Published Online June 2014 in SciRes. http://www.scirp.org/journal/ojas http://dx.doi.org/10.4236/ojas.2014.43016



Tree-Fall Gaps Effects on Spider (Araneae) Assemblages in an Atlantic Forest Landscape in Northeastern Brazil

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Received 15 April 2014; revised 20 May 2014; accepted 27 May 2014

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Abstract

The study investigates the effect of spatial and temporal tree-fall gaps structure on spiders' assemblage in an Atlantic forest fragmented area in Brazil. It was conducted in the Michelin Ecological Preserve-REM (Bahia), 190 ha forest remnant. Samples were collected on leaf-litter (50×50 cm) at five tree-fall gaps formations ($<150 \text{ m}^2$), within five adjacent primary forest and five inner edge parcels. During 16 months (between May 2009 and October 2012), 480 m² leaf-litter samples were collected, from which spiders were extracted using mini-Winkler traps. The observed and estimated richness of spider's species was higher at the edge (p < 0.01). The habitat structures differ significantly among the three habitat types (MRPP, p < 0.01) and also during the tree-fall gaps aging gradient (MRBP, p < 0.01). There were significant differences on spiders' species composition, comparing the three habitats (MRPP, p < 0.05). The composition of spider's species changed as tree-fall gaps aged (MRBP, p < 0.05). We argue that the tree-fall gaps play, on a local scale, an important role in acting on the time-space distribution dynamics of spider's species assemblages, although the time effect should still be evaluated.

Keywords

Atlantic Forest, Edge Effect, Habitat Selection, Spatiotemporal Effect, Neotropical Fauna

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1. Introduction

Natural disturbances role in shaping the tropical forests biological communities' structure is widely known [1]. Natural disturbances increase habitat heterogeneity by promoting specialization and resource partitioning among species, whereas at the same time, they prevent from competitive exclusion fostering diversity [2]-[4]. Gaps formed by the fall of one or more trees are, apparently, the most common disturbance in forest environments, and these forms an opening in the canopy structure [5]. However, tree-fall gaps are likewise considered one of the main contributors for tropical forests' regeneration, significantly adding to its floristic diversity [6] [7], as they alter the habitat structure.

The regeneration witnessed on tree-fall gaps promotes the development of primary and pioneer species, and the secondary one promotes remarkable changes on trees' population's dynamics, species composition and growth rate [8] [9]. Therefore, it has been considered as an essential mechanism for the forests diversity's maintenance [3] [10] [11]. Tree-fall gap regeneration can be divided into three phases: tree-fall gaps formation, building phase, and mature phase [12]. These phases duration vary, and depend on factors such as size [6] [13], alleviation [14], severity of disturbance [13], soil condition [7] and pre-existing vegetation [15] [16].

The tree-fall gap phase is considered the most important to determine floristic composition [17], since it is characterized by an intense gap, changing microclimatic conditions and plant community structures [15]. It is estimated to last from four to six years in tropical forests [9].

Tree-fall gaps influence the spatial and temporal distribution of plants, therefore, affect these organisms' interactions to other animals [18] [19]. However, few studies have focused on animals, whilst most of them have pointed out structural aspects, such as area, age, geometry and type of fall, as well as vegetal organisms rather than their interactions [6] [10] [13]. This knowledge bulk has found significant tree-fall gaps influence on plant community structure. Following a thorough literature review we can refer to: studies on trees [3], pioneer plants [6] [14], bamboos [20], seedling growth [21], and gap and grazing areas interactions with the establishment, growth and survival of pioneer species [22].

Previous studies of animal related tree-fall gaps include: birds [1], ants [23]-[25] and spiders [26] [27]. No significant differences were found, on the aforementioned publications, between tree-fall gaps and mature forests on birds and orb-weaver spiders' studies. However, studies on ants have revealed controversial results. In a forest in India, species richness differed between forest tree-fall formations [23], whilst in a study conducted in a forest in Panama, no difference was found on species' abundance, richness and composition [24]. More recently, a study in a forest in Costa Rica found that the estimated richness differ between mature forest and adjacent tree-fall gap, although species composition did not show significant difference [25]. Most studies tend to compare the fauna in young tree-fall gaps to intact forest, ignoring that tree-fall gaps may change over time [25]. Thus, time scale approaches are essential to understand the tree-fall gaps dynamics, especially when related to certain animal groups such as arachnids.

