Terrestrial arthropods from tree canopies in the Pantanal of Mato Grosso, Brazil

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ABSTRACT. Terrestrial arthropods from tree canopies in the Pantanal of Mato Grosso, Brazil. This study represents a contribution to the knowledge of the diversity of arthropods associated to the canopy of *Vochysia divergens* Pohl (Vochysiaceae). Three trees individuals were sampled during two seasonal periods in this region: a) by spraying one tree canopy during high water (February); b) by fogging two tree canopies during low water (September/October). The 15,744 arthropods (183.2±38.9 individuals/m^2) obtained from all three trees (86 m^2) represented 20 taxonomic orders, 87.1% were Insecta, and 12.9% Arachnida. The dominant groups were Hymenoptera (48.5%; 88.9 individuals/m^2), mostly Formicidae (44.5%; 81.4 individuals/m^2), followed by Coleoptera (14.0%; 25.5 individuals/m^2) and Araneae (10.2%; 19.5 individuals/m^2), together representing 62.5% of the total catch. Fourteen (70%) of all orders occurred on three trees. Dermaptera, Isoptera, Neuroptera, Odonata, Plecoptera and Trichoptera were collected from only one tree. Of the total, 2,197 adult Coleoptera collected (25.5±11.3 individuals/m^2), 99% were assigned to 32 families and 256 morphospecies. Nitidulidae (17.9% of the total catch; 4.6 individuals/m^2), Anobiidae (16.7%; 4.3 individuals/m^2), Curculionidae (13.2%; 3.4 individuals/m^2) and Meloidae (11.4%; 2.9 individuals/m^2) dominated. The communitiy of adult Coleoptera on *V. divergens* indicated a dominance of herbivores (37.8% of the total catch, 127 spp.) and predators (35.2%, 82 spp.), followed by saprophages (16.2%, 32 spp.) and fungivores (10.8%, 15 spp.). The influence of the flood pulse on the community of arboreal arthropods in *V. divergens* is indicated by the seasonal variation in evaluated groups, causing changes in their structure and composition.

KEYWORDS. Arthropods; canopy; diversity; Pantanal.

RESUMO. Artrópodes terrestres associados a copas de árvores no Pantanal de Mato Grosso, Brasil. Este estudo representa uma contribuição ao conhecimento da diversidade de artrópodes associados à copa de *Vochysia divergens* Pohl (Vochysiaceae). Três indivíduos foram amostrados durante dois períodos sazonais, um durante a cheia (árvore A: fevereiro) utilizando-se o método de pulverização com inseticida e dois durante a seca (árvore B: setembro, C: outubro), empregando-se a termonebulização. Um total de 15744 artrópodes (183,2±38,9 individuos/m^2) foram obtidos em 86m^2 de área representando 20 ordens taxonômicas, 87,1% Insecta e 12,9% Arachnida. O grupo dominante foi Hymenoptera (48,5%; 88,9 individuos/m^2), a maioria Formicidae (44,5%; 81,4 individuos/m^2), seguido por Coleoptera (14,0%; 25,5 individuos/m^2) e Araneae (10,2%; 19,5 individuos/m^2), que representaram 62,5% do total coletado. Com relação a freqüência, 14 de todas as ordens (70%) ocorreram nas tres árvores. Dermaptera, Isoptera, Neuroptera, Odonata, Plecoptera e Trichoptera foram coletadas em uma única árvore. Foram obtidos 2197 Coleoptera adultos (25,5±11,3 indivíduos/m^2), sendo 99% assinalados para 32 famílias e 256 morfoespécies. Nitidulidae (17,9%; 4,6 indivíduos/m^2), Anobiidae (16,7%; 4,3 indivíduos/m^2), Curculionidae (13,2%; 3,4 indivíduos/m^2) e Meloidae (11,4%; 2,9 indivíduos/m^2) foram dominantes. Os Coleoptera adultos associados à copa de *V. divergens* indicam dominancia de herbívoros (37,8% do total coletado, 127 spp.) e predadores (35,2%, 82 spp.), seguidos por saprófagos (16,2%, 32 spp.) e fungívoros (10,8%, 15 spp.). A influência do pulso de inundação sobre a comunidade de artrópodes arbóreos associados à *V. divergens* é indicada pela variação sazonal nos grupos avaliados, gerando mudanças em sua estrutura e composição ao longo dos períodos sazonais.

PALAVRAS-CHAVE. Artrópodes; copa; diversidade; Pantanal.

Terrestrial arthropods are important organisms with fundamental functions in natural ecosystems such as predation, pollination, and even with complex relations between species of vertebrates and invertebrates that evolved simultaneously (Jolivet 1992; Samways 1994). Despite this recognized importance, data on the biology and ecology of many groups are few, principally of those that inhabit environments of difficult access like canopies (Basset 2001).

Various techniques have been developed to reach the canopy and the use of insecticides is one of the most utilized, irrespective of specimens that are not collected like those hidden in crevices, under bark, and involuted or mining in leaves (Basset *et al.* 1997; Erwin 1989; Stork & Hammond 1997). Studies in forests demonstrated the efficiency of this methodology to describe the characteristics of arboreal communities like patterns in species abundance, body size, biomass, guild structure, dominance, eveness, richness, endemism, mode of nutrition, and seasonality (Basset *et al.* 2003; Linsenmair *et al.* 2001; Stork *et al.* 1997).

In Brazil, these studies concentrated in the Amazonian region, investigating forests on terra firme and of floodplains (Adis 1997; Adis *et al.* 1984, 1998b; Erwin 1983a, b; Harada &

Adis 1997, 1998; Hurtado-Guerrero *et al.* 2003). In the Pantanal of Mato Grosso, some aspects such as the guild structure of insects, patterns of herbivory and diversity on *Tabebuia aurea* and *T. ochraceae* (Bignoniaceae) have been approached by Ribeiro & Brown (1999).

The dynamic of perodical inundations defines the community structure of terrestrial arthropods that colonize floodplains (Adis & Junk 2002). The composition of this community both in the soil and in tree canopies of the Pantanal is virtually unknown. To evaluate the impact of the flood pulse (Junk *et al.* 1989, Da Silva *et al.* 2001) on terrestrial arthropods, preliminary studies over the past five years have focussed on both the terrestrial and the aquatic phase (Adis *et al.* 2001; Marques *et al.* 2001; Santos *et al.* 2003). The results presented in this contribution on arthropod orders, on families and morphospecies of Coleoptera from the canopy of a typical forest type in this region and comparison with results from other inventories in the same area provide data and observations on which hypotheses can be made for more detailed ecological studies in the future.

MATERIAL AND METHODS

Study area. The study was undertaken in 2000 in an area dominated by *Vochysia divergens* Pohl (Vochysiaceae), a typical tree species of the Pantanal of Mato Grosso, known as "cambará" that forms monodominant forest stands called "cambarazais" (Nascimento & Nunes da Cunha 1989). The study area is located at the Retiro Novo farm, in the district of Pirizal, municipality of Nossa Senhora do Livramento, situated on the right bank of Cuiabá river and the left bank of Bento Gomes river (16°15'12"S, 56°22'12"W). The study area is subjected to a rainy season from October to April and to annual flooding of 0.6-1.5m height, generally between December and March.

