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Is there a bottom-up cascade on the assemblages of trees, arboreal insects and spiders in a semiarid Caatinga?

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Abstract Predator–prey dynamics regulate the community structure of arthropods and may be affected by changes in their habitat. Bottom-up effects influence the distribution of arboreal insects changing, in turn, the availability of resources and shelter for the spider assemblage. This study examines the effect of habitat structure (tree richness and density) on the assemblages of herbivorous insects and spiders along a gradient of secondary forest succession in a semiarid Caatinga in northeastern Brazil. Insect and spiders were collected by beating the foliage during dry and wet seasons in 2010 and 2011. Plant richness and density varied significantly among stages of succession. In total, 2,590 arboreal insects were collected, corresponding to 14 orders and 151 morphospecies. In addition, we sampled 896 canopy spiders, encompassing 14 families and 53 morphospecies. Insect richness and abundance were negatively related with habitat structure, while spider richness increases with tree richness. We did not find any relationship among insects and spiders but there were differences in species composition of insects among all successional stages, determined by changes in vegetation structure. However, this effect does not extend to the species composition of spiders that remain similar in the different stages of secondary succession. We conclude that habitat structure had a partial bottom-up effect on arboreal insects and spider assemblages, indicating that this factor regulates the richness, abundance and species composition of arboreal insets and species richness of spiders. Thus, habitat structure promotes the maintenance of insects and spider diversity in fragments of Caatinga.

Keywords Arboreal spiders · Secondary succession · Habitat structure · Tropical dry forest

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Introduction

There is a consensus that bottom-up (host-plant resources) and top-down (predation) factors interact together to regulate the food webs in several ecosystems (Price et al. 1980; Hunter and Price 1992; Nakamura et al. 2005), and probably changes in habitat structure such as natural and anthropogenic disturbances can highlight the effects and direction of trophic cascades in these communities.

The conversion of large areas of native vegetation to earlier successional stages by direct and indirect human activities has reduced formerly connected habitats to smaller and increasingly isolated patches (Hunter 2002; Saunders et al. 1991; Vitousek and Farrington 1997). A mosaic of fragments with different stages of plant succession in the landscape may affect ecosystem function (Chapin et al. 1997) such as the trophic structure of food webs that ultimately influence species diversity and community structure (Hunter and Price 1992; Halaj et al. 2000).

According to the microspatial heterogeneity hypothesis (MacArthur and MacArthur 1961), habitats which are more diverse structurally will support more species. Thus, late secondary successional stages would have more species than early ones. For example, the habitat simplification through the replacement of native forests with pasture for livestock grazing results in significant losses of species and changes its composition (Schnell et al. 2003). In addition, changes in habitat structure play a bottom-up effect on prey availability and, in turn increases, spider abundance and richness (Greenstone 1984; Halaj et al. 1998).

Much attention has been directed toward changes in arthropod biodiversity throughout regeneration gradients in tropical forests (Hendrix et al. 1988; Siemann et al. 1999; Neves et al. 2010a, b, 2014). The underlying causes for observed changes, however, are almost unknown in tropical dry forests (TDFs), particularly those regarding bottom-up cascades. In semiarid regions such as the Brazilian TDF, known as Caatinga, the effects of changes on habitat structure, as a consequence of forest succession, on arthropod assemblages are an issue that remains inconclusive (see Neves et al. 2010a; Silva et al. 2012).

Bottom-up theory states that energy supply from the bottom of the food web limits the number of trophic levels, together with relative efficiency of the consumers (Lindeman 1942; Hunter and Price 1992). Hunter and Price (1992) suggested a model in which species at any trophic level can dominate other trophic levels due to feedback loops of top-down and bottom-up cascading effects. Thus, as a consequence of forest regeneration, plant diversity and abundance (a surrogate of habitat heterogeneity) often increase and become a bottom-up force, driving changes in population density, community structure and diversity for terrestrial food webs (Greenstone 1984; Hunter and Price 1992; Matos et al. 2013).

Although top-down cascades (the control of the biomass by consumers over lower trophic levels) commonly occur in a wide variety of aquatic and terrestrial systems (Strong 1992; Schmitz et al. 2000), some studies have shown that food webs with high diversity of plants and herbivores lead to the development of a myriad of defensive strategies of plants, because each additional plant species can have specialized consumers (Murdoch et al. 1972), indicating that bottom-up cascades could be the rule for terrestrial systems (Power 1992; Strong 1992; Polis and Strong 1996; Siemann 1998; Gratton and Denno 2003). Changes on vegetation structure, with the decrease of the richness and density of trees, may affect the distribution of arboreal insects and thereby reduce resource availability for natural enemies, like spiders (Fernandes et al. 2004; Bukovinszky et al. 2010; Neves et al. 2014).