Spiders (Arachnida: Araneae) are among the most abundant and diverse animal group, with 44,540 species currently described in the World [28]. They act as secondary predators on the trophic structure where they have a role [29]. They then, directly or indirectly regulate important taxa' abundance of ecosystem processes, such as predation, pollination, decomposition and dispersion [30]. Spiders' distribution and density are related to environmental factors such as temperature, relative humidity and luminosity [31] [32], habitat physiognomy, plant richness and composition [33]. In tropical forests such as any other natural landscape, habitat structure influences the richness and composition of spider's assemblages species [34]). Leaf litter structure also affects spiders' abundance [35], richness and composition [36] [37]. Therefore, natural disturbance caused by tree fall gaps may also influence the spider's assemblages [38] [39].

This study investigates whether tree-fall gaps show time-space scale effect on composition of spider's assemblages species in an Atlantic forest remnant at the Michelin Ecological Reserve, Igrapiúna, Bahia, northeastern Brazil. We addressed four questions: 1) Does the habitat structure of tree-fall gap (microclimate and microhabitat) significantly differ from that found in adjacent mature forest and inner edge? 2) Does the richness and composition of tree-fall gap species significantly differ from those found in adjacent mature forest and inner edge? 3) Does the habitat structure of natural tree-fall gaps (microclimate and microhabitat) significantly change during vegetation regeneration process? 4) Does the spider's species' assemblage composition of tree-fall gaps significantly change throughout the regeneration process?

2. Material & Methods

2.1. Study Area

The study was conducted at the Ecological Reserve Michelin (REM) (13°50'S, 39°10'W, 90 to 383 m above sea level), situated in the city of Igrapiúna and Ituberá (state of Bahia, Brazil). It is located 18 km away from the coast in a region known as "BaixoSul", 200 km south from the State capital city of Salvador. The 3096 ha REM area consists of a vegetation mosaic on different successional stages. Landscape id modified by different types of human disturbance, agriculture and pasture converted. And other forms of anthropogenic pressure (such as logging, hunting and exploitation of the palm). Approximately, 25% of the reserve is intended to rubber tree monoculture plantations [40]. The mean annual rainfall is 2000 mm and the temperature ranges from 21°C to 28°C. [40].

The reserve contains 1800 ha of lowland evergreen hill forest distributed in three main fragments: Vila 5/Pancada Grande fragment with 625 ha, the 140 ha Luis Inácio forest, and the 550 ha Pacangê forest, which is contiguous with a 13,000 ha forest [40]. This study was conducted in Mata da Vila Cinco with 190 ha, which is one of the remnants. The northern access to this fragment is constituted by a land mosaic dominated by mature and young primary forest, where the canopy reaches uniformly from 18 - 25 m. The southern access consists of mature second-growth forest, with trees ranging from eight to 13 m height, abundant vines and thick leaf litter. At higher slopes in the landscape there is a group of mature primary forest with several old trees. The local jussarapalm, bromeliads, vines and other epiphytes are abundant and well distributed in this remnant, which is crossed by a small river, two streams and several springs. The forest is surrounded by cocoa, rubber and banana plantations and is limited to the north by the "Mata do Rio" forest, another section of the reserve (K. Flesher, pers. comm.).

2.2. Sampling Design

Eight field surveys were conducted every two months, from July 2009 to October 2010. On the northern sector of Mata Vila Cinco we defined the tree-fall gaps and forest sampling points, both in the mature forest sections. In the mature forest stretches and along the main footpath edge sample points were set. The mature forest vegetation patch presents continuous canopy ranging from 18 and 25 m. Most trees had their Diameter at breast height (DBH) above 25 cm, moderate frequency of vines, moderate to high density of bromeliads and other epiphytes, abundant palm trees and moderately dense herbaceous vegetation [40]. We initially found 25 tree-fall gaps, originated from natural tree-fall, with similar structure in relation to: 1) age group: gaps with no more than two months of formation i.e., the treetops still had the antlers with green leaves [14]; 2) origin: by uprooting [41]; 3) area: minimum area of 25m², estimation based on Runkle (1981); 4) adjacent canopy height: visual estimation [14], thus tree-fall gaps had similar height; and 5) size class: (150 m²) [41]. Among the 25 gaps, we selected the five most recent in the mature forest. The minimum distance between the five tree-fall gaps of 150 m.

Having selected the five tree-fall gaps, we located the edge and forest sampling points. We established five forest's points in the stretch of primary forest, adjacent to the tree-fall gaps sampling points. We seek for points with no evidence of natural disturbance and which could characterize them as tree-fall gaps. We finally set the edge sampling points on the secondary-growth mature forest and distributed along the forest main footpath margin. After the selection of the 15 sampling points (SPs): five tree-fall gaps, five forest areas, and five edges, we then selected a 50 m^2 parcel within each SP. Each parcel was them randomly sampled applying four $50 \times 50 \text{ cm}$ quadrats in order to collect all the environmental metrics. In these parcels, we measured environmental metrics (microclimate and microhabitat) and we sampled spiders simultaneously as described below.

