Community structure of Neotropical wetland insects in Northern Venezuela.
II. Habitat type and environmental factors

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With 5 figures, 1 table and 1 appendix

Abstract: This study examined the spatial distribution of wetland insects in relation to selected environmental variables in northeastern Venezuela. Sampling was carried out over two sampling periods (rainy and dry season) in seven wetland types (brackish and freshwater herbaceous swamps, mangrove swamps, freshwater ponds, clear-cut marsh forests, small irrigation canals, and swamp forests), covering three environmental gradients (salinity, aquatic vegetation type, and habitat permanence). Using the partial redundancy analysis, we determined that occurrence and abundance of insects was significantly ($P < 0.05$) accounted for by the relative contributions of pure environmental (29–34 %) and habitat type-related (12–15 %) variations among wetlands. Water chemistry (salinity), wetland trophic state (phytoplankton), habitat heterogeneity (aquatic vegetation type), and habitat physical features (depth and habitat permanence) were significantly associated to community structure. Insect richness was higher in the less saline, more vegetated, and less temporary wetlands. Our findings add to previous results suggesting that adversity, productivity, heterogeneity and permanence of the habitat represent important axes along which Neotropical wetland insect communities are organized.

Key words: Aquatic insects, community structure, wetland type-related distribution.

Introduction

Wetlands and distributions of organisms that inhabit them are typically heterogeneous in space and time. Therefore, spatial and temporal variability are essential factors in the study of factors influencing wetland insect commu-

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nities. Habitat features as habitat permanence or habitat heterogeneity and biotic interactions such as predation are known to influence local assemblages of wetland insect species (BATZER & WISSINGER 1996, BATZER et al. 1999). Most of these generalizations are based upon studies in temperate ecosystems. By contrast, few studies have addressed these aspects in neotropical wetland insects (HECKMAN 1998, GRILLET 2000, GRILLET et al. 2002).

In a previous paper (GRILLET et al. 2002), we showed how the changes in insect community structure in several Neotropical wetlands in northeastern Venezuela could be partially accounted for by a temporal gradient representing seasonal variation in the wetlands and the overlap in temporal and environmental components. Seasonal changes in precipitation (as a broad-scale factor) were reflected in local wetland conditions (water depth, wetland trophic state, and water chemistry), which, in turn, correlated well with seasonal differences in taxa distribution. Insect strategies (life history patterns) for coping with the seasonal variation in the habitat were suggested as a possible explanation of their temporal distribution. In that study, the relative importance of different factors varied markedly between habitats, suggesting that purely local spatial variation related to the wetland type could also be important in the assessment of the factors influencing insects assemblages.

In the present paper, we explicitly address the spatial (among-habitat) variation in the distribution of wetland insect communities. The hypotheses that the wetland insect distributions are non-random at the scale of the study, and understandable, in part, by the relative contribution of abiotic and biotic factors as well as the habitat type was evaluated. Abundance and spatial distributions of insects in relation to habitat conditions are assessed and the community structure is investigated by partial ordination techniques, using the variation partitioning approach of BORCARD et al. (1992). The following explanatory variables for community assembly were considered: a) pure environmental variation, b) wetland type-related variation shared with environmental variation, c) pure wetland type-related variation, and d) undetermined variation.

Understanding insect distribution patterns along environmental gradients can provide insight into mechanisms structuring their communities. Thus, gradients of three environmental variables were chosen as the main axes along which the wetland insect communities should be organized: salinity, aquatic vegetation type, and habitat permanence (BATZER & WISSINGER 1996, BATZER et al. 1999). These gradients could be interpreted as measures of adversity (sensu SOUTHWOOD 1977), structural heterogeneity (sensu ORR & RESH 1989), and habitat permanence (sensu WIGGINS et al. 1980), respectively. It was expected that taxon richness would be lower in adverse, non-vegetated, and temporary aquatic habitats (BATZER & WISSINGER 1996).

In this study we addressed the following questions: (i) Are there positive or negative associations between abundance of some insects and selected envi-

ronmental factors? (ii) Are there particular associations between different wetland types and the abundance of taxa? (iii) How do these associations differ between the dry and rainy seasons?

Materials and methods

Study area

The study area has been described in detail elsewhere (GRILLET 2000, GRILLET et al. 2002). The wetlands were located and sampled in the coastal area of the Paria peninsula (10° 17′ N, 63° 57′ W), northeastern Venezuela. Mean annual temperature and rainfall in the area are 27–28 °C and 1200–1700 mm, respectively. There is a rainy season from May to November, and a dry period from December to April.

Sampled water bodies or habitats were classified according to water salinity, aquatic vegetation and hydroperiod (GRILLET et al. 2002). Permanent, seasonal and temporal wetlands were wet all year, for 9 or 8 months, and for 4–6 months each year, respectively. Most wetlands were generally shallow, having a mean depth <1 m and they were called brackish (*Bhs*) and freshwater herbaceous swamps (*Fhs*), ponds (*Pond*), mangrove swamps (*Mang*), clear-cut marsh forests (*Ccmf*), small irrigation canals (*Canal*), and swamp forests (*Sf*). The individual wetland types were described in detail elsewhere (GRILLET et al. 2002), except the *Canal* and *Sf* wetlands. *Canal* were permanent small agricultural irrigation canals, whereas the *Sf* wetland was a temporal swamp wood with a closed canopy of dominant trees of *Pterocarpus* sp. and palms of the genus *Euterpe*.