According to several studies, insect diversity increases with the increased plant diversity and heterogeneity in the course of forest regeneration (Southwood et al. 1979; Neves et al. 2014; Schuldt et al. 2011, 2013). Environments with greater diversity of herbivores may therefore harbor a higher diversity of predators, such as spiders (Rypstra et al. 1999; Halaj et al. 1998; Schuldt et al. 2008). Since spiders are generalist predators, feeding mainly on insects and occasionally small vertebrates (Brazil et al. 2005; Foelix 2011; Oliveira-Alves et al. 2005; Wise 1993), this group represents an important component of the community and is particularly sensitive to changes in the landscape (Johnson et al. 2010; Schuldt et al. 2011, 2012).

Although this issue is broadly recognized, there is no study in semiarid environments that supports or even investigates the effect of bottom-up forces as determinants in the structure of tri-trophic food chains consisting of plants, herbivorous insects and natural enemies. More information on the relationship between the habitat structure and biodiversity at different trophic levels is required to understand how semiarid ecosystems and their functioning are influenced by trophic interactions.

In this paper, we address how richness and abundance of the trees, insects and spiders change along a gradient of secondary succession in a semiarid Caatinga, a type of TDF in Brazil (Pennington et al. 2000; Santos et al. 2012). We test whether the secondary succession plays a bottom-up cascade altering richness, abundance and composition of arboreal insect and spider assemblages. Hence, we tested the hypothesis that the increased richness and density of trees that occurs along the Caatinga succession can determine a cascading effect on insects and spiders by increasing their richness and abundance, and by changing their species composition.

Materials and methods

Study area

This study was conducted in three areas with different stages of plant regeneration in the state of Sergipe, northeastern Brazil. All the areas are over sedimentary basins that surround the São Francisco River (Oliveira et al. 2013). The relief is formed by geomorphologic “Pediplanos Sertanejos,” and the predominant soil is classified as Eutrophic Litholic Neosol, according to the Brazilian System of Soil Classification (EMBRAPA 2006). The vegetation type matches the physiognomic forms of the Brazilian Caatinga, which range from seasonally TDF to scrub vegetation (Andrade-Lima 1981; Sampaio 1995; Pennington et al. 2000). Throughout the Caatinga domain (736,000 km^2), the climate is classified as Tropical Semiarid—Bshi (Köppen), with annual rainfall ranging from 250 to 900 mm and mean temperature of 24 and 26 °C (Andrade-Lima 1981).

The region of study currently has a number of fragments of secondary forest in diverse stages of plant regeneration, surrounded by a matrix of active and abandoned pastures (Souza et al. 2003).

Sampling design

Arthropods (arboreal insects and spiders) were sampled in 15 plots of 50 × 20 m (0.1 ha each) representing early, intermediate and late forest stages of natural regeneration (five plots per stage). We established a minimum distance of 200 m between each plot. The early stage of plant recovery is characterized by a 20 ha of abandoned pasture for 3 years before the experiment and composed of sparse patches of woody vegetation, shrubs, herbs and grasses, with a single stratum of tree crowns composing a very open canopy up to 2 m. Intermediate regeneration is located 2.5 km apart from early regeneration and is composed of deciduous trees 2–4 m in height within a Conservation Unit (Natural Monument Grota do Angico), in the municipality of Poço Redondo (9°41′S and 38°31′W) covering 2,183 ha. This area is formed by a secondary dry forest with approximately 12–15 years of regeneration. The third area is a forest fragment (115 ha) with more than 40 years of regeneration composed by taller deciduous trees which form a canopy 4–15 m high, located on a private farm, in the municipality of Porto da Folha, 30 km away from the other two regeneration stages (10°02′S 37°24′W).

Arthropod and plant sampling

For the assessment of vegetation structure, we measured the species richness and abundance of trees with circumference at breast height (CBH) higher than 6 cm. In each plot, we arbitrarily chose five trees (regardless of the species) with circumference at breast height ≥ 6 cm, at least 10 m apart from each other as sampling points, and the chosen trees were beaten over a beating tray, made of 1 m^2 of white cloth mounted on the frame of an umbrella drop net. Each tree was vigorously beaten over this umbrella with a stick. Sampling effort was standardized by estimated number of secondary branches per tree. Trees with 1–5 branches ($n = 60$) were beaten 30 times, including all branches. For the other trees with 6–10 branches ($n = 15$), we selected three sections of the tree canopy and performed 10 beatings in each section, totaling 30 beatings per tree. Trees with more than 3 m height were sampled using an articulate ladder (see Neves et al. 2014). We assessed arboreal insect abundance and spider abundance, species richness and composition in December 2010, March 2011, May 2011 and July 2011. We stored all of the arthropods that we collected from the beating samples in 80 % ethanol and later sorted, counted, and identified all spider individuals to the lowest possible taxonomic level (species/morphospecies) and arboreal insects to family level using taxonomic keys (Borror et al. 2002). After family identification, insects were sorted into morphospecies using external morphological characteristics. Voucher specimens of insects were deposited in the Entomological Collection of the Laboratório de Entomologia at Universidade Federal de Sergipe, Sergipe, Brazil, and the spiders were deposited in the Coleções Taxonômicas da Universidade Federal de Minas Gerais, Brazil.