Methods. Three individuals of *V. divergens* (Table I) with few or no epiphytes, nor flowers and fruits were sampled according to the criteria given in Adis *et al.* (1998a) during two seasonal periods in the Pantanal of Mato Grosso: a) by spraying one tree canopy (A) during high water (February: aquatic phase, forest inundated); b) by fogging two tree canopies (B, C) during low water (September/October: terrestrial phase, forest not inundated).

To collect the arthropods, 22-33 funnel-shaped trays ($1m^2$ in area) made of nylon were installed under the canopy with numbers (Table I) depending on the circumference of the tree crown. All collecting trays were individually numbered and mapped to indicate their position in the four quadrants (I-IV) assigned that related to the canopy range. Data from the two tree canopies fogged during low water were used to analyse the distribution pattern of arthropods (Figs. 1, 2).

The insecticide used, Lambdacialotrine 0.5%, is a non-residual synthetic pyrethrum that was diluted in diesel oil to 1% and applied from the ground to all parts of the canopy with an agricultural sprayer (Bomba Hatsuda Costal, type Pulverisador UBL, FP-4, JD22-2.T) (tree A) or a thermonebulizer Swing Fog SN50 (trees B, C).

Table I. Characteristics of *V. divergens* trees fogged in the inundation forest at Fazenda Retiro Novo.

	Tree A 21/II/2000 - high water	Tree B 29/IX/2000 - low water	Tree C 01/X/2000 - low water
Crown diameter	11m	35m	33m
Tree height	15m	12m	16m
Trunk diameter (dbh)	0.48m	0.80m	0.68m
Nº of collecting trays	22	31	33

The insecticide was applied to each tree canopy around 6:00 a.m. Arthropods intercepted on the collecting trays were collected twice. The first collection occurred two hours after fogging, a drop time recommended for falling arthropods (Adis *et al.* 1998a; Erwin 1983a; Stork & Hammond 1997). Thereafter each tree was thoroughly shaken by means of ropes attached to its limbs, so that remaining arthropods in the tree canopy would fall onto the collecting trays. The second collection occurred two hours later.

The arthropod material was transported to and deposited at the Entomological Laboratory of the Institute of Biosciences at the Federal University of Mato Grosso in Cuiabá, sorted and identified to the level of orders. Adult Coleoptera were identified to family level (Lawrence *et al.* 1999), assigned to trophic guilds (Erwin 1983b; Hammond *et al.* 1996) and their respective morphospecies (recognizable taxonomic units) determined.

Diversity indices of Shannon-Wiener (H'), eveness, richness of species of Margalef (R), using the natural logarithm (ln) as suggested by Magurran (1988), were used to evaluate species diversity of the Coleoptera community from three trees of *V. divergens* during two seasonal periods.

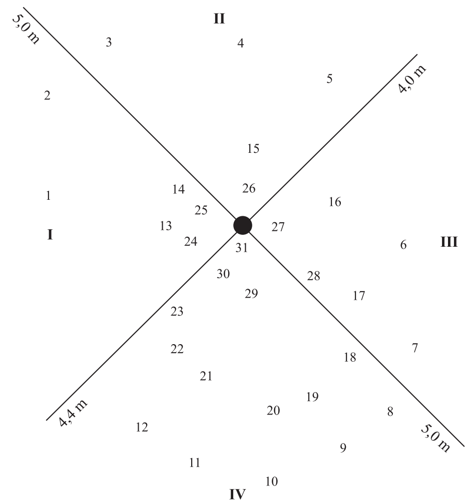

Fig. 1. Arrangement of collecting trays under the canopy of *V. divergens* during low water (tree B). I-IV = quadrants relating to canopy range.

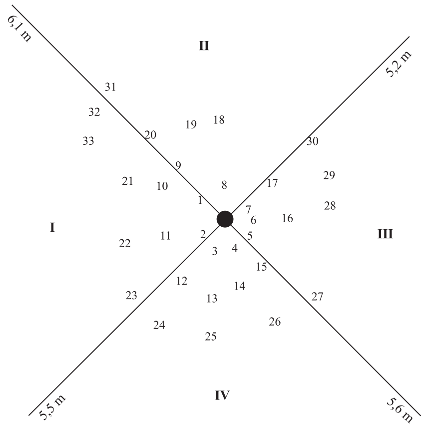

Fig. 2. Arrangement of collecting trays under the canopy of *V. divergens* during low water (tree C). I-IV = quadrants relating to canopy range.

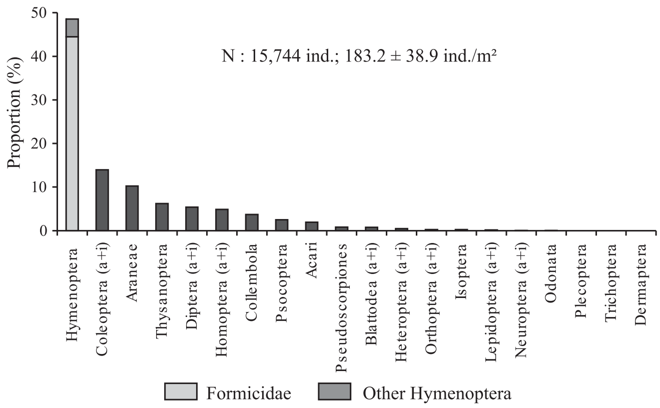

Fig. 3. Proportion (%) of arthropods obtained from the canopy of three trees of *V. divergens* in decreasing rank of dominance; a+i = adult+immatures, N = total number of arthropods collected.

RESULTS AND DISCUSSION

Composition and dominance of groups. The 15,744 arthropods (183.2±38.9 individuals./m^2) obtained from three trees (86 m^2) represented 20 taxonomic orders, 87.1% were Insecta, and 12.9% Arachnida.

The dominant groups (Fig. 3, Table II) were Hymenoptera (48.5%; 88.9 individuals/m^2), mostly Formicidae (44.5%; 81.4 individuals/m^2), followed by Coleoptera (14.0%; 25.5 individuals/m^2) and Araneae (10.2%; 19.5 individuals/m^2), together representing 62.5% of the total catch. Fourteen (70%) of all orders occurred on three trees. Dermaptera, Isoptera, Neuroptera, Odonata, Plecoptera and Trichoptera were collected from tree C only, during low water.

Santos *et al.* (2003) sprayed six canopies of the palm *Attalea phalerata* Mart. (Arecaceae; height 4-7 m) in this study area during low water (November/December 1999), using the same sampling method. The 17,188 arthropods (238.7±80.6 individuals/m^2) obtained represented 22 taxonomic orders, 90.8% were Insecta, 9.1% Arachnida, and 0.1% Chilopoda. Coleoptera (27.4%; 65.5 individuals/m^2), Hymenoptera (21.4%; 51.1 individuals/m^2), mostly Formicidae (19.0%; 45.3 individuals/m^2) and Collembola (13.6%; 32.4 individuals/m^2) dominated (Fig. 4), together representing 62.4% of the total catch. Seventeen of all orders (77%) occurred on all trees, except Dermaptera, Neuroptera, Mantodea, Odonata, Opiliones, and Chilopoda. The higher arthropod abundance obtained in comparison to *V. divergens* was due to a greater number of Coleoptera, Collembola, and Diptera (50.0% of the total catch) (Figs. 3, 4). Groups with low abundance and frequency on *V. divergens* and *A. phalerata* are considered occasional visitors.