2.3. Environmental Metrics (Microclimate and Microhabitat)

In order to characterize the tree-fall gaps, forest and edges environmental structure, we measured during the eight survey occasions, the environmental microhabitat and microclimate variables: 1) temperature and relative air moist (range); 2) soil temperature; 3) soil surface temperature; 4) leaf litter layer depth; 5) estimated leaf litter cover; 6) estimated herbaceous vegetation cover; 7) volume of rotten wood (logs and fallen trunks); and 8) light intensity.

1) Temperature (°C) and relative air moist (%) (range): metrics were taken at the center of the parcel, using a

digital thermo hygrometer. The equipment was set on the vegetation, at about 150 cm from the soil surface during all the leaf litter sampling period. We measured the temperature and moist (maximum and minimum), within o ne hour interval and from these measurements we then calculated thermal range; 2) and 3) Soil and soil surface temperature of soil and substrate (°C): these measurements were taken in 4 locations inside each parcel, at the center of the four quadrats (50×50 cm) where we collected the leaf-litter samples. To measure soil temperature we used a digital pen-type thermometer and for soil surface temperature, a digital infrared thermometer. The thermometer was then inserted in the soil; 4) Leaf-litter depth: These measurements were taken in cm, in the same fashion used for metrics two and three. In each quadrant $(50 \times 50 \text{ cm})$, a plastic ruler was inserted until it reached the soil and the metric sampled; 5) and 6) Leaf-litter and herbaceous vegetation coverage Estimates: Fournier's adapted technique was applied to measure the percentage index of leaf-litter and vegetation cover. Acategorical quantification method, where values are assigned to categories: 1—(covers 0% to 25%), 2—(26% to 50%), 3—(51% to 75%) and 4—(76% to 100%) [42]; 7) Decomposing fallen trunks and branches volume: Inside the 50 m² parcels we measured the all branches and trunks (>5 cm circumference) length and circumference rence. From the circumference value (m), we calculated the radius and using the formula $(\pi \times \text{radius}^2 \times \text{height})$. we then estimated the volume in m³. We finally, summed the values, obtaining the total volume (m) of fallen trunks and branches with in each parcel; 8) Light intensity: these measurements were taken with a digital lux meter positioned at the center of each quadrat and 1 meter above the soil surface.

2.4. Spider's Collection

In order to survey spiders, we sampled leaf-litter and extracted the associated fauna using a mini-Winkler trap. We collected four 50×50 cm leaf-litter samples of on each 50 m^2 parcels of and placed them in the sieve and strained it. The resultant material remained in the mini-Winkler for 24 h.

At each sampling survey occasion we took 60 leaf-litter samples, 20 in each sampling site (tree-fall gap, forest and edge), totalizing 480 leaf-litter samples over the eight surveys.

An additional night torching survey was applied [43]. A surveyor performed an active search in the 50 m² parcels for 60 minutes, 30 minutes searching spiders on the leaf-litter, fallen trunks and branches, and 30 minutes on vertical vegetation up to 180 cm. The spiders were captured with the use of forceps and fixed in alcohol 70%. We conducted eight 15 hours sampling occasions, summing 120 hours of active search. Each parcel was treated as statistically different sampling unit.

The spiders were identified and deposited in the arachnid collection at the Instituto Butantan, Sao Paulo, Brazil (IBSP, curator: Dr. Irene Knysak). A portion of the biological material was deposited in the UFBA Zoology Museum, Salvador, Bahia, Brazil (MZUFBA, curator: Dr. Adolfo R. Calor).

2.5. Statistical Analysis

The following analysis was performed:

- 1) Spiders species richness was estimated with EstimateS 8.2.0 [44]. The data was randomized 50 times. The spiders' richness (observed and estimated) were compared between the three formations (tree-fall gaps, forest and edge) using the one-way ANOVA test (Graph PadInstat 3.0).
- 2) We used the matrices to compare species composition among the three vegetation formations (tree-fall gaps, forest and edge). To do so, we have applied a Multiple Response Permutation Procedure (MRPP)-(PCORD® 6.0) [45], using the Sorensen (Bray-Curtis) *distance* measure. The values were standardized (n/sum (n)) by program default and the significance level was set at 0.05. Whereas we found a significant difference between the three vegetation types, we ran partial comparisons between sampling units. The MRPP is the most appropriated approach for community's studies since it not assumes multivariate normality and homogeneity of variances [46].
- 3) A tree-fall gap species composition matrix was created from the main sampling unit's formation matrix. This matrix was used to compare species composition among the tree fall gaps regeneration. In order to assess whether the spiders assemblage varied significantly over the tree-fall gaps regeneration, we compared four sub phases, between July 2009 and October 2010: *Sub phase* 1: July to September 2009, *Sub phase* 2: November 2009 to January 2010, *Sub phase* 3: March-May 2010 and *Sub phase* 4: August-October 2010. These sub phases are all included in the *gap phase* [12].

