Community structure of Neotropical wetland insects in Northern Venezuela.
I. Temporal and environmental factors

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With 3 figures, 3 tables and 1 appendix

Abstract: The temporal distribution of aquatic insects in relation to habitat conditions was assessed in some northern Venezuelan Neotropical wetlands. The hypothesis that abiotic and biotic factors interacting in time may simultaneously explain the community structure of aquatic organisms was evaluated. Larval insects were sampled over a one-year period in five wetland types; 13 variables were quantified to describe each habitat. Partial redundancy analysis was used on insect abundance data to partition the variance into four components: a) pure environmental variation without seasonal effect, b) seasonal variation of environmental factors, c) pure temporal factors (months), and d) unexplained variation. Our results showed that pure and temporally-structured environmental factors (a + b) explained between 30 % and 58 % of the variation of insect abundances within wetlands, whereas pure temporal factors also significantly contributed 13 % – 29 % to variation in taxa abundance. Physical factors (rainfall and water depth), wetland trophic state (phytoplankton), and water chemistry (mainly CO_2 and alkalinity) were significantly associated to community structure variability. We hypothesize that the interplay of trophic conditions, related chemical conditions, wetland duration, and insect life history patterns, all of which are mediated by seasonal fluctuation in rainfall, could largely account for the temporal distribution of the insect taxa in these wetlands.

Key words: Aquatic insects, temporal distribution, redundancy analysis, variance partitioning.

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Introduction

The interplay between physical factors (such as hydroperiod, habitat hetero-geneity, and/or physicochemical conditions) and biotic processes (such as predation) is known to influence local assemblages of wetland insect species in temperate ecosystems (BATZER & WISSINGER 1996, BATZER et al. 1999). It is uncertain whether these generalizations apply to neotropical populations be-cause few comparative data exist (e.g., HECKMAN 1998). Wetlands offer abun-dant, productive and extremely diverse habitats for insects, including pest and disease vector species (HECKMAN 1998, GRILLET 2000). However, in the Neo-tropical region, research on the ecology of such water bodies has lagged be-hind that of other natural inland aquatic ecosystems (HECKMAN 1994).

An assessment of the relative importance of biotic and abiotic factors influ-encing wetland communities should also consider the inherent spatial and tem-poral variation of natural assemblages (LEGENDRE 1993). For example, life cy-cles of invertebrates in Neotropical wetlands are profoundly influenced by the hydrological cycle produced by annual fluctuations in rainfall (HECKMAN 1998). Thus, temporal changes in community structure should be, in part, un-derstood in terms of species strategies for coping with this seasonal variation in habitat (WIGGINS et al. 1980). In addition, the analysis of such data should account for the overlap between seasonal and environmental variation in rela-tion to observed distributional patterns. Several analytical approaches have been developed to consider the spatial and temporal variability in the study of species-environmental relationships (e.g., TER BRAAK 1988, BORCARD et al. 1992, DOLÉDEC & CHESSEL 1994, FRANQUET et al. 1995). In particular, BOR-CARD et al. (1992) developed a quantitative statistical approach to this prob-lem, using canonical ordination techniques, in which the variation of the com-munity structure attributable to environmental and spatial components can be partitioned into: a) pure environmental variation, b) spatial component of the environmental variation, c) pure spatial variation, and d) undetermined varia-tion. The variation partitioning method has recently been extended to include more than two explanatory variables (ANDERSON & GRIBBLE 1998). Few pa-pers have applied this method to the assessment of aquatic invertebrate com-munities (RODRIGUEZ & MAGNAN 1993, PINEL-ALLOUL et al. 1996, VERSCHU-REN et al. 2000).

The present study was conducted to determine the temporal (monthly data collected at a single habitat) and habitat type-related (many sites sampled once at a specific time) variation in the distribution of aquatic insects in several wetlands in northeastern Venezuela. We used the approach of BORCARD et al. (1992) to test the hypotheses that, at the scale of the study, insect distributions are non-random, and understandable by the relative contributions of wetland abiotic and biotic conditions, season and habitat type. In this paper, we present

results of temporal distribution analyses, whereas the results on habitat type-related variation will be presented in a companion paper. This work was undertaken as part of a larger research effort aimed at characterizing the wetland insect fauna in northeastern Venezuela (GRILLET et al. 1998, GRILLET 2000). Because insects play an important trophic role in wetland ecosystems (MURKIN 1989, BATZER & WISSINGER 1996, BATZER et al. 1999), the processes documented here should contribute to an understanding of factors influencing Neotropical aquatic insect communities, forming the basis for future ecological studies.