Sampling design

To determine the distribution of aquatic insects among different wetland types, sampling was carried out at 28 habitats during the late rainy season (October 1994) representing 4 *Mang*, 6 *Bhs*, 3 *Fhs*, 4 *Pond*, 3 *Ccmf*, 4 *Canal*, and 4 *Sf* wetlands. An additional sampling was carried out at 16 habitats during the early dry season (February 1995) including 1 *Mang*, 3 *Bhs*, 5 *Fhs*, 2 *Pond*, 4 *Canal*, and 1 *Sf* wetlands. Organisms were sampled with a long-handled ladle or dipper (SOUTHWOOD & HENDERSON 2000), and the number of individuals per dip was calculated from 30 dips from each collection site (GRILLET et al. 2002). In the field, the water volume from each dip was sieved, and the collected individuals preserved in 80 % ethanol. In the laboratory, the insects were counted and identified to family (MERRITT & CUMMINS 1984).

Environmental variables

Before insect sampling, we characterized the following environmental variables (Table 1): type of aquatic vegetation (emergent, floating, or submerged: nominal variable), total cover (%) of aquatic vegetation, mean height of emergent vegetation above the water surface, water chlorophyll-a content, mean water depth, temperature, pH, salinity, conductivity, alkalinity, dissolved oxygen and, dissolved carbon dioxide. Wetland type

Table 1. Description and environmental variables (mean ± SE) used to characterize the wetlands during the rainy (top) and dry (bottom) season sampling in northeastern Venezuela.

Variables	Habitat types						
	Bhs	Fhs	Pond	Mang[1]	Cemf[2]	Canal	Sf[3]
Habitat duration[3]	P, S	P, S	P, S, T	S	T	P, T	T
Aquatic vegetation[4]	EV	EV	EV, FV	NV	EV, FV	NV	NV
Water depth	20±5	34±4	28±5	20±7	15±5	24±3	13±1
(cm)	16±1	29±6	26±11		–	27±5	
Vegetation	69±11	60±12	46±95	0	65±18	0	0
cover (%)	20+8	51±20	62±23		–	0	
Vegetation	71±10	208±27	99±18	0	91±19	0	0
height (cm)	63±6	216±35	110±56		–	0	
Temperature	28±1	28±1	29±1	27±1	22+8	28±0	26±0
(°C)	26±0	27±0.1	31±0		–	29±0	
pH	6.0±0	7.0±0	6.5±0	6.8±0	6.8±0	6.9±0	6.9±0
	7.3±0	7.7±0	7.3±0		–	8.2±0	
Oxygen	0.8±0.3	1.9±1.3	3.9±0.8	0.9±0.4	0.8±0.2	2.6±1	2.6±1
(mg/L)	0	1.6±1.2	6.7±1		–	5.9±0.5	
Salinity	4.0±2	0	0	13±4	0	0	0
‰	1.7±0	0.6±0	0		–	0	
Conductivity	7,617±3,931	917±169	136±92	21,750±6,434	917±292	637±90	750±409
(µS/cm, 21 °C)	3,333±667	1680±484	275±225		–	275±225	
Alkalinity	121±28	176±14	70±29	70±29	200±58	231±29	165±51
(mg/L)	482±11	234±118	109±79		–	202±26	
CO_2	118±30	27±10	24±6	24±6	93.3±3	54±26	31±51
(mg/L)	70±15	41±6	18±4		–	15±1	
Chlorophyll-a	42±12	37±24	30±2	30±2	32±6	7±0	67±16
(µg/L)	30±12	21±10	44±6		–	5.3±4	

[1] Only one habitat was sampled in the dry season.

[2] Wetland dried out completely during the dry season.

[3] P, permanent; S, seasonal; T, temporal.

[4] EV, emergent vegetation; FV, floating vegetation; NV, no vegetation.

Bhs = Brackish herbaceous swamp; Fhs = Freshwater herbaceous swamp; Pond = Pond; Mang = Mangrove; Cemf = Clear-cut marsh forest; Canal = canal; Sf = Swamp forest.

and habitat permanence data were incorporated *a posteriori* as nominal variables in the data matrix of each sampling occasion.

Data analyses

All statistical analyses were performed separately for the two sampling periods. Insect community structure was related to environmental variables using redundancy analysis (RDA). Taxa abundance data were transformed to preserve the Hellinger distance

among samples prior to the analysis following LEGENDRE & GALLAGHER (2001). Details about the use of this kind of transformation for the ordination of our insect data were provided elsewhere (GRILLET et al. 2002). In addition, partial RDA was used to determine whether the interpretation of insect abundance variation could be attributed to the environmental and wetland type-related factors separately, using the method of variation partition proposed by BORCARD et al. (1992). The variation partition procedure involved the following steps: (1) compute the variation accounted for by the environmental variables; (2) compute the variation accounted for by the wetland type; (3) compute the variation explained by the environmental variables after removing the effect of the wetland type by partial RDA; (4) compute the variation explained by the wetland type after removing the effect of the environmental variables by partial RDA. The total explained variation (component $a + b + c$) was the sum of the explained variations in (1) and (4) or in (2) and (3). The wetland type non-related (pure) environmental variation (component a) was given by step (3), and the (pure) wetland type-related variation (component c) that was not associated to the environmental variables was given by step (4). The variation shared by the wetland type-related and environmental variables (component b) was obtained by subtracting (3) from (1) or (2) from (4). The unexplained portion of variation (residual variation, component d) was calculated as $d = 1 - (a + b + c)$. The computer program CANOCO 4 (TER BRAAK & SMILAUER 1998) was used for all the analyses. A forward selection procedure permitted to select the most significant variables ($P < 0.05$) in the model. Finally, the significance of the overall model was tested using 999 Monte Carlo permutation tests.