We applied the Blocked Multi-Response Permutation Procedures (MRBP)-(PCORD® PC-6.0) [45] applying

the Sorensen distance measure (Bray-Curtis). The MRBP (=MRPP in blocks), when design is in blocks, it is required a blocked analysis, such as MRBP, thus removing the effect of temporal dependence between samples [46]. The values were standardized (n/sum (n)) by the program default and the level of significance was set at 0.05. When significant differences were observed among the four sub phases, we ran partial comparisons.

4) To compare the habitat structure between the three formations (gaps, forest and edge) and along the regeneration of tree fall gaps we built microhabitat and microclimate variables matrices.

To make comparisons between the three formations, we extracted the mean of the data collected over the 16 field surveys and we applied the MRPP. In order to reach that we adopted the same procedures applied in item 3. To compare the four sub phases along their regeneration, we applied the MRBP (Blocked Multi-Response Permutation Procedures = MRPP in blocks). In order to obtain this we adopted the same procedures applied in item

3. Results

The five selected tree-fall gaps presented areas between 86 and 110 m² (sd = 11.09). The gaps were originated by uprooting, were recent and adjacent canopy height was estimated between 20 and 30m (sd = 4.18).

3.1. Habitat Structure

The habitat structure was significantly different between the three vegetation types tree-fall gaps, forest and edge (MRPP: p < 0.001; T = -32.642779, A = 0.15145932). When the habitat structure of the formations were pair wise compared, differences between them were also significant. Leaf-litter (depth and coverage) and relative air moist was higher in the forest. The herbaceous vegetation cover, the wood (logs and fallen branches) total volume, temperature (soil and substrate), thermal air and light range were higher in tree-fall gaps (**Table 1** and **Table 2**).

Table 1. Mean and standard deviation (sd) of litter depth, litter cover, herbaceous cover and total volume of wood (fallen logs and branches) on decomposition. Standard deviation (sd) of tree-fall gap, adjacent forest and edges of Mata da Vila Cinco-Ecological Reserve Michelin (Igrapiúna-Bahia). Data collected between May 2009 and October 2012.

Habitat Variables	Tree-fall gap	Forest	Edge
Depth of litter (cm)	2.7 (±0.58)	3.2 (±0.70)	2.4 (±0.71)
Leaf Litter cover*	3.5 (±0.64)	3.9 (±0.35)	3.4 (±0.67)
Herbaceous cover*	3.3 (±0.82)	2.2 (±0.79)	3.1 (±0.85)
Total volume of fallen logs and branches (m ³)	2.05 (±0.04)	1.40 (±0.03)	1.71 (±0.04)

^{*}Measured in the scale of fournier.

Table 2. Mean and standard deviation (sd) of soil temperature, substrate temperature, air temperature range, relative air humidity and luminosity of tree-fall gap, adjacent forests and edges in Mata da Vila Cinco, Ecological Reserve Michelin (Igrapiúna-Bahia). Data collected between May 2009 and October 2012.

Environmental variables	Tree-fall gap	Forest	Edge
Soil temperature (°C)	23.8 (±1.88)	23.6 (±1.51)	23.8 (±1.34)
Substrate temperature (°C)	25.9 (±3.73)	24.3 (±3.20)	24.7 (±2.21)
Air temperature range $(^{\circ}C)^{^*}$	3.8 (±1.28)	3.3 (±1.52)	3.1 (±1.49)
Relative air humidity (%)	73 (±10.78)	76 (±10.14)	74 (±10.20)
Luminosity	4406 (±11,634)	412 (±1444)	2571 (±9181)

3.2. Spider Assemblages

A total of 4732 spiders, including juveniles and adults, divided into 41 families were collected. The most abundant families were Ctenidae (963-20.4%), Araneidae (906-19.15%) and Salticidae (534-11.3%). Among the adult spiders, we recorded a total of 1179 individuals, comprising 126 species, belonging to 36 families. We registered 87 species in tree-fall gaps, 92 in forest and 90 on edges (**Table 3**). The richest families in species were: *Araneidae* (22 species-17.2%), *Theridiidae* (18 species-14.1%) and *Ctenidae* (12 species-9.4%) (**Figure 1**).