Statistical analysis

We grouped the values of each sample point (the five trees per plot) to obtain a unique data for each plot. To compare the richness and abundance of trees, insects and spiders among successional stages, we used generalized linear models (GLMs) (Crawley 2007), when significant differences were observed that the data were submitted to contrast analysis by aggregating levels (Crawley 2007). If the level of aggregation was not significant and did not alter the deviance explained by the null model, the levels were pooled. To test the hypothesis that arthropod assemblages in this system are bottom-up controlled along a cascade from plants via insects to spiders, we first used GLMs, considering species richness and abundance of arboreal insects as response variables and richness and abundance of trees per plot and the interactions among this variables as explanatory variables. For spiders, we used richness and abundance of trees and arboreal insects, and the interactions among these variables as explanatory variables and richness and abundance of arboreal spiders as response variables (Crawley 2007), followed by analysis of residues to check for the suitability of error distribution (normal, Poisson or quasipoisson) and for model adjustment. The minimum adequate model (MAM) was obtained by extracting non-significant terms ($p < 0.05$) from the full model (Crawley 2007).

The influence of tree richness and density as well as secondary succession in species composition of arboreal insects, and the influence of tree richness and density, insect richness and abundance and secondary succession in species composition of spiders were tested using a PERMANOVA—permutational multivariate analysis of variance (Anderson 2001). We used of Bray-Curtis dissimilarity measures, and 999 permutations were generated. We also used non-metric multidimensional scaling (NMDS) to represent the results of the PERMANOVAs ($K = 2$). In NMDS, the ordination of species composition was undertaken using the Bray–Curtis index. All statistical analyses were conducted with the R (R Development Core Team 2014).