Results

Habitat characterization, insect community structure and spatial variation

Overall, the *Mang* habitats were the most brackish wetlands, and without macrophytes (Table 1). High CO_2 and phytoplankton levels were the main habitat conditions for the *Bhs* wetland. *Pond* habitats were the warmest and more oxygenated wetlands, with great amounts of phytoplankton and a low alkalinity. The deeper and emergent vegetation dominated sites were found in the *Fhs* wetland. The *Canal* wetland was the habitat with the lowest level of phytoplankton, but high values of oxygen, pH and alkalinity (Table 1).

A total of 38 insect taxa were collected for the 44 habitats during the rainy and dry sampling sessions; however, a maximum of 31 taxa were considered in the analyses (see Appendix). The total mean density of insects ranged from 25 (rainy season) to 38 (dry season) individuals/dip among wetlands. During the rainy season, the fauna was dominated in abundance and occurrence by the dipterans Culicidae, Ceratopogonidae and Chironomidae, whereas a more diverse group of taxa predominated during the dry season (Culicidae, Helodidae, Veliidae, and Baetidae). Spatially, the highest taxon richness was observed in

the vegetated and permanent wetlands (e.g., 28 taxa each: *Fhs* and *Canal* wetlands, see Appendix), whereas the lowest richness was recorded in the most saline (*Mang*: 11 taxa) followed by the most temporary (e.g., *Ccmf*: 14 taxa) wetlands. Seasonally, the highest richness and insect abundance (28 taxa with 1,448 individuals in total at the *Bhs*) was recorded in the dry season.

General and partial ordination, and associated factors

The relationship between insect abundance and the environmental and wetland type-related variables together was highly significant in both sampling periods (component $a + b + c$, $P < 0.001$), accounting for 48 % (rainy season) and 61 % (dry season) of the total variation of the community (Fig. 1). Insect abundance was more predictable during the dry season than rainy season. Components a (pure environmental variation) and c (pure wetland type-related variation) also were significant ($P < 0.001$) in both periods, ranging, respectively, from 29 % and 12 % (rainy season) to 34 % and 15 % (dry season). Component b meant the fraction of variation of insect taxa explained and equally attributed to the environmental and the wetland type-related variables. The amount of unex-
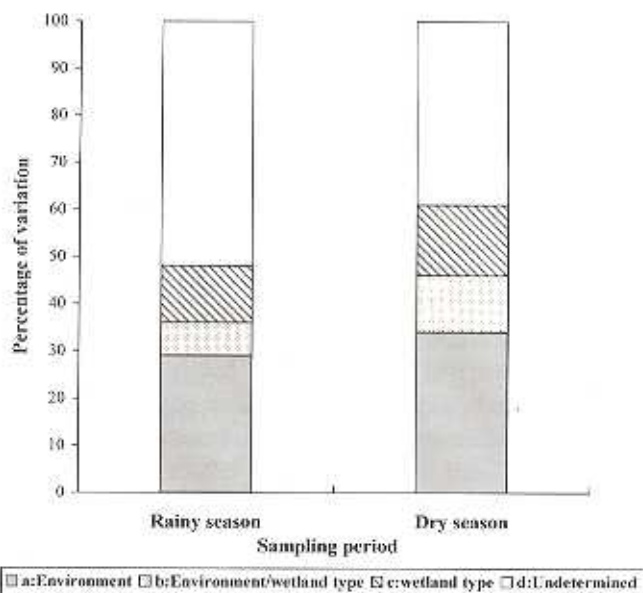

Fig. 1. Variation partition of the total variation in the wetland insect community from northern Venezuela based on a partial RDA ordination. Insect variation attributed to environmental variation independent of any wetland type-related variation (component *a*), variation shared by the wetland type-related and environmental variables (component *b*), pure wetland type-related variation (component *c*) independent of any environmental variable, and unexplained variation (component *d*).

plained variation (rainy season: 52 % and dry season: 39 %) indicated that other external factors, not taken into account in our study, were also important in influencing the insect assemblages in these wetlands.

For the rainy season, the first two canonical axes in the RDA model accounted for 22 % of the variation in the insect community, although only the first axis was significant ($P < 0.001$; Fig. 2). Ten taxa were well-represented in the diagram and three families of dipterans (Culicidae, Ceratopogonidae and Chironomidae) dominated the ordination (Fig. 2). Insect distribution along ordination axes was mostly related with water chemical (salinity and CO_2), wetland trophic condition (phytoplankton), habitat features (aquatic vegetation type, vegetation cover, habitat permanence, and water depth), and wetland type (*Mang, Fhs, Bhs,* and *Ccmf*; Fig. 2). The eutrophic, brackish and high CO_2 level sites of the *Bhs* wetland (positive and negative side of axis 1 and 2, respectively) were characterized by the biting midges (Ceratopogonidae), whereas the Culicidae (positively) and Chironomidae (negatively) were asso-
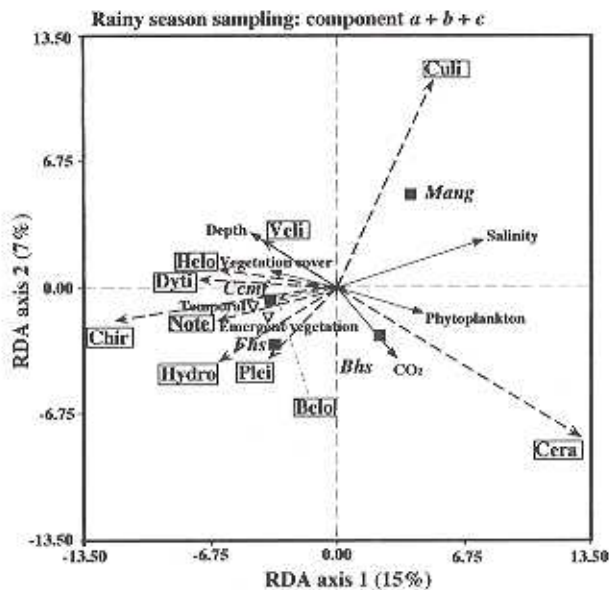