The specific objectives of this study were to: 1) characterize the physico-chemical, structural (physical features of the habitat such as depth and aquatic vegetation type), and biotic factors of different wetland types; 2) describe seasonal patterns of insect abundance in different wetland types; and 3) identify the factors that influence the abundance and distribution of insects in these wetlands.

Methods

Study site

The study area, vegetation, and physical and chemical features of the wetlands were described in detail by GRILLET (2000); only a brief description is given here. The study was carried out in the southern coastal lowland areas of the Paria peninsula (10° 17′ N, 63° 57′ W), 0–10 km from the littoral zone, in Sucre State, northeastern Venezuela. Mean annual temperature is 27–28 °C and total annual rainfall is 1200–1700 mm, with a rainy season from May to November and a dry season from December to April. Maximum water levels in lentic ecosystems occur after heavy rains in September–November. Water levels are at their lowest at the end of the dry season (March–April). Thus, four water-level periods during a year can be recognized in the study area: a) early rainy season (May–August) when flooding first occurs; b) late rainy season (September–November) when the highest water levels occur; c) early dry season (December–February) when the water level rapidly decreases because of diminished rainfall and runoff; and d) late dry season (March–April) when the flood plain progressively dries. The vegetation of the area is mostly composed of deciduous forests, a relatively undisturbed area of coastal mangroves, and herbaceous or woody swamps (HUBER & ALARCÓN 1988).

Habitat types

In a previous work (GRILLET 2000), five wetland types were selected for the study as a representative subset of contrasting natural wetlands prevailing in this region. Wetland classification was based on a combination of dominant aquatic vegetation type (species with >60 % of vegetation cover), water salinity, and the seasonal pattern of the water level (hydroperiod) of the habitat. Hydroperiod was determined as the number of

months per year the habitat contained any standing water. Permanent wetlands were wet all year. Seasonal wetlands were dry for 3 or 4 months each year. Temporal wetlands were dry for 6–8 months each year. Categories of salinity for wetlands were: freshwater, oligosaline, mesosaline, and polysaline and refer to saline contents of <0.5, 0.5 to 5, 5.1 to 18, and >18 ppt, respectively (WETZEL & LIKENS 1991). Most of the studied wetlands were generally shallow, having a mean depth <1 m and they were called brackish and freshwater herbaceous swamps, ponds, mangrove swamps and clear-cut marsh forests (FANSHAWE 1952). The individual wetland categories can be briefly characterized as follows. Mangroves *(Mang)* were mesosaline and polysaline seasonal swamps with a partially closed canopy of mangroves trees of *Avicennia germinans, Rhizophora mangle* and *Laguncularia racemosa.* Brackish herbaceous swamps *(Bhs)* were oligosaline and mesosaline permanent extensive swamps dominated by the *Eleocharis mutata* emergent cyperaceous communities. Freshwater herbaceous swamps *(Fhs)* were permanent and seasonal wetlands composed of dense patches of the emergent dominant species *Typha dominguensis.* Ponds *(Pond)* were permanent and seasonal freshwater bodies with a high diversity of aquatic vegetation, composed by emergent vegetation such as *Cyperus* spp., *Typha dominguensis, Colocasia* spp. and *Ludwigia affinis,* and floating and submersed vegetation, mostly of Lemnaceae, *Nymphaea* spp. and filamentous algae. Finally, the clear-cut marsh forests *(Ccmf)* were temporal marshes of *Colocasia* spp. during the rainy season, with dense cover of floating vegetation such as *Lemna* spp. and *Pistia* spp. Overall, the *Mang* habitats were the most saline wetlands, with high dissolved carbon dioxide and phytoplankton, and with fewer aquatic macrophytes. *Pond* wetlands were the warmest and most oxygenated habitats, with high phytoplankton abundance, and low CO_2 and alkalinity. *Fhs* habitats were deeper with more emergent vegetation than the other habitats (Table 2, GRILLET 2000).