Regarding the estimated species richness, the estimated value of the 2nd-order Jackknife (Jack 2) was the highest, indicating a richness of 185 species, whereas the Bootstrap showed the lowest estimates, with 140 species. The remaining estimators Estimates were similar to each other and showed intermediate Jack 1 and Bootstrap values. The estimated species accumulation curve and observed species curves, did not reach an asymptote for any of the three formations (**Figure 2**). There was no significant difference among the three formations in observed (p = 0.7415, F = 0.2998), estimated richness Jackknife 2 (p = 0.6751, F = 0.3942) and Bootstrap (p = 0.8094, F = 0.2118).

The first four field surveys (July 2009 to January 2010) data, when tree fall gaps reached eight months, we found significant differences in spiders, species composition, between the three vegetation formations (MRPP, p = 0.00398857, A = 0.01368813, T = -3.0830481). However, when we compared the formations in pairs, no significant difference was found between tree-fall gaps and edges (**Table 4**). When data from the last four field surveys (March 2010 to October 2010), when the tree-fall gaps were between 10 to 16 months old, we found a significant difference in species composition of spiders among the three vegetation formations (p = 0.0456, A = 0.0090, T = -1.8376). However, when running pair wise comparisons among the formations, no significant difference was found between the tree-fall gaps and forest formations (p = 0.8520, A = -0.0052, T = -1.005).

We recorded 10 (7.8%) exclusive species in tree-fall gaps, 17 (13.3%) in forests and 14 (11.0%) on edges. However, in partial pair comparisons, these values were higher: tree-fall gaps vs. forest, presented respectively (19 unique species-14.9%; 26% - 20.3%); forest vs edge, respectively (27 unique species-21.0%; 24% - 18.8%) and tree-fall gaps vs. edge, respectively (20 unique species-15.6%; 23% - 18.0%) (Table 4).

3.3. Temporal Effect of Tree-Fall Gaps on Habitat Structure

The habitat structure showed significant difference among the four gap sub phases (MRBP, p= 0.0056, T = -3.2479, A = 0.1292). When sub phases were compared pair wise, significant differences were found only between sub phases (1 vs. 3) and (1 vs. 4) (**Table 5**).

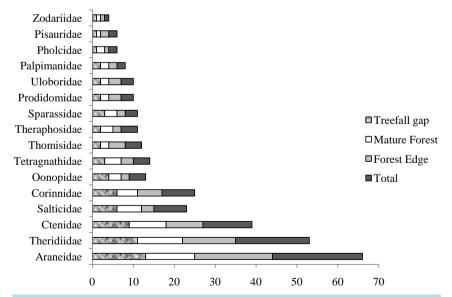


Figure 1. Species richness by family of spiders in Mata Vila Cinco-Ecological Reserve Michelin-REM (Igrapiúna-Bahia). We considered families representing at least 1% of total abundance. Data collected between May 2009 and October 2012.

Table 3. Abundance of spider species in Mata da Vila Cinco-Ecological Reserve Michelin (Igrapiúna-Bahia). Data collected from July 2009 to October 2010.

	Trefall gap	Mature forest	Forest edge	Total
ANYPHAENIDAE				
Hibana sp.1	1	2	0	3
Isigonia sp.1	2	2	1	5
ARANEIDAE				
Acacesia sp.1	0	0	1	1
Alpaidagr. negra	2	0	4	6
Alpaida delicata (Keyserling, 1892)	1	1	1	3
Alpaida sp.1	11	14	14	39
Alpaida sp.2	0	0	1	1
Araneus sp.1	3	2	2	7
Cyclosa fililineata Hingston, 1932	2	0	1	3
Cyclosa sp.1	0	3	2	5
Dubiepeira sp.1	1	0	0	1
Eustala sp.1	6	2	5	13
Gasteracantha sp.1	0	0	1	1
Hypognatha sp.1	0	0	3	3
Kaira sp.1	0	0	1	1
Mangora sp.1	2	9	1	12
Melychiopharis sp.1	2	0	0	2
Metazygia sp.1	3	3	2	8
Micrathena sp.1	19	22	13	54
Micrathena sp.2	3	3	3	9
Micrathena sp.3	0	0	1	1
Ocrepeira sp.1	0	1	0	1
Parawixia sp.1	6	1	1	8
Wagneriana sp.1	0	2	1	3
CAPONIIDAE				
Nops sp.1	1	1	1	3
CORINNIDAE				
Castianeira sp.1	4	1	4	9
Corinna sp.1	7	10	10	27
Corinnidae sp.1	7	2	4	13
Ianduba sp.1	1	0	1	2
Myrmecium sp.1	1	0	0	1
Orthobula sp.1	3	5	2	10

