparent trend of co-occurrence. For instance, whereas the highest richness of true weevils was in the riparian clayey landscape unit (RiClaB), plants had more species in canyons with soil (CoMouR). The plant and true weevil species dominance among landscape units also had no trend. While *P. pyramidalis* was the most abundant plant species in almost all landscape units (except in ravines—ErForW), the dominant true weevil species differed among the landscape units. Together, these results indicate that, despite each landscape unit determining the taxonomic diversity of woody plants and true weevils, plants diversity presents no clear relationships with true weevil diversity in this region of the Caatinga TDF.

Contrary to our expectations, habitat type affected true weevil and plant species richness and diversity in different ways, and the landscape units that encompassed a more diverse true weevil assemblage were not the same as those that had a more diverse plant assemblage. The Resource Specialization Hypothesis suggests that areas with higher plant diversity may favor the establishment of more diverse insect herbivore fauna (Hutchinson 1959), which has been proved in previous empirical studies (Cuevas-Reyes *et al* 2004, Haddad *et al* 2009, Leal *et al* 2016, Ebeling *et al* 2017a). Besides the food resource of insect herbivorous (i.e., plants), habitat structural complexity and microhabitat availability also affect the distribution of such insects (Cuevas-Reyes *et al* 2004 Joern & Laws 2013). Our results suggest habitats with a high plant diversity (potential food resources) may not promote a diverse assemblage of true weevils. Given dry ecosystems have harsh climatic conditions (e.g., elevated temperatures, low air humidity), the vegetation structure in these landscapes may promote a stronger effect on insect herbivores than the food availability by itself. Analyzing arboreal arthropods in Caatinga, Sousa-Souto *et al* (2014) suggest that tree identity or vegetation stage as possible main drivers in insect richness since they found a greater diversity of insects in environments with less plants diversity. Also, there are other factors related to vegetal structure like vegetation cover, plant architecture, and productivity can apparently be highly influential to insect communities because they affect directly the amount of resource on the environment, climate, locomotion, etc. (Allan *et al* 1975, Schmidt *et al* 2013 Stinson & Brown 1983). Therefore, we suggest further studies should aim at understanding the effects of diversity of food resources and vegetation structure on insect herbivores in the Caatinga TDF.

Previous studies found a positive relationship between plant and true weevil species assemblages (e.g., Murdoch *et al* 1972 Humphrey *et al* 1999 ter Braak & Schaffers 2004, Schaffers *et al* 2008). In arid and semi-