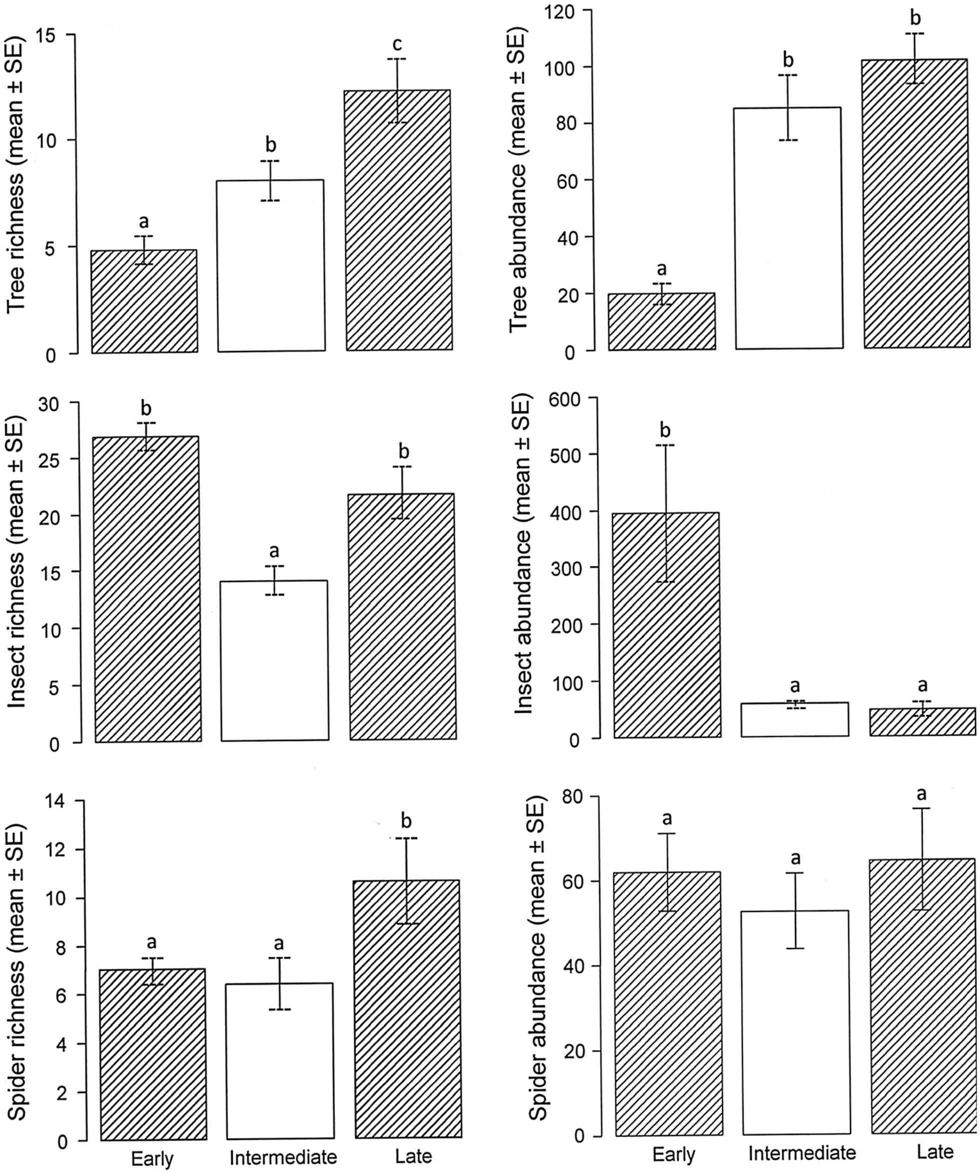


Fig. 1 Abundance and richness of woody plants, arboreal insects and spiders among three stages of forest regeneration in a Caatinga environment. *Different letters* indicate significant differences among stages (GLM with a MAM adjustment; $\alpha < 0.05$)

Results

The three areas were characterized by marked differences in tree species richness and abundance ($p < 0.001$, Fig. 1) since plant richness increased with succession, and tree abundance was higher in intermediate and late successional stages, when compared to the early stage. The mean tree species richness varied from 3 to 5 (early succession), 7 to 9 (intermediate succession) and 10 to 17 (late succession), while tree density had a range from 9 to 127 plants/plot (1,000 m^2).

In general, we sampled 2,590 adults of arboreal insects (151 morphospecies) distributed in 14 orders (Table 1). Larvae and nymphs (97 individuals) were recorded only for analysis of abundance. Coleoptera (70 morphospecies), Hymenoptera (34) and Hemiptera (23) accounted for 84 % of all individuals sampled (Table 1). Only 13 morphospecies (8 %) were common to all areas sampled: Blattelidae sp. 1 (Dictyoptera), Bruchinae sp. 3 (Coleoptera), *Camponotus vittatus*, *Crematogaster* sp. 1, *Crematogaster stolli* (Hymenoptera), Eumolpinae sp. 7, Galerucinae sp. 2, Monommatinae sp. 1 (Coleoptera), *Pseudomyrmex* sp. 1, *Pseudomyrmex gracilis* (Hymenoptera), Scotytilidae sp. 1, *Sibinia* sp. 1 and Tenebrionidae sp. 3 (Coleoptera). In plots of early plant recovery, we sampled 83 morphospecies (53 unique to that stage); plots of the intermediate stage of plant recovery had 46 morphospecies (17 unique); and 71 morphospecies were collected (40 unique) in plots of late regeneration.

Additionally, we sampled 896 spiders (183 adults) corresponding to 53 morphospecies, 20 genera and 14

Table 1 Spider species found in 15 plots in three stages of forest regeneration (early, intermediate and late) in a Caatinga environment, Sergipe, Brazil

Morphospecies	Regeneration stage		
	Early	Intermediate	Late
Anyphaenidae			
Anyphaenidae sp. 1	10	8	7
Anyphaenidae sp. 2	0	0	1
Araneidae			
Alpaida sp. 1	8	10	1
Alpaida sp. 2	0	0	2
Ciclosa sp.	0	0	1
Eustala sp.	1	0	0
Mecynogea sp.	0	1	0
Metepeira sp.	3	0	1
Wagneriana sp.	0	0	1
Corinnidae			
Castianeira sp.	0	1	3
Dictynidae			
Dictynidae sp. 1	0	0	3
Linyphiidae			
Linyphiidae sp. 1	0	1	0
Linyphiidae sp. 2	0	0	1
Mimetidae			
Mimetus sp.	1	1	0
Miturgidae			
Cheiracanthium inclusum	23	3	7
Oxyopidae			
Hamataliwa sp.	0	0	2
Peucetia rubrolineata	0	1	1
Philodromidae			
Philodromidae sp.	0	0	1
Salticidae			
Salticidae sp. 1	0	1	0
Salticidae sp. 2	0	1	2
Salticidae sp. 3	0	1	0
Salticidae sp. 4	0	3	4
Salticidae sp. 5	0	1	0
Salticidae sp. 6	0	0	1
Salticidae sp. 7	1	0	0
Salticidae sp. 8	2	0	0
Salticidae sp. 9	0	0	1
Salticidae sp. 10	1	0	0
Salticidae sp. 11	1	0	0
Salticidae sp. 12	0	1	0
Salticidae sp. 13	0	1	0
Salticidae sp. 14	0	1	0
Salticidae sp. 15	0	1	0
Salticidae sp. 16	0	0	1
Salticidae sp. 17	0	0	2
Salticidae sp. 18	0	0	1
Salticidae sp. 19	0	0	1
Cotinusa sp.	0	1	0
Scytodidae			
Scytodes sp.	5	1	4
Tetragnathidae			
Leucage sp.	1	2	2
Theridiidae			
Anelosimus sp.	4	0	0
Chrysso sp.	5	1	5
Cryptachaea sp.	1	0	1
Faiditus sp.	0	1	0
Theridiidae sp. 1	0	3	3
Theridiidae sp. 2	1	0	1
Theridiidae sp. 3	0	0	2
Theridiidae sp. 4	0	0	1
Theridiidae sp. 5	2	0	0
Theridiidae sp. 6	0	0	2
Theridiidae sp. 7	0	0	1
Thomisidae			
Misumenops maculisparssus	0	1	1
Tmarus sp. 1	0	0	1
Tmarus sp. 2	0	0	1
Tmarus sp. 3	0	0	2