Arthropod abundances in inundation forests of Central Amazonia were lower in both the blackwater region (igapó: 61.6 individuals/m^2) and the whitewater region (várzea: 32,1 individuals/m^2) (Adis *et al.* 1984). Ants were the dominant group (43.4 and 52.2%, respectively) on three trees (2 species) fogged in each forest type. However, in a second study with four trees (4 species) fogged in the whitewater region (Adis 1997), abundances varied between 134 and 534 individuals/m^2. Adult Coleoptera (21%), Formicidae (20%) and adult Diptera (13%) represented more than half of all arthropods obtained (23,689 individuals). The predominant taxa varied with the tree species sampled, being either Coleoptera (40.5%), Formicidae (38.4%), Homoptera (29.5%) or Psocoptera (26.0%). This demonstrates the necessity of broader studies like that on terra firme in Central Amazonia (Hurtado-Guerrero *et al.* 2003). Here Formicidae represented 51.7% (143-877 individuals/m^2)

Table II. Total capture (Individuals), proportion (%) and abundance (Individuals/m^2) with standard deviation (S.D.) of arthropod taxa obtained from the canopy of three trees of *V. divergens*; [ ] = immatures.

Táxon	Total (individuals)	Proportion (%)	Individuals/m^2±S.D.
Acari	304	1.9	3.5±5.5
Araneae	1608	10.2	19.5±16.2
Blattodea	122 [77]	0.8 [0,5]	1.4±0.5
Coleoptera	2197 [20]	14.0 [0,1]	25.5±11.3
Collembola	582	3.7	6.8±6.1
Dermaptera	1	<0.1	<0.1±0.1
Diptera	847 [17]	5.4 [0.1]	9.8±3.7
Heteroptera	70 [26]	0.4 [0.2]	8.8±0.5
Homoptera	764 [192]	4.9 [1.2]	8.9±5.6
Hymenoptera	7642	48.5	88.9±42.8
- Formicidae	(7002)	(44.5)	(81.4±45.6)
- Others	(640)	(4.0)	(7.4±3.0)
Isoptera	34	0.2	0.4±0.6
Lepidoptera	27 [14]	0.2 [0.1]	0.3±0.2
Neuroptera	3 [2]	<0.1 [<0.1]	<0.1±0.1
Odonata	2	<0.1	<0.1±0.1
Orthoptera	41 [9]	0.3 [0.1]	0.5±0.4
Plecoptera	1	<0.1	<0.1±0.1
Pseudoscorpiones	129	0.8	1.5±1.1
Psocoptera	392	2.5	4.6±5.9
Thysanoptera	977	6.2	11.4± 9.2
Trichoptera	1	<0.1	<0.1±0.1
Total	15,744	100.0	183.2±38.9

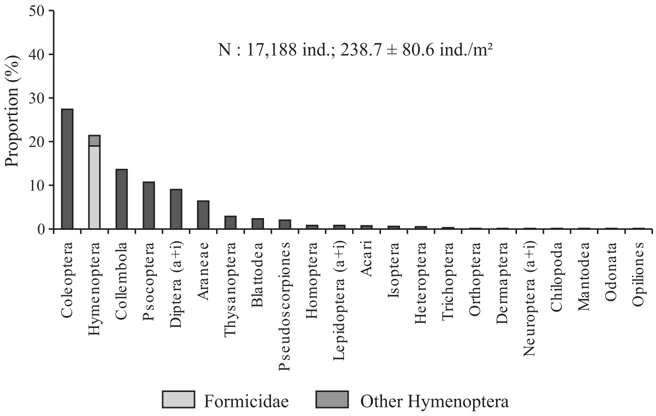

Fig. 4. Proportion (%) of arthropods obtained from the canopy of six trees of *A. phalerata* in decreasing rank of dominance; a+i = adults+immatures, N = total number of arthropods collected.

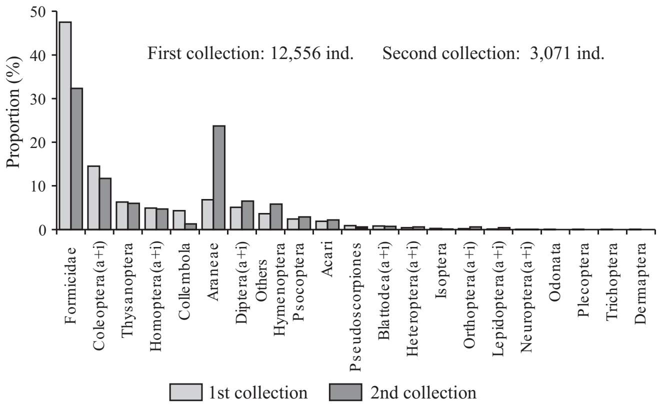

Fig. 5. Proportion (%) of arthropods obtained per collecting event from three trees of *V. divergens*; a+i = adults+immatures.

of all arthropods obtained by fumigating the canopy of 40 trees (787 m^2) of nine tree species. Other dominant groups were Diptera (12.7%), Psocoptera (5.9%), and Collembola (4.2%).

In the canopy of tropical forests, Formicidae generally represent the dominant taxa both in abundance and biomass (e.g., Adis *et al*. 1984; Basset 1991; Erwin 1983b; Floren & Linsenmair 1997, 1998b; Harada & Adis 1997, 1998; Stork 1988, 1991; Stork & Brendell 1990, 1993; Tobin 1991; Wilson 1987). Its dominance with respect to biomass is partly explained by a greater body compared to terricolous ants (Tobin 1995). Soil inhabiting species are primarily predators and decomposers, whereas canopy species show a broad nutritional range using e.g., floral and extrafloral nectar, saps of plants and fruits, and exudates of arthropods and seeds (Davidson 1997; Tobin 1995).

Knockdown rates. Of the total arthropods sampled from *V. divergens,* 80.3% (146.4 individuals/m^2) were obtained in the first two hours and the remaining 19.7% (36.8 individuals/m^2) after the trees had been shaken. Formicidae were the dominant group in both samples (47.5 and 32.3%, respectively). To the contrary of the first sample event, Araneae (23.7%) was more abundant in the second sample than Coleoptera (11.7%) (Fig. 5). During high water, 57.5% of the total spiders was obtained in the second sample. They supposedly hang on their spinning thread after dying and only fall with the tree being shaken.

On *A. phalerata,* 58.9% of the total arthropods were sampled in the first two hours, 37.6% after palms had been shaken, and only 3.5% after leaves were cut and rinsed with water (Santos *et al*. 2003). The discrepancy with *V. divergens* is attributed to the different leaf structure in palms and a trunk that accumulates organic matter.

When fogging 39 trees of *Calophyllum brasiliense* (Guttiferae) on terra firme in Central Amazonia, about 75% of all arthropods were obtained in the first two hours and the rest after trees had been shaken (Adis *et al*. 1997).