Sampling design

To determine the temporal (within-year) distribution of aquatic insects, sampling was performed at 10 sites, two in each wetland type *(Mang, Bhs, Fhs, Pond* and *Ccmf),* at approximately three-week intervals over a 14 month period (July 1993–August 1994) as long as sites had water. Previously (GRILLET M. E., unpublished data), we found that a long-handled ladle or dipper (SOUTHWOOD & HENDERSON 2000) was effective in capturing active, free-swimming aquatic insects from the water surface as well as those living near the macrophytes or in the water column of the littoral region of the very shallow and vegetated wetlands (depth <1 m). Dippers could be used to compare these communities between habitats provided the samples were taken in great number (n = 30 samples). Thus, samples were taken along a transect extending through the littoral region and at less than 2 m from the shore by dipping the water column to a depth of 0.5 m. The number of individuals per dip was calculated from 30 dips (replicates) from each collection site. Dipping was always done by the same person. In the field, the water volume of each dip was sieved (pore size = 0.5 mm), and the collected individuals preserved in 80 % ethanol. In the laboratory, the samples were washed, emptied into sorting trays and the insects removed, counted and identified. Since there are

no reliable taxonomic keys for neotropical aquatic insects, invertebrates were identified to family using North American taxonomic keys (MERRITT & CUMMINS 1984).

Environmental variables

Each time a site was visited, 11 environmental variables were measured prior to insect sampling. These variables were: 1) aquatic vegetation or macrophyte cover (n = 6 replicates; 0.5 × 0.5 m quadrats; Braun-Blanquet method, MUELLER-DUMBOIS & ELLENBERG 1974), 2) mean height of emergent vegetation above the water surface (n = 6), 3) water chlorophyll-*a* content (WETZEL & LIKENS 1991), 4) mean water depth (n = 6), 5) temperature (n= 6), 6) pH, 7) salinity, 8) conductivity, 9) alkalinity, 10) dissolved oxygen and, 11) dissolved carbon dioxide. Water chemistry estimates were means based on six water samples taken at each wetland. Portable field meters were used for pH (Model 5996–70, Cole Palmer), salinity, conductivity and water temperature (Model 33, YSI). Chemical Kits (Standard LaMotte®, LaMotte Chemical Products Company) were used for dissolved oxygen, dissolved carbon dioxide, and alkalinity. Phytoplankton density was estimated by measuring the chlorophyll-a concentration at each collection site from a 500 mL sample of water taken 30 cm below the surface in a plastic bottle. Chlorophyll-*a* was concentrated using two Whatman (membrane filter pore size = 0.45 μm) GF/F filters and stored at 4 °C in the dark. It was extracted from filters using 90 % methanol (for freshwater samples) or acetone (for saline water samples). Rainfall data were supplied by the metereological station closest (15 km) to the study area.

Data analyses

To test for an interaction between the factors time (months) and wetland type (different habitats) on the response variables (taxa abundance data), we used distance-based redundancy analysis (db-RDA, LEGENDRE & ANDERSON 1999). This is a nonparametric multivariate technique for testing the significance of individual terms in a multifactorial analysis of variance model for multispecies response variables. The technique uses permutation tests and thus is free of the assumption of multivariate normality required by parametric MANOVA. It is based on the known method of redundancy analysis (RDA) but allows the analysis to be done on measures of association (distance measures such as the Hellinger distance, see LEGENDRE & GALLAHER 2001) through the use of a previous principal coordinate analysis (PcoA, see LEGENDRE & ANDERSON 1999). A significant interaction ($P < 0.05$) was detected between months and habitats, indicating that there were significant seasonal differences in insect abundances in the wetlands and that they varied according to habitat type. Therefore, all statistical analyses hereafter were performed separately for each wetland type (samples from 2 habitats per wetland type were combined) to focus on temporal variation and avoid confounding effects of habitat type on community structure.

Insect community structure was related to environmental variables using RDA. This is a canonical technique used in ecology for ordination by direct gradient analysis, where a matrix of species variables or response variable, Y, is analyzed with regard to a corresponding matrix of environmental or explanatory variables, X (LEGENDRE &

LEGENDRE 1998). In addition, partial RDA was used to determine if the variation of the response variable could be attributed to the set of factors previously chosen as explanatory variables, once the effect of other undesired variables (matrix W, co-variables) had been removed from the analysis (LEGENDRE & LEGENDRE 1998). RDA is recommended for the analysis of sites representing short ecological gradients where a linear relationship between species and environmental factors is assumed (TER BRAAK & SMILAUER 1998, LEGENDRE & LEGENDRE 1998). We corroborated that the length of the gradient of our data was short (<4.0 standard deviation units) through the use of a detrended correspondence analysis (DCA, TER BRAAK & SMILAUER 1998). In the full-dimensional space, the RDA preserves the Euclidian distance among sites which is an inappropriate distance for raw species abundance data involving null abundances (LEGENDRE & LEGENDRE 1998). For that reason, LEGENDRE & GALLAGHER (2001) propose to transform the species data matrix (matrix Y), previous to the use of the RDA, in such way that the Euclidean distance computed among sites of the new matrix (matrix Y′) results in some other distance more appropriate to species abundances. The net result is an ordination that will preserve the said distances among sites while retaining the identity of individual species in biplots. In the present work, the Hellinger distance was used for transforming the taxa abundance data, previous to the use of RDA (LEGENDRE & GALLAGHER 2001).