Table 2 Arboreal insects sampled in three different regeneration stages in Caatinga vegetation, Sergipe, Brazil

Taxon	Regeneration stage (number of morphospecies)		
	Early	Intermediate	Late
Coleoptera	37	25	37
Hemiptera	15	4	9
Orthoptera	2	4	1
Hymenoptera	22	9	17
Lepidoptera	2	1	1
Mantodea	2	0	2
Blattodea	2	2	2
Isoptera	1	1	2
Thysanoptera	1	0	1
Pscoptera	1	1	0
Dermaptera	0	0	1
Diptera	2	1	2
Neuroptera	0	1	0
Phasmatodea	0	0	1
Total	87	49	76

families. Spiders represented between 19 and 54 % of all canopy arthropods among the stages of plant regeneration. Salticidae (38 %), Theridiidae (21 %) and Araneidae (11 %) were the most representative families, comprising 41 morphospecies. The families with more individuals were Anyphaenidae (243 individuals), Salticidae (197) and Araneidae (143). Six morphospecies were common to all stages of succession (11 %), seven were unique in abandoned pastures (early succession), eleven morphospecies occurred only on the intermediate stage, and 21 morphospecies were unique to late stage (Table 2).

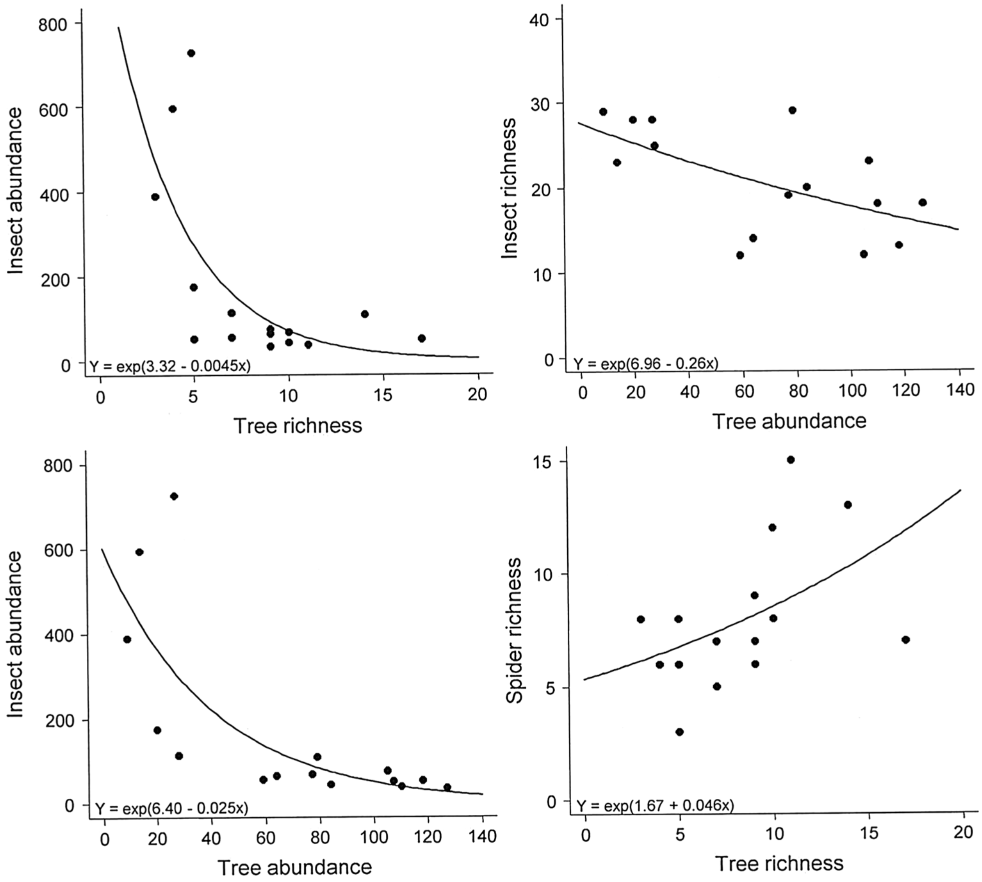
Fig. 3 Non-metric multidimensional scaling ordination for species composition of arboreal insects (**a**, **b**) and spiders (**c**), sampled among three stages of forest regeneration in a Caatinga environment. The difference in the size of symbols is proportional to the abundance (**a**) or richness (**b**) of trees ▶