Capturing rates of trays. The distribution of collecting trays under each tree varied in dependence on the architecture of the tree crown and by avoiding crown gaps (Adis *et al.* 1998a).

For tree B (Fig. 1), the coefficient of variation (Zar 1974) for the number of individuals in each collecting tray was 76%, with 60% of the fauna being represented by Formicidae, followed by Coleoptera, Thysanoptera, Araneae, Diptera and Collembola. The spacial distribution for the most representative groups in the canopy was evaluated by means of the four quadrants, revealing a higher abundance in trays close to the trunk and particularly in quadrant IV (Fig. 6). This distribution might possibly be related to a greater concentration of branches in this quadrant, permitting a greater area for migration and foraging, besides the greater availability of food, indicating in that way a heterogeneity in the canopy architecture. The great variation can also be explained by the aggregation pattern of some taxa, principally of ants. In adult Coleoptera, the Cocinellidae represented an aggregated pattern of distribution in one single tray (morphospecies 09 in funnel 1 of tree C) which might be related to the oviposition behaviour of these specimens.

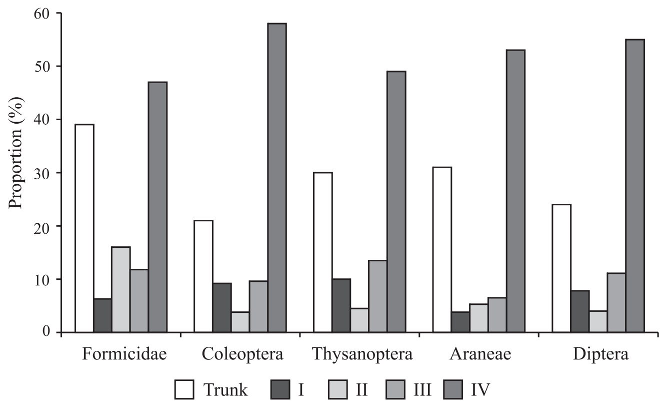

Fig. 6. Proportion (%) of five arthropod groups obtained from *V. divergens* during low water (tree B) in collecting trays close to the tree trunk and in the four quadrants assigned.

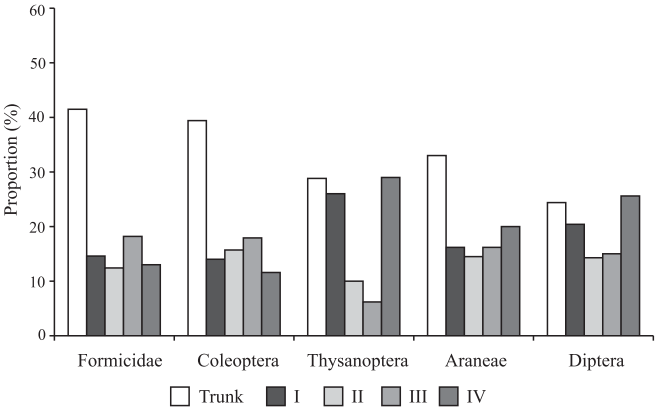

Fig. 7. Proportion (%) of five arthropod groups obtained from *V. divergens* during high water (tree C) in collecting trays close to the tree trunk and in the four quadrants assigned.

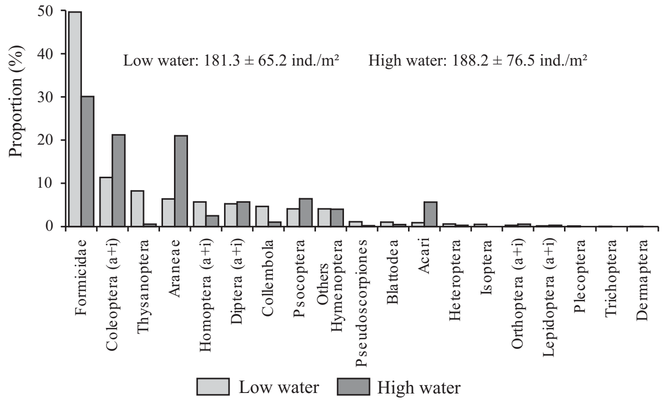

Fig. 8. Proportion (%) of arthropods obtained from the canopy of *V. divergens* during low water (trees B, C) and high water (tree A); a+i = adults+immatures.

For tree C (Fig. 2), the coefficient of variation for the number of individuals in each collecting tray was 55%, with 40% of the fauna being represented by Formicidae, Coleoptera, Collembola, Diptera, Araneae and Thysanoptera. The majority of these groups occurred in trays close to the trunk, a pattern found in tree B. However, distribution of groups between the four quadrants was more uniform (Fig. 7), indicating a more homogeneous canopy architecture.

Seasonality. Arthropod abundance of 181.3±65.2 individuals/m² (11,604 individuals from 64 m²) during low water was comparable to that during high water. Formicidae (49.6% of the total catch; 91.3 individuals/m²), Coleoptera (11.4%; 20.6 individuals/m²), Thysanoptera (8.2%; 15.1 individuals/m²) and Araneae (6.4%; 11.5 individuals/m²) dominated (Fig. 8).

During high water, 188.2±76.5 individuals/m² (4,141 individuals from 22 m²) were obtained, with Formicidae (30.1% of the total catch; 56.6 individuals/m²), Coleoptera (21.2%; 39.9 individuals/m²), Araneae (21.0%; 39.5 individuals/m²) and Psocoptera (6.4%; 12.1 individuals/m²) being dominant (Fig. 8).

When spraying one tree of *V. divergens* (height 12 m) in the study area during receding waters (June 1999: forest without inundation), Formicidae (44.0% of the total catch; 19.2 ind/.m²) predominated as well, followed by Coleoptera (14.1%; 6.2 individuals/m²), Araneae (14.0%; 6.1% individuals/m²) and Diptera (7.4%; 3.2 individuals/m²) (Marques *et al*. 2001).

Formicidae and Coleoptera, apart from being frequent, dominated independent of season, indicating that the canopy represents an important habitat. Some groups like Coleoptera, Acari, Araneae and Psocoptera showed greater abundances during high water, while Thysanoptera, Homoptera and Collembola during low water, thus indicating seasonality (Fig. 8). Basset (2001) considered Thysanoptera seasonal as they frequently occur on flowers of tropical trees, representing potential pollinators. Flowering of *V. divergens* occurs during low water and when 97.6% of the total Thysanoptera have been collected.

More than 85% of immature Blattodea, Homoptera and Heteroptera (307 individuals) were obtained during high water, indicating that the canopy is used by some groups for reproduction.

In Central Amazonian inundation forests, many terricolous species pass the aquatic phase on trees (Adis 1997). In the Pantanal this survival strategy was observed for *Acromyrmex lundi carli* (Myrmicinae). The ant species temporarily abandons its subterraneous nest and constructs a new one on limbs of *Licania parvifolia* (Chrysobalanaceae), above the water level (Adis *et al*. 2001). Araneae was the third most abundant group obtained with canopy fogging during high water which is possibly related to a migration from the soil to trees, too.