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Parachemmis sp.1	0	1	0	1
Stethorrhagus sp.1	0	0	2	2
CTENIDAE				
Ancylometes rufus (Walckenaer, 1837)	0	1	0	1
Celaetycheus sp.1	4	0	10	14
Ctenidae sp.1	1	2	2	5
Ctenus ornatus (Keyserling, 1877)	0	4	4	8
Ctenus rectipes F. O. P. Cambridge, 1897	14	8	14	36
Ctenus sp.1	4	5	6	15
Enoploctenus cyclothorax (Bertkau, 1880)	6	2	4	12
Enoploctenus maculipes Strand, 1909	1	0	0	1
Gephyroctenus sp.1	0	2	0	2
Isoctenus sp.1	4	10	9	23
Nothroctenus sp.1	5	3	6	14
Nothroctenus sp.2	1	0	3	4
CYRTAUCHENIIDAE				
Cyrtaucheniidae sp.1	1	14	4	19
DEINOPIDAE				
Deinopis sp.1	3	5	0	8
DIPLURIDAE				
Masteria sp.1	5	2	3	10
GNAPHOSIDAE				
Gnaphosidae sp.1	1	1	0	2
HERSILIIDAE				
Ypypuera sp.1	4	8	5	17
IDIOPIDAE				
Idiops sp.1	3	1	2	6
LINYPHIIDAE				
Meioneta sp.1	5	3	1	9
LYCOSIDAE				
Aglaoctenus sp.1	0	1	0	1
MIMETIDAE				
Ero sp.1	0	1	0	1
Gelanor sp.1	1	3	6	10
MITURGIDAE	-	-	~	
Eutichurus sp.1	0	0	1	1
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Miturgidae Gen. Novo	1	3	2	6
NEMESIIDAE				
Nemesiidae gen.1	1	3	0	4
OCHYROCERATIDAE				
Theotima sp.1	0	1	0	1
OECOBIIDAE				
Oecobius sp.1	0	1	0	1
OONOPIDAE				
aff. Oonops sp.1	1	3	1	5
Neoxyphinus sp.1	4	0	0	4
Oonops sp.1	3	2	0	5
Gr. Capitato	3	3	1	7
PALPIMANIDAE				
Fernandezina sp.1	12	21	29	62
Otiothops atlanticus Platnick, Grismado & Ramírez, 1999	18	12	22	52
PHOLCIDAE				
Carapoia sp.1	0	1	0	1
Mesabolivar sp.1	5	6	8	19
PISAURIDAE				
Architis sp.1	6	6	16	28
Thaumasia sp.1	0	0	1	1
PRODIDOMIDAE				
Lygromma sp.1	4	16	16	36
Lygromma sp.2	1	0	1	2
Lygromma sp.3	0	1	3	4
SALTICIDAE				
Breda sp.1	1	0	0	1
Corythalia sp.1	0	0	2	2
Cotinusasp.1	1	1	0	2
Lyssomanes sp.1	4	3	0	7
Noegus sp.1	2	6	0	8
Salticidae sp.1	4	7	4	15
Salticidae sp.2	2	7	3	12
Thiodina sp.1	0	2	0	2
SCYTODIDAE				
Scytodes sp.1	2	2	0	4

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SENOCULIDAE				
Senoculus sp.1	1	1	2	4
SPARASSIDAE				
Olios sp.1	16	19	8	43
Sparianthinae sp.1	4	7	0	11
Thomasettia sp.1	3	3	3	9
SYNOTAXIDAE				
Synotaxus sp.1	0	2	1	3
TETRAGNATHIDAE				
Aziliahistrio Simon, 1895	13	7	11	31
Chrysometa sp.1	0	1	0	1
Cyrtognatha sp.1	1	1	6	8
Leucauge sp.1	2	3	6	11
THERAPHOSIDAE				
Ischnocolinae sp.1	1	1	0	2
Magulla sp.1	0	3	0	3
Plesiopelma sp.1	0	0	4	4
Theraphosidae sp.1	1	4	2	7
THERIDIIDAE				
Achaearanea sp.1	1	0	0	1
Argyrodes elevatus Taczanowski, 1873	0	1	0	1
Argyrodes sp.1	0	1	1	2
Chrosiothes sp.1	0	0	1	1
Chrysso sp.1	7	4	3	14
Dipoena sp.1	3	11	5	19
Dipoena sp.2	1	0	1	2
Dipoena sp.3	0	1	2	3
Dipoena sp.4	3	0	3	6
Episinus gr. cognatus	10	10	13	33
Episinus sp.1	1	9	10	20
Episinus sp.2	0	0	2	2
Episinus sp.3	1	1	2	4
Euryopis sp.1	0	0	1	1
Nesticodes rufipes (Lucas, 1846)	10	1	0	11
Spintharus sp.1	0	6	3	9
Theridiidae sp.1	4	2	1	7
Theridion sp.1	4	0	2	6