Differences in habitat structure affected the richness and abundance of arboreal insects and spiders differently. For insects we found that species richness was higher in early and late successional stages, when compared to the intermediate stage ($p < 0.0001$, Fig. 1). Additionally, insect abundance was higher in early stage than in intermediate and late successional stages ($p < 0.0001$, Fig. 1). There was a negative effect of tree species richness on arboreal insect richness, and we found a negative effect of tree

Table 3 Analyses of deviance of MAM, showing the effects of explanatory variables (tree species richness and density and secondary succession) on the richness and abundance of arboreal insects and on the richness of spiders, in a semiarid Caatinga, state of Sergipe, Brazil

Response variable	Explanatory variable	*df*	Deviance	*p*	Error distribution
Insect richness	Stage of succession	1	20.1	<0.001	Poisson
	Plant abundance	1	14.28	>0.001	Poisson
Insect abundance	Stage of succession	1	2.083	<0.001	Poisson
	Plant richness	1	1.513	<0.01	Quasipoisson
	Plant density	1	497	0.037	Quasipoisson
Spider richness	Stage of succession	1	6.2	0.04	Poisson
	Plant richness	1	3.84	0.04	Poisson
	Insect abundance	1	0.48	0.49	Poisson

Fig. 2 Abundance and richness of arboreal insects and richness of spiders in response to tree abundance or tree richness in a Caatinga environment