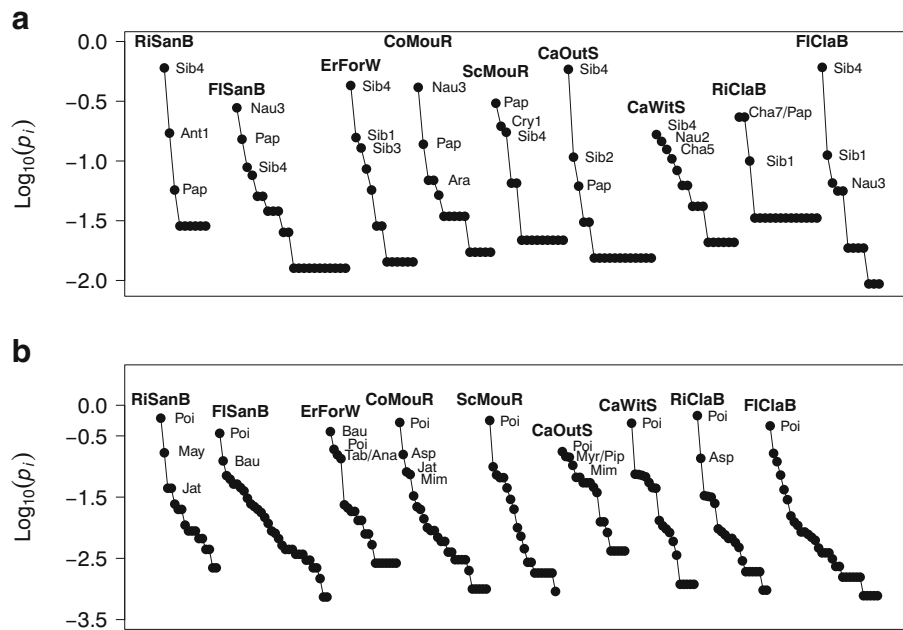


Fig 1 Ranking abundance plot of true weevils (A) and plants (B) in each landscape unit: FISanB: riparian sandy board; RiSanB: plane sandy board; ErForW: ravina; CoMouR: counterfort mountain range; ScMouR: scarp mountain range; CaOutS: canyon without soil; CaWitS: canyon with soil; RiClaB: riparian clayey board; FiClaB: plane clayey board. We only show the most abundant species in each landscape unit: true weevils: Ant1: *Anthonomus* sp1; Ara: *Aracanthus* sp.; Cha 3: *Chaldermus* sp3; Cha 7: *Chaldermus* sp7; Cry1: *Cryptorhynchini* sp1; Nau2: *Naupactus* sp2; Nau3: *Naupactus* sp3; Pap: *Pappista* sp.: Sib1: *Sibinia* sp1; Sib2: *Sibinia* sp2; Sib3: *Sibinia* sp3; Sib4: *Sibinia* sp4. Plants: Ana: *Anadenanthera colubrina* (Vell.) Brenan; Bau: *Bauhinia* sp.; Jat: *Jatropha molissima* (Pohl) Baill.; May: *Maytenus rigida* Mart.; Mim: *Mimosa tenuiflora* (Willd.) Poir.; Pip: *Piptadenia stipulacea* (Benth.) Ducke; Poi: *Poincianella pyramidalis* (Tul.) L. P. Queiroz. The relative abundance was log-transformed (base 10).

arid ecosystems, insect herbivores may present adaptations to surpass climatic conditions. For example, in arid regions of the USA, the herbivore *Uroleucon ambrosiae* (Thomas, 1878) (Aphididae, Hemiptera) presents a generalist diet, which is associated with scarce and ephemeral food availability (Funk & Bernays 2001). Likewise, in a Brazilian TDF, insect herbivores may feed on specific plant species that do not lose their leaves during the dry season (Silva *et al* 2017). In the studied landscape units, *Sibinia* sp4 was the only true weevil species that had a positive relationship with plant species abundance (Fabaceae–Mimosoideae). The correlation between *Sibinia* and Mimosoideae is known, since the seed of this plant is the oviposition site to *Sibinia* species (Clark 1978,

Heard *et al* 1997). In fact, Mimosoideae species produce many seeds per plant and in some areas, a large amount of resource is available to true weevils (Cuevas-Reyes *et al* 2004). Based on these results, we suggest there are true weevil species in the Caatinga which occupy narrow trophic niches, feeding and developing on specific plant species.

Based on our results, we can conclude that plant and true weevil diversity is not affected similarly in different habitats of the Caatinga dry forest, despite each landscape unit influences the species composition in both groups. This suggests the mechanisms that regulate herbivore–plant diversity relationships do not always follow a positive relationship, as observed in most tropical and temperate ecosystems. By

Table 3 Generalized linear models with Poisson distribution corrected by overdispersion between true weevil species and sub-family (Fabaceae–Mimosoideae) and family (Euphorbiaceae) plants.

True weevil	Plant	Estimate	Deviance	Deviance residuals	F [†]	P
<i>Sibinia</i> sp1	Mimosoidea	0.06	10.18	29.64	2.3	0.17
<i>Sibinia</i> sp2	Mimosoidea	0.01	0.05	23.34	0.01	0.9
<i>Sibinia</i> sp3	Mimosoidea	- 0.06	1.49	35.94	0.18	0.68
<i>Sibinia</i> sp4	Mimosoidea	0.08	86.43	83.05	7.65	0.02
<i>Pappista</i> sp.	Euphorbiaceae	- 0.01	0.25	19.17	0.09	0.77

These relationships were previously recorded in previous studies (Clark 1978, Espinelli *et al* 2016).

[†] Degrees of freedom of F test were 1 and 7.