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THERIDIOSOMATIDAE				
Chthonos sp.1	0	2	0	2
Naatlo sp.1	1	6	2	9
Plato sp.1	3	4	0	7
Theridiosomatidae Gen. Novo	2	0	2	4
THOMISIDAE				
aff. Tmarus sp.1	0	0	1	1
Aphantochilusrogersi O. PCambridge, 1870	0	0	1	1
Tmarus sp.1	2	5	15	22
Tmarus sp.2	0	1	1	2
TRECHALEIDAE				
Trechalea sp.1	4	2	2	8
ULOBORIDAE				
Uloborus sp.1	0	0	4	4
Miagrammopes sp.1	3	11	3	17
Zosis sp.1	7	1	3	11
ZODARIIDAE				
Tenedos sp.1	3	38	3	44
Species richness	87	92	90	126

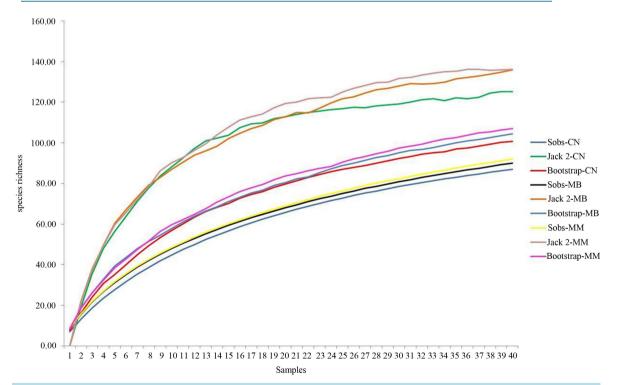


Figure 2. Estimates of species richness of spiders in the three formations: Tree-fall gap (TG), edge (FE) and forest (MF); in Mata Vila Cinco-Ecological Reserve Michelin-REM (Igrapiúna-Bahia). S_{obs}: Species observed. Estimated richness: Jack2 = 2nd order Jackknife.

Table 4. Peer-to-peer comparisons spider species composition between vegetation formations: Tree-fall gap, forest and edges, considering the first four field campaigns in Mata da Vila Cinco-Ecological Reserve Michelin (Igrapiúna-Bahia). MRPP test (multi-response permutation procedure). T = variation between groups, A = variation within groups and p = statistical significance. US = number of exclusive species in the peer-to-peer comparisons. The bold letters are statistically significant values.

	T	A	p	US
Tree-fall gap vs. Edge	-1.671	0.0079	0.0608	20 and 23
Tree-fall gap vs. Forest	-1.830	0.0827	0.0470	19 and 26
Edge vs. Forest	-3.053	0.0152	0.0059	24 and 27

Table 5. Peer-to-peer comparisons of habitat structure among the four sub phases of a tree-fall gap in Mata of Vila Cinco-Ecological Reserve Michelin (Igrapiúna-Bahia). MRBP (*Blocked* Multi-Response Permutation Procedures): T = variation between groups; A = variation within groups and p = statistical significance. The bold letters are statistically significant values.

Sub phases	Estimated age (in months)*	T	A	p
1 vs. 2	4 vs. 8	-1.247	0.0692	0.1107
1 vs. 3	4 vs. 12	-1.986	0.1167	0.0477
1 vs. 4	4 vs. 16	-2.313	0.1732	0.0339
2 vs. 3	8 vs. 12	-0.249	0.0064	0.3910
2 vs. 4	8 vs. 16	-0.989	0.0630	0.1420
3 vs. 4	12 vs. 16	-1.358	0.1280	0.0973

^{*}Maximum estimated age.

3.4. Temporal Effect of Tree-Fall Gaps on Spider Assemblages

The spider species' composition differ significantly among the four sub phases (MRBP, p = 0.0047, T = -3.007, A = 0.2994). When we compared the sub phases pair wise, we found significant differences only between the sub phase four and the other sub phases (Table 6).

4. Discussion

4.1. Habitat Structure

The tree-fall gaps formations in fact promoted significant changes in environmental structure in relation to the adjacent forest, specifically in relation to microclimatic and microhabitat variables. Such differences have been reported in several studies in tropical forests [1] [15] [24]-[26] [47] [48]. We also found that throughout the regeneration within tree-fall gaps, major changes in habitat structure occurred, as reported on other studies [49] [50]. Moreover, the gradual closure of canopy promotes microclimate changes in areas originally open [19] [50]. Thus, our results confirm the role of natural disturbances in increasing habitat heterogeneity in time-spatial scales [2]-[4].