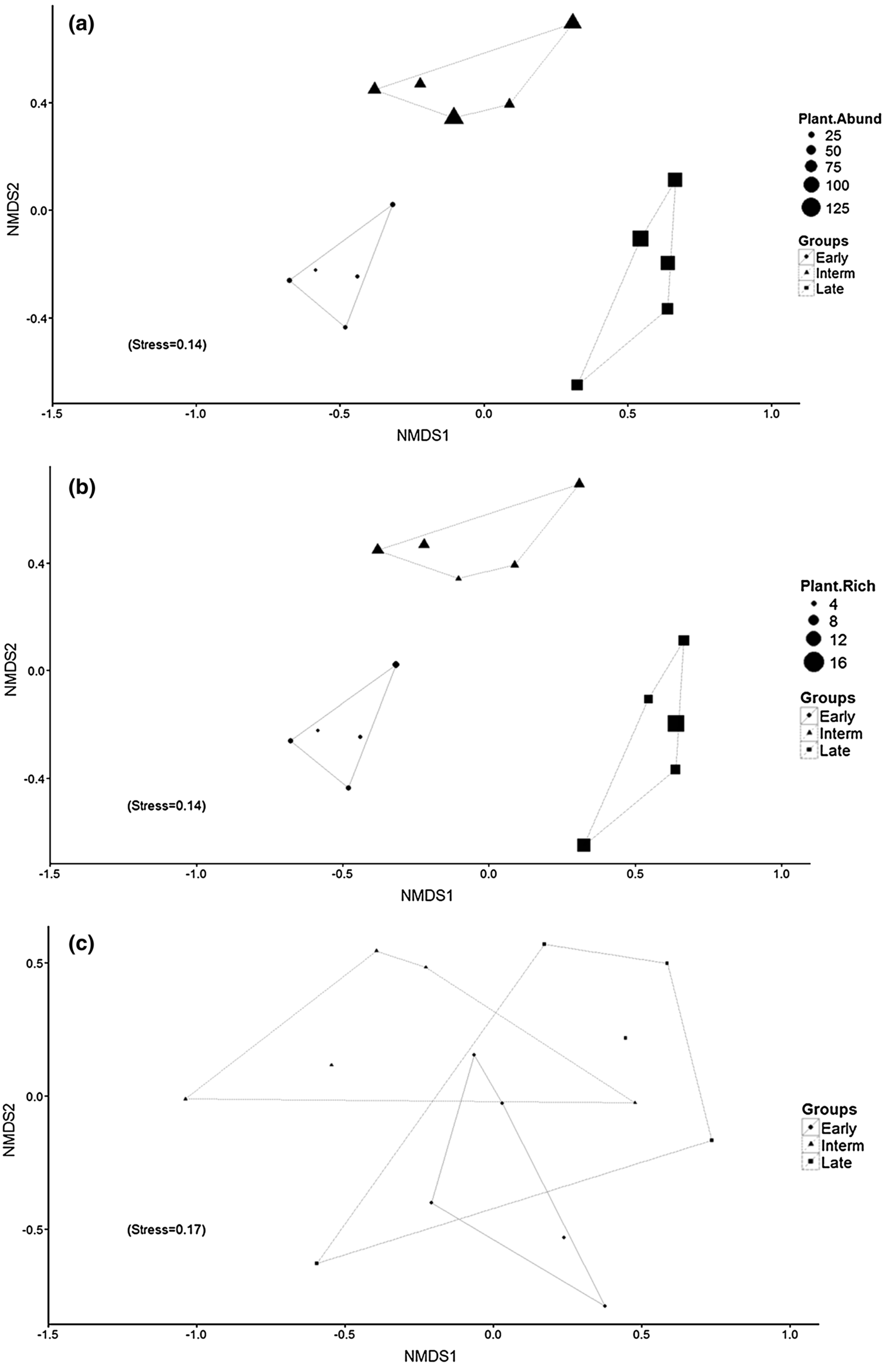

(a)
Plant.Abund
25
50
75
100
125
Groups
Early
Interm
Late
(Stress=0.14)
NMDS1
NMDS2
0.4
0.0
-0.4
-1.5
-1.0
-0.5
0.0
0.5
1.0
(b)
Plant.Rich
4
8
12
16
Groups
Early
Interm
Late
(Stress=0.14)
NMDS1
NMDS2
0.4
0.0
-0.4
-1.5
-1.0
-0.5
0.0
0.5
1.0
(c)
Groups
Early
Interm
Late
(Stress=0.17)
NMDS1
NMDS2
0.5
0.0
-0.5
-1.5
-1.0
-0.5
0.0
0.5
1.0

Table 4 PERMANOVA main tests for differences in assemblage composition of arboreal insects and spiders among successional stages and habitat structure (plant richness and density), in a semiarid Caatinga, state of Sergipe, Brazil

Response variable	Terms of the model	*df*	*F*-model	R^2	*p*
Insect composition	Stage of succession	2	3.07	0.249	0.001
	Plant richness	1	5.22	0.211	0.006
	Plant abundance	1	3.32	0.134	0.003
Spider composition	Stage of succession	2	1.38	0.178	0.19
	Plant richness	1	1.63	0.105	0.06
	Plant density	1	1.27	0.082	0.23
	Insect richness	1	1.26	0.041	0.83
	Insect abundance	1	0.64	0.081	0.21

richness and abundance on the abundance of arboreal insects (Table 3, Fig. 2).

For spiders, we found that species richness was higher in late successional stage ($p = 0.014$ in a GLM with Poisson errors), when compared to the intermediate and early stages (Fig. 1). On the other hand, the MAM indicated that species richness of spiders was positively influenced by tree richness (Table 3; Fig. 2). The abundance of spiders did not change in response to secondary succession (Fig. 1), and tree or insect structure ($p > 0.05$).

Regarding species composition, arboreal insects presented clear difference in all successional stages in response to changes of the richness and abundance of trees (Fig. 3; Table 4). The composition of spiders did not change in response to secondary succession, nor tree or the assemblage structure of insects (Fig. 3; Table 4).

Discussion

In this study, we tested whether habitat structure (plant richness and density) promoted by secondary succession could drive a bottom-up cascade on the assemblages of arboreal insects and spiders in a semiarid Caatinga, and we found some results that partially support this hypothesis. Early successional stage (abandoned pastures) presented lower heterogeneity and complexity, determined by lower richness and density of trees, higher insect abundance than intermediate or late areas of succession, and lower species richness of spiders compared with late stage. Thus, habitat structure has made changes on arboreal spider richness as well as insect richness, abundance and species composition. However, there was no relationship between insects and spiders; only the richness of trees determines the species richness of spiders. Sites in advanced stage of secondary succession, which present greater complexity and heterogeneity of vegetation, can support increased insect diversity (Lassau and Hochuli 2005, 2007; Ober and Hayes 2008; Neves et al. 2014) and as such, habitats of early succession could negatively impact insects and subsequently spiders. Arboreal insects, however, were more abundant in sites of early successional stage, despite the higher complexity and heterogeneity of vegetation in intermediate and late stages. This result, in turn, corroborates previous studies that argue that insect densities can be greater in human-altered areas (Christie et al. 2010; Silva et al. 2012; Matos et al. 2013, but see Dennis et al. 1998), and in our study site, it can be explained by two factors.