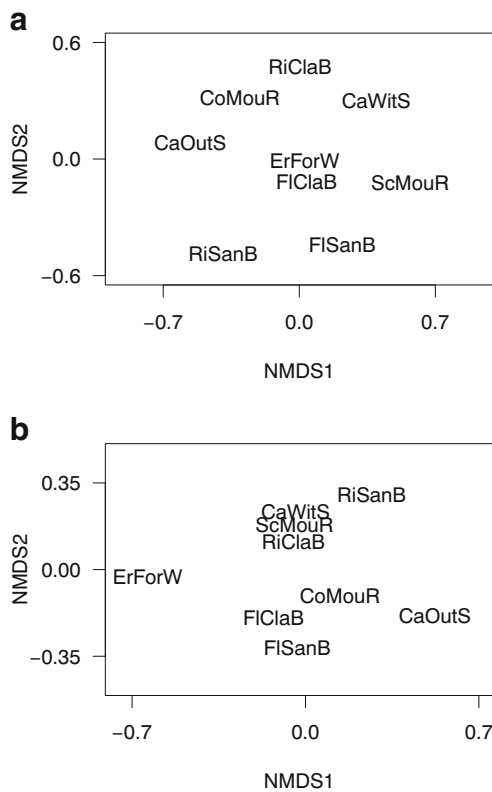


Fig 2 Nonmetric multidimensional scale of species assemblage dissimilarities of true weevils (A) and plants (B). We used the Bray–Curtis distance among landscape unit. FISanB: riparian sandy board; RiSanB: plane sandy board; ErForW: ravina; CoMouR: counterfort

evaluating how other factors regulate herbivore-insect distribution in dry ecosystems, we can improve the knowledge of diversity dynamics in such harsh environments. Knowing which factors regulate true weevil distribution, we can infer about ecological strategies of insects in dry forests, since herbivorous species tend to prefer a younger environment devoid of natural defenses. In TDFs, it is possible that specific plant traits, as being an evergreen species, may play a more

Table 4 Cross-validation fit, percentage of explained variance, and P value of permutation test of co-correspondence analysis (CoCa) to test if true weevil assemblage is predicted by plant assemblage.

	Cross-validation fit	% variance explained	P
COCA 1	0.58	14.51	0.11
COCA 2	-13.08	8.01	0.97
COCA 3	-28.31	11.80	0.99
COCA 4	-32.91	13.00	0.95
COCA 5	-80.91	10.27	1.00
COCA 6	-335.86	14.61	0.98
COCA 7	-443.4	12.57	0.78
COCA 8	-443.12	12.85	0.02

The number of axes (COCA 1 to 8) is the same of the number of sites.

important role on the distribution of herbivorous insects than plant diversity itself.

Acknowledgments We are thankful to GR-N for the help with true weevil specific identification. We thank the Xingó Program (CHESF/CNPq) for funding. JCS was supported by Capes (Grant as Best Thesis of 2012 on Biodiversity and Post-doc grant process #88881.120150/2016-01). RPS was supported by CONACYT and PNP/CAPES. LI is grateful to Conselho Nacional de Desenvolvimento Científico e Tecnológico–CNPq for the grant PQ2 (process number 309750/2019-9).

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s13744-020-00809-3>) contains supplementary material, which is available to authorized users.

Authors’ Contributions All authors contributed to the study conceptualization and writing. Material preparation and data collection were performed by Luciana Iannuzzi and João C. S. Regueira. Analysis was performed by Julia C. S. Regueira and Renato P. Salomão. Project supervision was performed by Luciana Iannuzzi. Authors read and approved the final manuscript.

Compliance with Ethical Standards

Declaration of Ethical Procedures The experimentation was no invasive and complied with Brazilian law. At the end of the experiment, the voucher specimens are deposited at Entomology Collection of Federal University of Pernambuco (UFPE) and plants voucher are at UFP Herbarium (Recife, Pernambuco, Brazil), following standard procedures and there are no conflicts of interest (financial and non-financial)

Conflict of Interest The authors declare that they have no conflict of interest.

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