Adult Coleoptera: Families and morphospecies. Of the total 2,197 adult Coleoptera collected (25.5±11.3 individuals/m²), 99% were assigned to 32 families and 256 morphospecies. Nitidulidae (17.9% of the total catch; 4.6 individuals/m²), Anobiidae (16.7%; 4.3 individuals/m²), Curculionidae (13.2%;

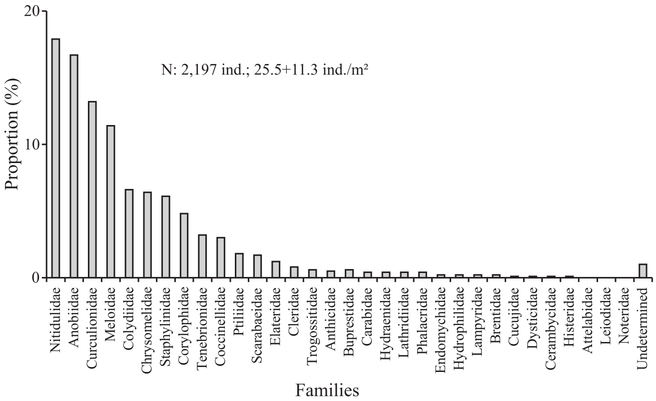

Fig. 9. Proportion (%) of families of adult Coleoptera obtained from the canopy of three trees of *V. divergens* in decreasing rank of dominance; a+i = adults+immatures, N = total number of arthropods collected.

3.4 individuals/m^2) and Meloidae (11.4%; 2.9 individuals/m^2) dominated (Fig. 9, Tables III, IV and VII). Eighteen families occurred on three trees, ten on two trees, and four on one tree (Table III). Curculionidae (56 spp.), Chrysomelidae (34 spp.) and Staphylinidae (31 spp.) had the highest number of morphospecies (Table VII). Twenty-two morphospecies had 100% frequency, 65 occurred on two trees (66.6%), and 169 on only one tree (33.3%).

During receding waters, Marques *et al.* (2001) obtained 26 families of adult Coleoptera from one tree of *V. divergens*. Curculionidae (21.6% of the total catch), Scolytidae (19.3%), Elateridae (17.4%) and Dryopidae (13.2%) were dominant.

Of the total 4,715 adult Coleoptera (65.5±21.7 individuals/m^2) collected from *A. phalerata,* 99% were assigned to 44 families and 326 morphospecies. Tenebrionidae (24.4% of the total catch; 16.0 individuals/m^2), Curculionidae (22%; 14,7 individuals/m^2) and Carabidae (10.8%; 7.1 individuals/m^2) dominated. The highest number of morphospecies was in Curculionidae (54 spp), Chrysomelidae (55 spp.) and Staphylinidae (44 spp.) (Santos *et al.* 2003) (Fig. 10, Tables III and IV).

Studies on arboreal Coleoptera communities in different regions of the tropics showed no predominance of the same families. Lathridiidae, Chrysomelidae, Staphylinidae, Apionidae and Curculionidae dominated in Uganda (Wagner 2000), whereas Chrysomelidae, Curculionidae and Staphylinidae on Borneo (Floren & Linsenmair 1998b). Chrysomelidae and Curculionidae were more abundant in Amazonia of Peru (Farrell & Erwin 1988), Bruchidae and Curculionidae in Venezuela (Davies *et al.* 1997). However, Chrysomelidae, Curculionidae and Staphylinidae represented the highest richness of species (Allison *et al.* 1993, 1997; Davies *et al.* 1997; Erwin 1983b; Erwin & Scott 1980; Farrell& Erwin 1988; Hammond *et al.* 1996, 1997; Wagner 2000), being valid for the Pantanal as well.

The number of individuals in Coleoptera inhabiting one tree of *V. divergens* (732.3±125.0) was comparable to that of A. *phalerata* (785.8±260.1). However, population density on *A. phalerata* was two times greater (65.5±21.7 vs. 25.5±11.3),

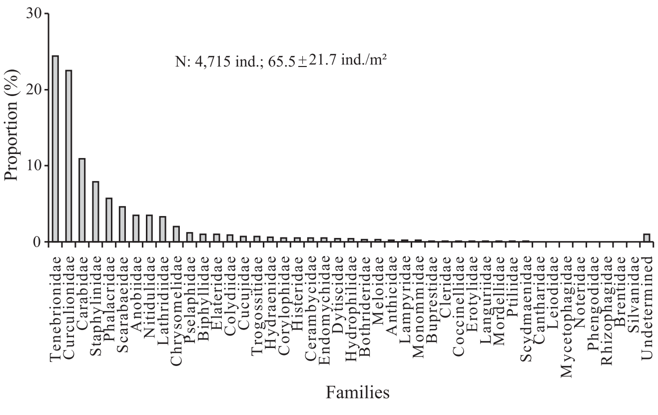

Fig. 10. Proportion (%) of families of adult Coleoptera obtained from the canopy of six trees of *A. phalerata* in decreasing rank of dominance; a+i = adults+immatures, N = total number of arthropods collected.

Table III. Total capture (Individuals), proportion (%) and frequency (%) of adult Coleoptera families (Lawrence *et al.* 1999) obtained from the canopy of three trees of *V. divergens* and six trees of *A. phalerata* (Santos *et al.* 2003).

	V. divergens			*A. phalerata*		
Family	Total (ind.)	Proportion (%)	Frequency (%)	Total (ind.)	Proportion (%)	Frequency (%)
Anobiidae	367	16.7	100	167	3.5	100
Anthicidae	12	0.5	66.6	10	0.2	50
Attelabidae	1	<0.1	33.3	-	-	-
Biphyllidae	-	-	-	45	1.0	100
Bothrideridae	-	-	-	14	0.3	50
Brentidae	12	0.5	66.6	10	0.2	50
Apioninae	(5)	(0.2)	(33.3)	(2)	(<0.1)	(16.6)
Buprestidae	12	0.5	66.6	2	<0.1	33.3
Cantharidae	-	-	-	1	<0.1	16.6
Carabidae	9	0.4	33.3	511	10.8	100
Cerambycidae	2	0.1	66.6	22	0.5	100
Chrysomelidae	140	6.4	100	94	2.0	100
Bruchinae	(5)	(0.2)	(100)	(18)	(0.4)	(83.8)
Cleridae	18	0.8	100	6	0.1	50
Coccinellidae	65	3.0	100	2	<0.1	33.3
Colydiidae	144	6.6	100	42	0.9	100
Corylophidae	105	4.8	100	25	0.5	83.3
Cucujidae	3	0.1	100	35	0.7	66.6
Curculionidae	290	13.2	100	1057	22.4	100
Platypodinae	(37)	(1.7)	(100)	(5)	(0.1)	(50.0)
Scolytinae	(74)	(3.4)	(100)	(13)	(0.3)	(33.3)
Dytiscidae	3	0.1	66.6	18	0.4	50
Elateridae	26	1.2	100	45	1.0	100
Endomychidae	4	0.2	66.6	22	0.5	100
Erotylidae	-	-	-	3	0.1	50
Histeridae	2	0.1	66.6	23	0.5	83.3
Hydraenidae	9	0.4	66.6	28	0.6	66.6
Hydrophilidae	4	0.2	100	16	0.3	83.3
Lampyridae	4	0.2	66.6	9	0.2	66.6
Languriidae	-	-	-	4	0.1	33.3
Lathridiidae	8	0.4	100	158	3.4	100
Leiodidae	1	<0.1	33.3	1	<0.1	16.6
Meloidae	250	11.4	100	13	0.3	83.3
Monommidae	-	-	-	9	0.2	33.3
Mordellidae	-	-	-	3	0.1	50
Mycetophagidae	-	-	-	1	<0.1	16.6
Nitidulidae	393	17.9	100	165	3.5	100
Noteridae	1	<0.1	33.3	1	<0.1	16.6
Phalacridae	8	0.4	100	271	5.7	100
Phengodidae	-	-	-	1	<0.1	16.6
Ptiliidae	39	1.8	66.6	4	0.1	50
Rhizophagidae	-	-	-	1	<0.1	16.6
Scarabaeidae	30	1.4	100	216	4.6	100
Scydmaenidae	-	-	-	8	0.2	33.3
Silvanidae	-	-	-	1	<0.1	16.6
Staphylinidae	136	6.1	100	430	9.1	100
Pselaphinae	(4)	(0.2)	(33.3)	(56)	(1.2)	(100.0)
Tenebrionidae	70	3.2	100	1149	24.4	100
Alleculinae	(1)	(<0.1)	(33.3)	(69)	(1.5)	(100.0)
Trogossitidae	14	0.6	100	33	0.7	83.3
Undetermined	22	1.0	100	47	1.0	-
Total	2197	100	100	4715	100	