Fig. 2. Correlation biplot based on a RDA ordination of insect abundance (dashed arrows) and the environmental (solid arrows and triangles) and wetland type-related factors (squares) during the rainy season sampling period (component $a + b + c$). Qualitative variables are indicated by triangles and squares. Only the environmental factors retained in the model by the forward selection procedure ($P < 0.05$) and the taxa with > 30 % of their variance accounted for by the diagram are shown. Culi = Culicidae, Chir = Chironomidae, Cera = Ceratopogonidae, Note = Noteridae, Dyti = Dytiscidae, Hydro = Hydrophilidae, Helo = Helodidae, Veli = Veliidae, Plei = Pleidae, Belo = Belostomatidae.

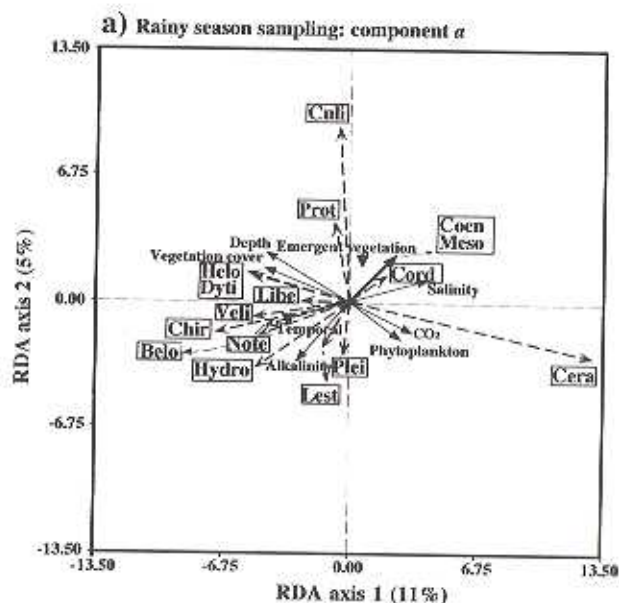**a)** **Rainy season sampling: component** *a*

Fig. 3. a

ciated to the water salinity. Additionally, mosquitoes dominated the *Mang* wetland (Fig. 2). The more vegetated (*Fhs* and *Ccmf*), temporary (*Ccmf*) and deeper (*Fhs*) wetlands were characterized by the water beetles (Helodidae, Dytiscidae, Hydrophilidae and Noteridae) and water bugs (Pleidae, Belostomatidae, and Veliidae).

Results of the variation partitioning of the insect assemblages during the rainy season sampling (Fig. 3) showed how the community pattern could be partly due to the purely environmental (component *a*) and wetland type-related (component *c*) variation. In component *a* (Fig. 3 a), on the one hand, we identified a true environment-insect relationship that remained even after partialling out the effect of wetland type. Indeed, the chemical, trophic condition, and aquatic vegetation gradients described previously (Fig. 2) separated insect taxa along this new ordination biplot. On the other hand, the results revealed new insect distribution patterns that came out when we removed wetland effects (Fig. 3 a). For example, six new families belonging to the group of the odonates (Corduliidae, Coenagrionidae, Protoneuridae, Libellulidae, and Lestidae) and hemipterans (Mesoveliidae) appeared in this model as a result of their positive relationships with the emergent vegetation and water depth. Likewise, mosquitoes were linked to the emergent vegetation (Fig. 3 a). In component *c* (Fig. 3 b), although all 7 wetlands were retained in the partial model, the *Fhs, Canal, Pond, Mang* and *Ccmf* habitats contributed most to the spatial variation of insect taxa. Families of soldier flies (Stratiomyidae), water
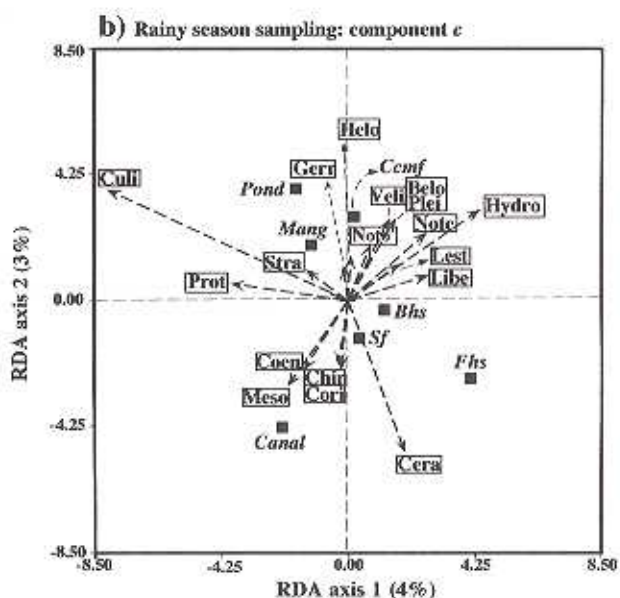
b) Rainy season sampling: component *c*