First, probably insect abundance was affected by tree identity, since we have sampled different species of trees in the three different habitats and it is strongly expected that the insect attraction by specific trees (e.g., leaf thickness specially for chewing insects and phloem quality for sucking insects) might be different along a gradient of plant succession. Arthropod sampling in different tree species in this study is justified because differences in tree species composition are a consequence of the own plant succession, where pioneer species are dramatically reduced in late succession. Thus, sampling in a unique tree species was not possible.

Second, more disturbed sites have greater abundance of some tree species than undisturbed environments (Silva et al. 2012; Matos et al. 2013), and greater abundance of insects in trees of the early regeneration sites in the present study can be explained primarily by the occurrence of *Sibinia* sp. (Coleoptera: Curculionidae), which occurred in all stages of succession but had massive presence only in the early succession plots (1,535 individuals or 60 % of total insects sampled). *Sibinia* sp. is a small (<0.5 mm) herbivore insect that was common in individuals of *Mimosa hostilis* (Mart.) Benth (Fabaceae), a pioneer arboreal species which is very conspicuous in abandoned pastures (early stages of succession) in Caatinga environments (Ribeiro et al. 2013). In fact, the occurrence of *M. hostilis* was restricted to plots of early succession stage, as well as this species was the most representative of those plots (80 % of all tree individuals sampled). The high frequency of *M. hostilis* can explain the high insect abundance in the abandoned pastures due to the “resource concentration hypothesis” (Root 1973). This hypothesis predicts that the abundance of specialist herbivores will be higher in simplified environments, since it is more likely that they will be able to locate their host-plant in such areas (Bach 1980; Andow 1991). Besides, abandoned pasture can influence the diversity and density of specialist grass arthropods (Brown et al. 1992; Curry 1994). This can explain why the intermediate successional stage had the smaller number of insect species compared with the early and late stages. It is possible that in the early stage, some generalist species of insects sampled in the trees were simultaneously using several plant species in the two strata (pasture/tree), even pasture specialist species captured occasionally, and thus, a high richness can be found, similar to the effect found in later successional stages, in response to a greater species richness of trees. In opposition, the herbaceous strata in the intermediate stage were negligible.

The greater abundance of the coleopteran *Sibinia* sp. in the early succession, however, did not promote a high species richness or abundance of spiders in this environment, corroborating previous studies that have suggested little evidence that spider populations cause significant density-dependent mortality in prey populations (Wise 1993) or that plant species richness changes spider assemblages (Schuldt et al. 2011).

We did not verify any change in spider species composition among the three stages of succession, although we found that from the 55 sampled morphospecies, only six (11 %) occurred in all stages and 20 morphospecies (36 %) were exclusive from the late stage. Divergent results were found for spider assemblages in different habitats (Hatley and Macmahon 1980; Hurd and Fagan 1992; Hore and Uniyal 2008), with spider assemblages differing along a gradient of habitat types or perturbation and having similar composition according to habitat structure. It may occur due to the high dispersion capacity of spiders, as observed in studies performed in the Azores islands (Ribeiro and Borges 2010). Thus, our result shows that spider species are insensitive to habitat changing across Caatinga regeneration in our study site, contrasting with previous studies that found that predators, such as spiders, might be expected to have relatively predictable assemblages based on habitat structure (Uetz 1991; Wise 1993; Borges and Brown 2001).

The similarity of spider assemblages among all successional stages suggests that the patchy tree populations are someway connected in the landscape, maintaining the spider diversity in the studied Caatinga environment. Thus, according to these observations, spider diversity does not necessarily correlate with a high insect abundance neither it depended on the spatial heterogeneity of the habitat. Another possibility is that 40 years of forest succession is not enough to restore spider diversity in this semiarid habitat, since approximately 30 years were necessary for the recovery of spider assemblages on *Handroanthus ochraceus* (Bignoniaceae) along a successional gradient in a seasonally dry tropical forest in southeastern Brazil (Silva et al. 2012) and in temperate environments—boreal and coniferous forests (McIver et al. 1992; Buddle et al. 2000), after clear-cutting or fire disturbances.

Hence, our results indicate that changes in habitat structure as a result of forest succession do partially drive a trophic cascade involving arboreal insect and spider assemblages, but it is evident that arboreal spiders have low sensitivity to resource availability or habitat quality in TDFs. Based on the regeneration patterns observed in the Caatinga studied here, it is likely that 40 years of forest regeneration is not enough to restore species composition of arboreal spiders; however, this period is enough to restore species composition of arboreal insects, strengthening the importance of secondary habitats to biodiversity maintenance in these ecosystems. We conclude that changes in habitat structure (tree richness and density) along a gradient of plant succession in a semiarid Caatinga can lead to changes on both arboreal insect and spider assemblages; however, the strength of these variables is more pronounced for the consumers than for predators.

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