Table IV. Density per tree (Individuals/tree) and abundance (Individuals/m^2) of families of adult Coleoptera (Lawrence *et al.* 1999) obtained from the canopy of three trees of *V. divergens* and six trees of *A. phalerata* (Santos *et al.* 2003) with their assigned trophic guilds. H = herbivores, P = predators, F = fungivores, X = xylophages, S = saprophages, ( ) = habit of nutrition in adults ranked secondary; S.D. = standard deviation.

Family	*V. divergens* ind./tree ±S.D.	*A. phalerata* ind./tree ±S.D.	*V. divergens* ind./m^2 ±S.D.	*A. phalerata* ind./m^2 ±S.D.	Guild
Anobiidae	122.3±91.2	27.8±28.6	4.3±3.2	2.3±2.4	H (F)
Anthicidae	4.0±6.1	1.7±2.7	0.1±0.2	0.1±0.2	S
Attelabidae	0.3±0.6	-	<0.1±0.0	-	H
Biphyllidae	-	7.5±4.6	-	0.6±0.4	F
Bothrideridae	-	2.3±3.4	-	0.2±0.3	P
Brentidae	4.0±6.1	1.7±2.7	0.1±0.2	0.1±0.2	S
Apioninae	(1.7±2.9)	(0.3± 0.8)	(0.1± 0.1)	(<0.1± 0.1)	H
Buprestidae	4.0±6.1	0.3±0.5	0.1±0.2	<0.1±0.0	H
Cantharidae	-	0.2±0.4	-	<0.1±0.0	H
Carabidae	3.0±4.4	85.2±64.7	0.1±0.2	7.1±5.4	P
Cerambycidae	0.7±0.6	3.7±3.7	<0.1±0.0	0.3±0.3	H
Chrysomelidae	46.7±37.7	31.3±5.51	1.6±1.2	1.3±0.3	H
Bruchinae	(1.7 ±1.2)	(3.0± 3.0)	(0.1± 0.0)	(0.3± 0.2)	H
Cleridae	6.0±3.6	1.0±1.3	0.2±0.1	0.1±0.1	P
Coccinellidae	21.7±21.8	7.0±7.2	0.8±0.8	0.6±0.6	P
Colydiidae	48.0±43.4	0.3±0.5	1.7±1.5	<0.1±0.0	P (F)
Corylophidae	35.0±52.9	4.2±5.3	1.2±1.8	0.3±0.4	P
Cucujidae	1.0±0.0	5.8±7.7	<0.1±0.0	0.5±0.6	P (F)
Curculionidae	96.7±3.7	173.2±61.9	3.4±0.1	14.7±13.5	H
Platypodinae	(12.3 ±14.7)	(0.8 ±1.0)	(0.4 ±0.5)	(0.1± 0.1)	F
Scolytinae	(24.7 ±13.3)	(2.2± 4.0)	(0.9± 0.5)	(0.2 ±0.3)	H (F)
Dytiscidae	1.0±1.0	3.0±5.1	<0.1±0.0	0.3±0.4	P
Elateridae	8.7±3.2	7.5±1.8	<0.1±0.0	0.6±0.1	H (P)
Endomychidae	1.3 ±1.2	3.7±2.4	<0.1±0.0	0.3±0.2	F
Erotylidae	-	0.5±0.5	-	<0.1±0.0	F
Histeridae	0.7±0.6	3.8±3.7	<0.1±0.0	0.3±0.3	P
Hydraenidae	3.0±4.4	4.7±7.2	0.1±0.2	0.4±0.6	P
Hydrophilidae	1.3±0.6	2.7±3.4	<0.1±0.0	0.2±0.3	S
Lampyridae	1.3±1.5	1.5 ±1.6	<0.1±0.0	0.1±0.1	P
Languriidae	-	0.7±1.0	-	0.1±0.1	H
Lathridiidae	2.7±0.6	26.3±21.1	0.1±0.0	2.2±1.8	F
Leiodidae	0.3±0.6	0.2±0.4	<0.1±0.0	<0.1±0.0	S
Meloidae	83.3±64.9	2.2±2.9	2.9±2.3	0.2±0.2	H
Monommidae	-	1.5±2.8	-	0.1±0.2	H
Mordellidae	-	0.5±0.5	-	<0.1±0.0	H
Mycetophagidae	-	0.2±0.4	-	<0.1±0.0	F
Nitidulidae	131.0±86.8	27.5±31.4	4.6±3.0	2.3±2.6	S
Noteridae	0.3±0.6	0.2±0.4	<0.1±0.0	<0.1±0.0	P
Phalacridae	2.7±2.1	45.2±30.3	0.1±0.1	3.8±2.5	H
Phengodidae	-	0.2±0.4	-	<0.1±0.0	P
Ptiliidae	13.0±17.6	0.7±0.8	0.5±0.6	0.1±0.0	S (F)
Rhizophagidae	-	0.2± 0.4	-	<0.0±0.0	P
Scarabaeidae	10.0±14.7	36.0±35.8	0.3±0.5	3.0±3.0	H (S)
Scydmaenidae	-	1.3±2.4	-	0.1±0.2	P
Silvanidae	-	0.2±0.4	-	<0.1±0.0	F
Staphylinidae	44.0±42.7	62.3±34.7	1.5±1.5	5.2±2.9	P (S,F)
Pselaphinae	1.3±2.3	9.3±8.1	<0.1±0.1	0.8±0.7	F
Tenebrionidae	24.6±30.4	180.0±91.6	0.8±1.1	16.0±7.6	S (F)
Alleculinae	(0.3± 0.6)	(11.5 ±13.3)	(<0.1± 0.0)	(1.0 ±1.1)	H
Trogossitidae	4.7±2.9	5.5±7.1	0.2±0.1	0.5±0.6	P (S)
Undetermined	7.3±1.5	7.8±2.2	0.3±0.1	0.7±0.2	-
Total	732.3±125.0	785.8±260.1	25.5±11.3	65.5±21,7	-

Table V. Richness of morphospecies, number of individuals (N), and proportion (%) of singletons of adult Coleoptera obtained from the canopy of three trees of *V. divergens* during high water (A) and low water (B, C).