Fig. 3. a) Partial RDA correlation biplot for the rainy season sampling representing the environmental variation independent of any wetland type-related variation (component *a*). Environmental variables are represented by solid arrows and triangles, insect families are displayed by dashed arrows. Only the first axis was significant ($P = 0.001$) b) Biplot of the component *c* (partial RDA of the taxa against wetland type-related variables while controlling for the environmental variables). Wetland type-related variables are represented by squares. Only the first axis was significant ($P = 0.001$). Culi = Culicidae, Chir = Chironomidae, Cera = Ceratopogonidae, Stra = Stratiomyidae, Note = Noteridae, Hydro = Hydrophilidae, Helo = Helodidae, Meso = Mesoveliidae, Veli = Veliidae, Noto = Notonectidae, Plei = Pleidae, Belo = Belostomatidae, Cori = Corixidae, Gerri = Gerridae, Coen = Coenagrionidae, Prot = Protoneuridae, Cord = Corduliidae, Libe = Libellulidae, Lesti = Lestidae.

bugs (Corixidae, Notonectidae, Gerridae and Mesovellidae) and odonates (Coenagrionidae, Protoneuridae, Libellulidae, and Lestidae) came out in this ordination diagram, emphasizing particular wetland association. The distribution of mosquitoes (Culicidae), soldier flies (Stratiomyidae) and protoneurid damselflies was accounted for by the *Mang* wetland. *Canal* wetland was characterized by midges, some damselflies (Coenagrionidae), and some water bugs (Mesoveliidae and Corixidae). Most of the water bugs (Gerridae, Notonectidae, Veliidae, Belostomatidae and Pleidae) and the taxa Helodidae occurred in the *Ccmf* and *Pond* wetlands, whereas the other water beetles (Hydrophilidae and Noteridae) and odonates (Lestidae and Libellulidae) characterized the *Fhs* and *Bhs* wetlands. Finally, the biting midges (Ceratopogonidae) were linked to *Sf* and *Fhs* wetlands.

For the dry season sampling, the total explained variation ($a + b + c = 62\%$) in the insect community was highly significant ($P < 0.001$). Fourteen taxa were selected in the model, whereas four of them (Culicidae, Helodidae, Baetidae, and Veliidae) dominated the ordination (Fig. 4). RDA axis I clearly represented site-specific variation in trophic (positive side) and physicochemical condition (negative side) among habitats. Ordination of insect taxa along this axis provided evidence that the mosquitoes, coleopterans (Helodidae, Noteridae and Dytiscidae) and the giant water bug (Belostomatidae) occurred in eutrophic and emergent vegetation dominated wetlands (*Bhs* and *Fhs*). At the opposite end of Axis I (Fig. 4), the warmer and oxygenated *Pond* wetland was dominated by dipterans (Ceratopogonidae, Stratiomyidae and Tipulidae), hemipterans (Mesoveliidae and Notonectidae) and ephemeropterans (Ephemeridae). The Tipulidae, Ceratopogonidae, Stratiomyidae, Notonectidae and Mesoveliidae also were associated with the high-conductivity sites in the *Mang* wetland (along axis 2 negative side), whereas the deeper, more oxygenated and non-vegetated *Canal* habitat, on the opposite side, was characterized by Baetidae, Veliidae, and Corixidae.

The insect taxa discriminated either in component *a* or *c* during the dry season sampling are shown in Fig. 5. The Chironomidae, Dixidae, Gerridae and Corduliidae came out in the component *a* (Fig. 5 a), showing positive associations with deeper (Gerridae), eutrophic (Corduliidae), warmer and emergent vegetation dominated (Chironomidae and Dixidae) sites. Here (Fig. 5 a), we newly confirmed the importance of the trophic and aquatic vegetation gradients in the insect spatial distribution. In component *c* (Fig. 5 b), the wetlands that contributed most to the variation of organisms were *Bhs*, *Pond*, *Mang*, and *Fhs*. Some dipterans (Culicidae, Tipulidae and Dixidae), the marsh beetle (Helodidae), the narrow-winged damselfly (Coenagrionidae) and the common burrower (Ephemeridae) characterized the *Bhs* wetland. The small minnow mayfly (Baetidae), the midges (Chironomidae) and some hemipterans (Veliidae and Pleidae) predominated in the *Pond* wetland. Finally, a group belonging to the Diptera (Ceratopogonidae and Stratiomyidae) and Hemiptera (Corixidae, Gerridae and Mesoveliidae) as well as the water scavenger beetle (Hydrophilidae) appeared as taxa closely linked to the *Mang* and *Fhs* wetlands (Fig. 5 b).