4.2. Spiders' Assemblage

The tree-fall gaps formation triggered significant changes in the spiders' assemblage in relation to the adjacent forest. This differentiation was observed in habitat structure and thus corroborated the association of spider assemblage's with microclimate and microhabitat variables, as reported by other studies. The habitat structure influence the spider's species' assemblages' composition and/or richness [26] [34] [36] [37]. The remarkable changes printed by canopy openings on luminosity, moist and temperature in the interior of tree-fall gaps affect spiders' population distribution and density, since they are closely associated with these environmental factors [26] [31] [32]. Changes in vegetation density also promote alterations in spiders' richness and diversity [51] [52].

Table 6. Peer-to-peer comparisons of spider species composition among the four sub phases in tree-fall gaps in Mata da Vila Cinco-Ecological Reserve Michelin (Igrapiúna-Bahia). MRBP test (Multiple-response Blocked Procedure): T = variation between groups, A = variation within groups and p = statistical significance. In bold letters, statistically significant values.

Sub-phases	Estimated age (in months)*	T	A	p
1 vs. 2	4 vs. 8	-0.9087	0.0088	0.1765
1 vs. 3	4 vs. 12	0.0363	-0.0004	0.5229
1 vs. 4	4 vs. 16	-2.4134	0.0454	0.0200
2 vs. 3	8 vs. 12	-0.0153	0.0001	0.4832
2 vs. 4	8 vs. 16	-1.9200	0.0199	0.0357
3 vs. 4	12 vs. 16	-2.7010	0.05411	0.0157

^{*}Maximum estimated age.

Higher habitat heterogeneity allows orb-weaver spiders' occurrence, since this habitat quality increases the shelter offer for species settlement [53]. The orb-weavers Araneidae, Linyphiidae and Tetragnathidae families also showed strong dependence on relative air humidity [54]. These three families represent over 20% of the collected spiders, where Araneidae family was the richest. They also showed similar abundance in the three formations; however the highest number of exclusive species occurred in the forest. Indeed, richness in the forest was four times higher than in tree fall gaps and eight times higher than on edges. Dominance of forest exclusive orb-weaver spiders can be related to more stable microclimatic conditions found under more closed canopy.

Certainly, light in tree-fall gaps is the main variable that controls microclimate and other variables that make tree-fall gaps different from adjacent forest [10]. Another study compared tree-fall gaps in the Brazilian Northeast and adjacent forest showed that orb-weaver spiders exhibited preference for forest formations [26]. The high abundance of the Ctenidae spiders' family can be partially explained, because the size and intensity of bright in their eyes make them more conspicuous when sampling [55], which may have biased the effort. These spiders do not spin webs and many species of *Ctenus* actively forage on leaf-litter and vegetation [56], and also use the vegetation to molt [personal observation]. These spiders' higher abundance in the forest formation is associated with lower fallen trunks frequency [55], and higher moist [57]. Differences in leaf-litter structure and herbaceous cover between the three formations can also explain differences found in spider assemblages, since vegetation richness positively influence orb-weavers spiders' abundance [58] and plant density affects richness and diversity [51] [52]. Finally, habitat heterogeneity can increase spider's richness and thus favoring the occurrence of orb-weaver species [53].

The leaf-litter complexity affects the spider assemblages [37] [59]; a study conducted in a deciduous forest revealed that spiders are stratified distributed on leaf-litter [60]. Thus, a thicker leaf-litter on forest formations offers spiders' greater refuge and prey availability [35] [59]; favoring vertical distribution [60], and thus reducing competition. Furthermore, thicker leaf-litter reduces thermal amplitude and increases moist [61], creating microclimatic conditions with positive effect on spider's assemblages [31].

In contrast, higher luminosity in tree-fall gaps and edges promotes greater herbaceous vegetation cover, also contributing to increase of herbivores [62], important spiders' prey that forage on the foliage (Churchill, 1997). Besides, high coverage of herbaceous vegetation and fallen trunks in tree-fall gaps and edges boosts suitable supports for fixing the webs [63]. Therefore, tree-fall gaps, forest and edges have different habitat structure, marked by singularities on microclimate and microhabitat variables which in turn can have positive or negative associations with spiders, and therefore harbor distinct assemblages.

5. Conclusion

In conclusion, tree-fall gaps, even the small ones, have a crucial role in the dynamics of spider's assemblages in the Atlantic forest. The spatial effect is pronounced but the temporal effect, although detected by in the spiders' assembly, should be evaluated in the long-term (>4 years).

Acknowledgments

The authors are grateful to the Ecological Reserve Michelin for their excellent support, by providing us with necessary infrastructure and logistics during field campaigns. To Lacerta Ambiental by lending field equipment. M. C. L. P. is supported by Programa de Regime de Tempo Contínuo (RTC) of Universidade Católica do Salvador. J.H.C.D. is a CNPq fellow.

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