Tree	A	B	C
Nº of morphospecies (S)	138	118	109
Nº of individuals (N)	868	671	636
Ratio (N/S)	6.3	5.7	5.8
Proportion of singletons (%)	44.2	54.2	55.0
Nº of abundant morphospecies	9	8	5

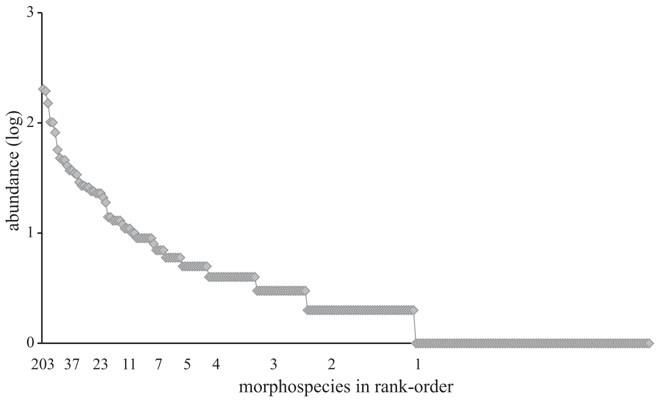

Fig. 11. Rank-abundance plot (log scale) of morphospecies of adult Coleoptera obtained from the canopy of three trees of *V. divergens*.

indicating a less homogeneous distribution (Table IV). This is possibly related to the more complex leaf structure and accumulation of organic matter on the trunk in palms.

The composition of predominating families in adult Coleoptera between *A. phalerata* and *V. divergens* differed. Only Curculionidae was common on both (Figs. 9, 10). In this family, *Celetes* Schoenherr, 1836 was the dominant and exclusive genus on *A. phalerata*, suggesting a possible host specifity.

The diversity of adult Coleoptera on *V. divergens* was high during both low and high waters, showing a great number of species with low abundance and even distribution. Of the 256 identified morphospecies, 102 (39.8%) were "singletons" (= one specimen collected in total), 47 (18.3%) "doubletons" (= only two specimens collected), and 68 (26.6%) with at least ten individuals obtained. Curculionidae (15 spp.), Staphylinidae (14 spp.), and Chrysomelidae (13 spp.) had the highest number of singletons. Abundance and richness of morphospecies was greater during high water (Fig. 11, Tables V and VI).

Of the 326 morphospecies obtained from *A. phalerata*, 41.7% were singletons, 10.4% doubletons and 26.1% comprised less than 10 individuals (Santos *et al.* 2003). Chrysomelidae (25 spp.) and Staphylinidae (16 spp.) had the highest number of singletons.

Studies on adult Coleoptera in the canopy of different tropical and subtropical forests revealed that 40-50% of the species obtained represented singletons. In forests of Uganda, they accounted for 41.6% of the total catch (Wagner 2000) and on Papua New Guinea for 47.6 and 50.7% (Allison *et al.* 1993, 1997). On Borneo singletons even represented 75% of the total species (Floren & Linsenmair 1998a). In Venezuela almost 50% of the families were represented by fewer than five species (Davies *et al.* 1997). Considering the great occurrence of rare species, an understanding of their ecological function in the canopy is needed (Basset 2001). The richness of herbivorous communities on plants and particularly of rare species can increase due to a constant influx of species originating from adjacent plants, named "mass effect" theory (Shmida & Wilson 1985). This influx is important for insects in humid forests, where numerous plant species grow in close vicinity. However, it is possibly of less importance for the species richness on *A. phalerata* and *V. divergens*, considering that these trees cover great areas in the Pantanal of Mato Grosso as monodominant forest stands.

Table VI. Diversity indices and species richness of adult Coleoptera obtained from the canopy of three trees of *V. divergens* during high water (A) and low water (B, C).

Index	Tree A	Tree B	Tree C
Shannon-Wiener (H')	3,89	3,65	3,46
Evenness	0,79	0,77	0,74
Species richness - Margalef (R)	137,8	117,85	108,8
Nº of morphospecies	138	118	109

With regard to seasonality of adult Coleoptera on *V. divergens*, data showed that 5 families occurred in greater abundances during low water (Anobiidae, Meloidae, Curculionidae, Tenebrionidae, and Coccinellidae), whereas eight families were more abundant during high water (Nitidulidae, Corylophidae, Colydiidae, Staphylinidae, Chrysomelidae, Ptiliidae, Scarabaeidae, and Anthicidae). Abundances in the remaining families were similiar during both low and high waters (Fig. 12, Table VII). Of the total 256 morphospecies, the majority (46.1%, 118 spp.) was obtained exclusively during low water, 29.3% (75 spp.) only during high water and 24,6% (63 spp.) during both low and high waters (Fig. 13, Table VII). All morphospecies representing the Brentidae, Buprestidae, Dytiscidae, Endomychidae, Hydraenidae and Pselaphinae were obtained during low water. In other families such as Anobiidae and Tenebrionidae, 72.7% of the morphospecies occurred solely during this period. Attelabidae, Leiodidae and Noteridae were represented by only one specimen each collected during high water (Table VII).

The seasonality of arboreal Coleoptera in humid forests, particularly of taxa with different trophic requirements, is poorly known (Basset 1991). In the Pantanal both seasonal changes in the host plant (e.g., flowering and fruiting, age, chemistry and savouriness of foliages) and the flood pulse certainly influence adults, in particular herbivores and their reproduction. For families with mainly terricolous larvae like Ptiliidae and Scarabeidae, data indicated that part of their adults pass the aquatic phase on trees.

Table VII. Number of morphospecies of adult Coleoptera obtained exclusively from the canopy of *V. divergens* during low water (trees B, C) or high water (tree A) and common during both low and high waters.