Discussion

The spatial (among habitats) and temporal (among seasons) distribution of insects in our study was predictable on the wetland type and measured habitat variables. In particular, our results suggest that the water chemistry (salinity), wetland trophic state (phytoplankton), habitat heterogeneity (due to aquatic
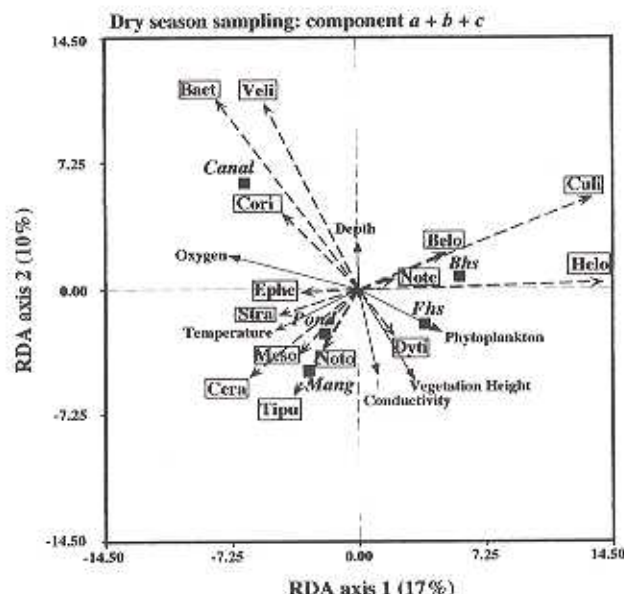
Fig. 4. RDA correlation biplot representing each set of environmental (solid arrows) and wetland type-related factors (squares) as well as insect taxa (dashed arrows) during the dry season sampling period (component $a + b + c$). The first two canonical axes in the model accounted significantly ($P < 0.001$) for 27 % of the variation. Culi = Culicidae, Cera = Ceratopogonidae, Tipu = Tipulidae, Stra = Stratiomyidae, Note = Noteridae, Dyti = Dytiscidae, Helo = Helodidae, Meso = Mesoveliidae, Veli = Veliidae, Noto = Notonectidae, Belo = Belostomatidae, Cori = Corixidae, Baet = Baetidae, Ephe = Ephemeridae.

vegetation type), and habitat physical features such as depth and habitat permanence are important habitat axes along which Neotropical wetland insect communities are organized. In general, the taxonomic richness was larger in the freshwater, more vegetated, and less temporary wetlands, agreeing with previous results for temperate insect communities (BATZER & WISSINGER 1996, BATZER et al. 1999). Additionally, insect richness was higher in the early dry season than in the late rainy season, supporting previous results for Neotropical wetlands (GRILLET et al. 2002, HECKMAN 1998).

Among habitats, extremely saline wetlands, such as *Mang*, were characterized mainly by high densities of only a few taxa belonging to Diptera such as mosquitoes (Culicidae), soldier flies (Stratiomyidae), biting midges (Ceratopogonidae), and crane flies (Tipulidae). In general, these families fare particularly well across adverse habitat conditions (WILLIAMS & FELTMATE 1992). Faunal diversity and salinity tend to be negatively correlated (BATZER & WISSINGER 1996); however, this relationship is not straightforward and may be confounded by other concomitant effects. Here, the saline habitats had no
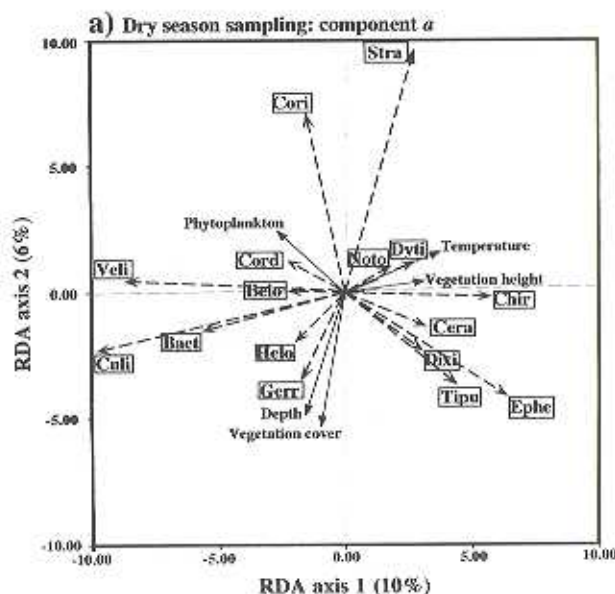
a) Dry season sampling: component *a*

Fig. 5. a

aquatic vegetation, were non-permanent and had typically high nutrient levels presumably due to increased primary production. Consequently, the lower observed diversity in the *Mang* wetland could be due to reduced habitat heterogeneity (BATZER & WISSINGER 1996), low habitat predictability (WILLIAMS 1987), and/or the anoxic conditions due to excessive nutrient enrichment (TIMMS 1983, WOLLHEIM & LOVVORN 1996).

The distribution of taxa changed between the two sampling periods mainly in response to phytoplankton concentration; the effect of this factor was more significant and predominant during the dry season (GRILLET et al. 2002). Indeed, the higher insect richness observed during the early dry season was due mainly to an increase in the herbivore-detritivore group (such as the Tipulidae, Dixidae, Stratiomyidae, Ephemeridae, and Baetidae), which, in turn, could be explained by an increase in algae, algal detritus, and/or plant detritus as the dry season progresses. The temporal eutrophication of these wetlands was described previously (GRILLET et al. 2002).