Family	Low water	High water	Low+High water	Total
Anobiidae	8	1	2	11
Anthicidae	1	3	-	4
Attelabidae	-	1	-	1
Brentidae	4	-	-	5
Apioninae	(4)	(-)	(-)	(4)
Buprestidae	2	-	-	2
Carabidae	1	1	-	2
Cerambycidae	1	1	-	2
Chrysomelidae	11	15	8	34
Bruchinae	(-)	(2)	(1)	(3)
Cleridae	6	-	3	9
Coccinellidae	6	-	5	11
Colydiidae	-	1	3	4
Corylophidae	1	1	2	4
Cucujidae	2	2	-	4
Curculionidae	23	20	13	56
Platypodinae	(1)	(3)	(2)	(6)
Scolytinae	(5)	(4)	(3)	(12)
Dityscidae	3	-	-	3
Elateridae	5	4	-	9
Endomychidae	3	-	-	3
Histeridae	-	-	1	1
Hydraenidae	4	-	-	4
Hydrophilidae	1	-	1	2
Lampyridae	1	-	1	2
Lathridiidae	-	-	2	2
Leiodidae	-	1	-	1
Meloidae	3		3	6
Nitidulidae	2	4	5	11
Noteridae	-	1	-	1
Phalacridae	3	1	1	5
Pitiliidae	-	1	2	3
Scarabaeidae	2	2	1	5
Staphylinidae	11	13	7	31
Pselaphinae	1	-	-	1
Tenebrionidae	9	2	1	12
Alleculinae	(1)	(-)	(-)	(1)
Trogossitidae	4	-	2	6
Total	118	75	63	256

Trophic guilds. The communitiy of adult Coleoptera on *V. divergens* indicated a dominance of herbivores (37.8% of the total catch, 127 spp.) and predators (35.2%, 82 spp.), followed by saprophages (16.2%, 32 spp.), and fungivores (10.8%, 15 spp.) (Fig. 14). In herbivores, Anobiidae, Meloidae, Curculionidae and Chrysomelidae dominated, in predators Colydiidae, Staphylinidae and Coccinellidae, in saprophages Nitidulidae and Tenebrionidae, and in fungivores Lathridiidae and Endomychidae (Table IV).

The predominance of herbivores during low water (64.1% of the total catch vs. 27.7% at high water) was due to Anobiidae (10 spp.) and Meloidae (6 spp.). The predominance of predators during high water (33.1% vs. 9.6% at low water) was due to Staphylinidae (20 spp.), Colydiidae (4 spp.) and Corylophidae (3 spp.) (Fig. 12, Table VII). Saprophages and fungivores showed similar abundances during both low and high waters. Herbivores also predominated during receding waters (42% of the total catch), followed by xylophages (21%), saprophages (21%), predators (15%) and fungivores (1%) (Marques *et al.* 2001).

In *A. phalerata*, herbivores (37.5% of the total catch) and predators (35.4%) prevailed fungivores (14.6%) and saprophages (12.5%) as well (Fig. 15).

Studies of trophic guilds in other tropical regions indicated a dominance of herbivores or predators in the canopy. In Sulawesi and Australia predators dominated over fungivores, xylophages and herbivores (Hammond 1990; Hammond *et al.* 1996, 1997). In Venezuela herbivores predominated, followed by fungivores and predators (Davies *et al.* 1997). In Rwanda and Zaire herbivores and fungivores were more abundant (Wagner 1997). In Central Amazonia herbivores (74.4%) from three inundation forests and one forest on terra firme predominated over predators (13.6%), saprophages (9.3%) and fungivores (2.7) (Erwin 1983b).

Evergreen and monodominant forests like *V. divergens and A. phalerata* in the Pantanal offer nutritional resources over the year. This might be an explication for the predominance of herbivores in their canopies. The greater abundance of

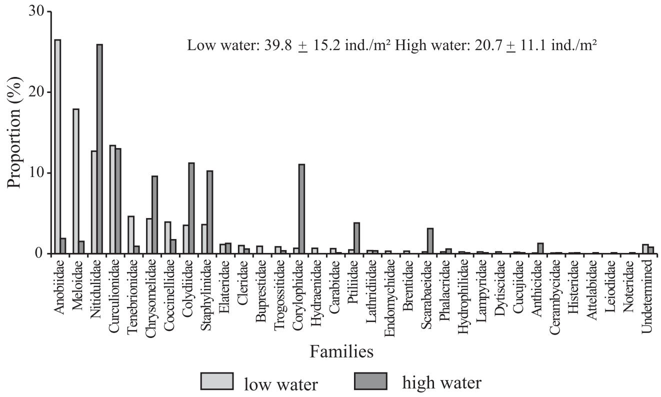

Fig. 12. Proportion (%) of families of adult Coleoptera obtained from the canopy of *V. divergens* during low water (trees B, C) and high water (tree A); a+i = adults+immatures.

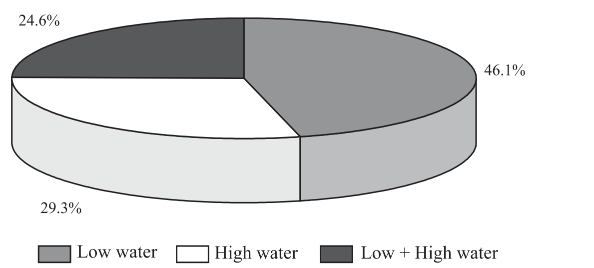

Fig. 13. Proportion (%) of morphospecies in adult Coleoptera obtained during low or/and high water from the canopy of *V. divergens*.

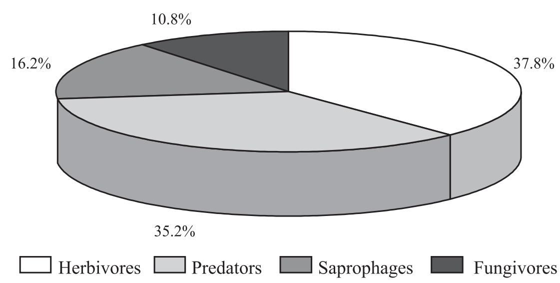

Fig. 14. Proportion (%) of trophic guilds assigned to adult Coleoptera obtained from the canopy of three trees of *V. divergens*.

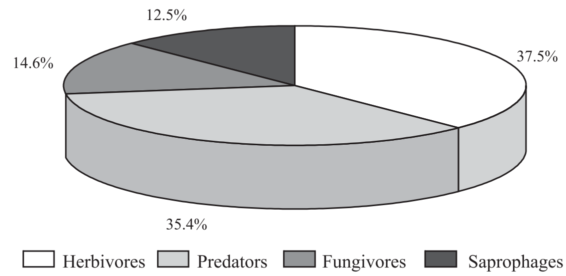

Fig. 15. Proportion (%) of trophic guilds assigned to adult Coleoptera obtained from the canopy of six trees of *A. phalerata*.

herbivores on *V. divergens* during low water (September/October) may be related to the preceding flowering and fruiting of trees (July/August). The greater number of predators during high water may represent a reaction to the flood pulse due to a greater availability of prey, considering that terricolous arthropods use trees as refugium during the aquatic phase. Clarification of the function and life cycle of dominant morphospecies in the canopy both during low and high waters is mandatory for future studies.

CONCLUSIONS

The influence of the flood pulse on the community of arboreal arthropods in *V. divergens* is indicated by the seasonal variation in evaluated groups, causing changes in their structure and composition.

Formicidae was the predominating group both during low and high waters. Seasonality in Thysanoptera is attributed to flowering of the host plant during low water, and seasonality in Araneae to the temporary use of trees by terricolous species during high water.

The canopy represents a reproduction place for Blattodea, Homoptera and Heteroptera during high water.

Rare species (singletons, doubletons) cause the great diversity in adult Coleoptera. Distribution of species was even, however their abundance and richness was greater during high water. Five families were more abundant during low water (above all Nitidulidae), and nine families during high water (above all Anobiidae). Herbivores and predators were the dominating trophic groups. Predominance of predators during high water is attributed to the flood pulse, that of herbivores during low water to seasonal changes in the host plant.

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