The highly vegetated wetlands, such as the freshwater *Bhs, Fhs, Pond* and *Ccmf* habitats, had high taxon richness (Diptera, Hemiptera, Coleoptera, Odonata, and Ephemeroptera) as well as higher numbers of less common taxa such as the Ephemeroptera or the dipterans Dixidae and Stratiomyidae. This is presumably because macrophytes increase the habitat heterogeneity, with plants serving as cover and habitat for invertebrates and as a substrate for algal growth, thus allowing more taxa to coexist (BATZER & WISSINGER 1996). In
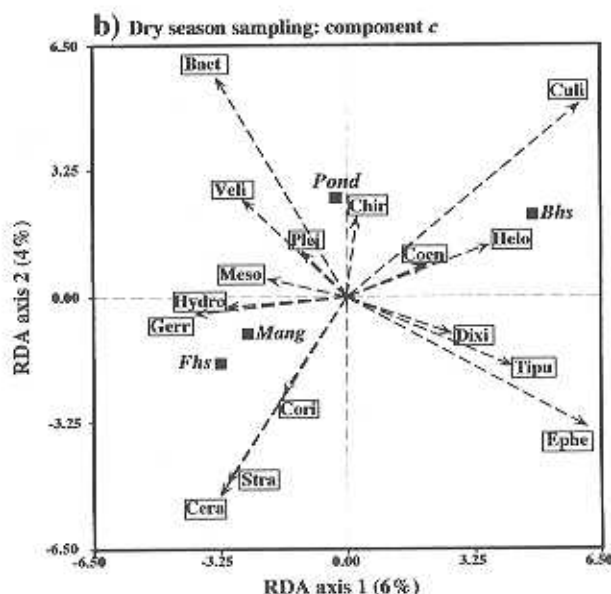
b) Dry season sampling: component *c*

RDA axis 2 (4%)

RDA axis 1 (6%)

Fig. 5. a) Correlation biplot for the dry season sampling representing each set of environmental (solid arrows) and the insect families (dashed arrows) as identified in the partial RDA of the taxa against environmental variables while controlling for the wetland type-related (component *a*). Only the first axis was significant ($P = 0.001$). b) Biplot of the component *c* (partial RDA of the taxa against wetland type (squares) while controlling for the environmental variables). Only the first axis was significant ($P = 0.001$). Culi = Culicidae, Chir = Chironomidae, Cera = Ceratopogonidae, Tipu = Tipulidae, Stra = Stratiomyidae, Dixi = Dixidae, Dyti = Dytiscidae, Hydro = Hydrophilidae, Helo = Helodidae, Meso = Mesoveliidae, Veli = Veliidae, Noto = Notonectidae, Plei = Pleidae, Belo = Belostomatidae, Cori = Corixidae, Gerri = Gerridae, Coen = Coenagrionidae, Cord = Corduliidae, Baet = Baetidae, Ephe = Ephemeridae.

particular, these habitats were dominated by emergent plants, a growth form that seems to support more taxa than other macrophyte growth forms such as submerged vegetation (WOLLHEIM & LOVVORN 1996). In addition, low dissolved oxygen in the emergent vegetation-dominated habitats (e.g., *Fhs*, *Bhs* and *Ccmf*) also can limit fish predators (MURKIN 1989, WOLLHEIM & LOVVORN 1996).

We found that highly oxygenated habitats such as *Pond* and the *Canal* wetlands also had high taxon richness belonging mainly to Odonata and Ephemeroptera. The positive relationship among these taxa and oxygen is well-documented (BATZER & WISSINGER 1996). Additionally, changes in insect abundances linked to water level through the space and season in these wetlands also were important. Most taxa belonging to the Coleoptera, Hemiptera, Odonata and Ephemeroptera, as well as the Chironomidae, showed positive rela-

tionships with depth (which is a function of habitat size), agreeing with previous observations (e.g., BAZZANTI et al. 1996, GRILLET et al. 2002) and suggesting that large water bodies support a greater diversity of insects than small ones. Indeed, the deeper habitats in our study were the *Fhs*, *Pond* and *Canal* wetlands. In particular, deeper areas of habitats are more likely to be inhabited by mayflies, some chironomids (mainly predators) and dragonflies (WILLIAMS & FELTMATE 1992, WARD 1992). In contrast, in our study, mosquitoes and other dipterans such as the Stratiomyidae, Ceratopogonidae and Tipulidae predominated in shallow water conditions with high CO_2 and phytoplankton levels, indicating their association with detritus food (MERRITT & CUMMINS 1984).

The non-vegetated but less temporary wetlands such as the *Canal* habitat also had high insect richness, mainly during the dry season. In contrast, habitats flooded for short periods during the year, such as the *Ccmf* and *Sf*, had low taxon richness. Frequent drying may limit the number of predators (mainly odonates) in these habitats (BATZER & WISSINGER 1996). Longer hydroperiods (more seasons) can support a greater variety of phenologies and thus more insect species. Additionally, temporary waters exhibit much greater amplitudes in the physical and chemical variables than permanent aquatic habitats, making them adverse habitats at certain times. Temporary water species within these groups invariably show special traits in either their physiology or life cycle, thus allowing them to be successful in these habitats. Chironomidae, Ceratopogonidae, Culicidae, Hemiptera (some taxa), and Coleoptera (some taxa) do particularly well in temporary freshwater habitats (WILLIAMS & FELTMATE 1992, WARD 1992), as was observed in this study.

The variance partitioning technique used in this paper permitted a quantification of "pure habitat type-related" variation, which substantially increased our capacity to predict insect community structure. This ecological information could have been classified as "unexplained variation" if we would have used only a simple RDA analysis (BORCARD et al. 1992). We identified particular habitat type-insect associations not related to the measured environmental variables despite of the broad taxonomic level here examined. Water striders were positively associated with ponds and mangroves, the protoneurid damselflies did with mangroves, the small minnow mayflies were linked to ponds, and finally the common skimmers (Libellulidae), the spreadwinged damselflies (Lestidae) and the common burrowers (Ephemeridae) were related with brackish herbaceous swamps. Unmeasured factors such as species-specific life histories, habitat selection behavior, local community and population dynamics, small-scale temporal and spatial variation or other abiotic and biotic variables could be explaining this insect-habitat relationship. For example, the spatial arrangement of the habitat within the landscape could largely influence the rates of colonization and dispersion of insects among habitats in these wet-

lands and explain the spatial distribution of some taxa. An experimental approach and a better insect taxonomic resolution are needed to account for these pure habitat type-related variation in the community.

Finally, the wetland type and environmental variables used seem to have higher predictive power of insect distribution in the dry season than in the rainy season. This could be understandable, in part, because during the dry season the phytoplankton had a significant effect on taxa distribution as we mentioned before. On the other hand, concerning the wetland type, this could be comprehensible because during the dry season habitats are more limited and the insect populations are more aggregated in few places than during the rainy season. Our results illustrate the importance of a temporal and spatial scale approach to characterize different aspects of community structure.

In summary, the fraction of the total variation of the community that could be attributed to the environmental and wetland type-related factors together supported our hypothesis that multiple factors varying among habitats and seasons determine the broad-scale spatial patterns of aquatic insects in these wetlands.

Acknowledgements

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Appendix 1. List, code and occurrence (+, −) of the insect taxa collected during the rainy (left) and dry (right) season sampling in the northern Venezuela wetlands.

Taxon	Code	Bhs	Fhs	Pond	Mang	Ccmf	Canal	Sf
Diptera								
Culicidae*	Culi	+, +	+, +	+, +	+, +	+, /	+, +	+, +
Dixidae*	Dixi	−, −	−, −	−, −	−, −	−, /	−, +	−, −
Chironomidae*	Chir	+, +	+, +	+, +	+, +	+, /	+, +	+, +
Ceratopogonidae*	Cera	+, +	+, +	+, +	+, +	+, /	+, +	+, +
Tipulidae*	Tipu	+, −	−, −	+, +	−, +	−, /	−, +	+, −
Stratiomyidae*	Stra	+, +	+, +	+, +	+, +	+, /	+, +	+, +
Ephydridae*	Ephy	+, −	+, +	−, −	+, −	−, /	−, +	−, +
Psychodidae	Psyc	−, −	+, −	−, −	+, −	+, /	−, +	−, −
Sciomyzidae	Scio	−, −	−, +	−, −	−, −	−, /	−, −	−, −
Empididae	Empi	−, +	−, −	−, −	−, −	−, /	−, −	−, −
Muscidae	Musc	−, −	−, −	−, −	−, −	−, /	−, +	−, −
Coleoptera								
Noteridae*	Note	+, +	+, +	+, −	+, −	+, /	+, −	+, +
Dytiscidae*	Dyti	+, +	+, +	+, +	+, +	+, /	+, +	+, +
Hydraenidae*	Hydra	+, +	+, +	−, −	−, +	−, /	+, +	−, −
Hydrophilidae*	Hydro	+, +	+, +	+, +	+, +	+, /	+, +	+, +
Helodidae*	Helo	+, +	+, +	+, −	+, −	+, /	+, +	+, −
Elmidae	Elmi	−, +	−, −	−, −	−, −	−, /	−, −	−, −
Chrysomelidae	Chry	−, −	−, +	−, −	−, −	−, /	−, +	−, −
Hemiptera								
Mesoveliidae*	Meso	+, +	+, +	+, +	−, +	−, /	+, +	−, −
Veliidae*	Veli	+, +	+, +	+, +	+, +	+, /	+, +	+, +
Nepidae*	Nepi	−, +	−, +	−, −	−, −	−, /	−, +	−, −
Gerridae*	Gerr	−, −	−, +	+, +	−, +	−, /	+, +	+, +
Notonectidae*	Noto	−, +	+, −	+, +	−, −	+, /	−, −	+, −
Pleidae*	Plei	+, +	+, +	+, +	−, −	+, /	+, +	+, −
Belostomatidae*	Belo	+, +	+, +	+, −	+, −	+, /	+, +	+, +
Naucoridae*	Nauc	+, +	+, −	−, +	−, −	−, /	+, −	−, −
Hebridae*	Hebr	+, +	+, +	+, −	−, −	−, /	+, +	+, +
Hydrometridae*	Hydrom	+, +	+, −	+, −	−, −	−, /	+, +	+, +
Corixidae*	Cori	−, +	+, −	−, −	−, −	−, /	+, +	+, −
Odonata								
Coenagrionidae*	Coen	+, +	+, +	+, +	−, −	+, /	+, +	+, +
Lestidae	Lest	+, +	−, −	+, −	−, −	−, /	−, −	−, −
Protoneuridae*	Prot	+, +	+, +	+, −	−, −	−, /	−, −	−, −
Corduliidae*	Cord	+, +	+, +	+, +	−, −	−, /	+, +	+, +
Libellulidae*	Libe	+, +	+, −	+, −	+, −	−, /	+, −	−, −
Aeshnidae	Aesh	−, −	−, −	+, −	−, −	−, /	−, −	−, −
Ephemeroptera								
Baetidae*	Baet	−, +	−, +	−, +	−, −	−, /	+, +	−, +
Ephemeridae*	Ephe	−, +	−, +	+, +	−, −	−, /	+, +	−, +
Trycoridae*	Tryc	−, −	−, +	−, −	−, −	−, /	−, +	−, −
Number of taxa		23, 28	24, 25	24, 17	13, 11	14, 0	23, 28	20, 17

* Taxa retained in the analysis (those comprising > 5 % of occurrence).
(/) Wetlands not sampled during the dry season sampling.