For each wetland type, three types of matrices were created: a) the transformed taxa abundance matrix, Y′ (taxa x samples, where samples = no. dips per habitat x 2 habitat per wetland type x no. of sampled months per wetland); b) the matrix X of environmental data (composed of the abiotic and biotic variables); and c) the matrix of temporal descriptors, W (composed of the pure temporal factors, with months coded as dummy variables). A series of simple and partial RDA were performed to partition the variation of the insect data (matrix Y′) between the environmental (matrix X) and temporal (matrix W) explanatory variables, following BORCARD et al. (1992). *Step 1.* The total variation in the insect data explained by the environmental and temporal variables (component $a + b + c$) was obtained by running a simple RDA on the Y′ matrix constrained by a matrix containing the variables of matrices X and W. The variation explained by neither the temporal nor the environmental variables (the residual variation, component d) was calculated as $d = 1-(a + b + c)$. *Step 2.* We partitioned the explained total variance into three components corresponding to: 1) the environmental variation independent of any temporal structure (component a), which was estimated by performing a partial RDA on matrix Y′ constrained by matrix X while controlling for the influence of month (matrix W); 2) the temporal patterns in the insect data that were not shared by the environmental data (component c); estimated as the variation explained by a partial RDA of matrix Y′ constrained by matrix W, and using matrix X as co-variables; 3) the temporal structure in the insect data shared by the environmental factors was calculated as $b = [(a + b + c) - a - c]$. The computer program CANOCO 4 (TER BRAAK & SMILAUER 1998) was used for all the analyses. We used a forward selection procedure, where the most significant variables ($P < 0.05$) were incorporated in the analysis. For each analysis, the statistical significance of the overall model (relationship between the set of variables and the taxa abundances) was tested using 999 Monte Carlo permutations tests and the value of the sum of all canonical eigenvalues was recorded (TER BRAAK & SMILAUER 1998).

Results

Temporal changes in the habitat

Wetlands exhibited an annual cycle of rain with flooding and either seasonal drying (non-permanent habitat) or low-lying water (permanent habitats), characterized by eutrophic conditions. At the beginning of the rainy season, there was an increase in dissolved CO_2 levels and conductivity in the water, followed by a progressive growth of macrophytes. Throughout this period, the water became clear due to the absence of phytoplankton and suspended matter and decreasing levels of free inorganic nutrients. During the late rainy season, water depth increased, and there was an additional decline in the concentrations of inorganic nutrients and levels of dissolved oxygen. Throughout the dry season (early and late period), water level and dissolved CO_2 rapidly decreased, whereas levels of conductivity, phytoplankton, and (as a consequence of the latter) alkalinity and DO gradually increased. The macrophyte cover and height of emergent vegetation increased as the dry season progressed, followed by the death and decay of these plants at the end of the period.

Insect community structure, temporal variation and general ordination

A total of 24,483 individuals belonging to 43 taxa were collected; however, a maximum of 31 taxa was considered in the analyses (Appendix). The total mean density of insects ranged from 8 (*Ccmf* habitat) to 301 (*Mang* habitat) individuals/sample among wetlands. The fauna was dominated in abundance and occurrence by Diptera, specifically Culicidae and Chironomidae. The highest insect density (16,790 individuals in total) was recorded at the *Mang* wetland during the late rainy season (October).

The RDA ordination of samples in relation to the insect families reflected the difference in taxa composition among the four periods of the year (Fig. 1). Overall, 21 taxa were well-represented in the ordination diagram, which meant that more than 20 % of their variance was accounted for, with the number of taxa being low at the start of the rainy season, increasing during the late rainy and early dry season, and then rapidly decreasing during the late dry season (Fig. 1 a–d). Culicidae dominated during the early rainy season, whereas the Chironomidae (dry-rainy or rainy-dry season) and Stratiomyidae (rainy-dry season) occurred mostly during the transition periods between seasons and the dry season (Fig. 1 a–e). Additionally, mosquitoes (Culicidae) were also associated with the rainy-dry season transition period in the *Ccmf* temporal habitat (Fig. 1 e) and the early dry season (January) in the *Pond* habitat (Fig. 1 c). Tipulidae, Ceratopogonidae, Hydrophilidae, Dytiscidae, Helodidae, Belostoma-
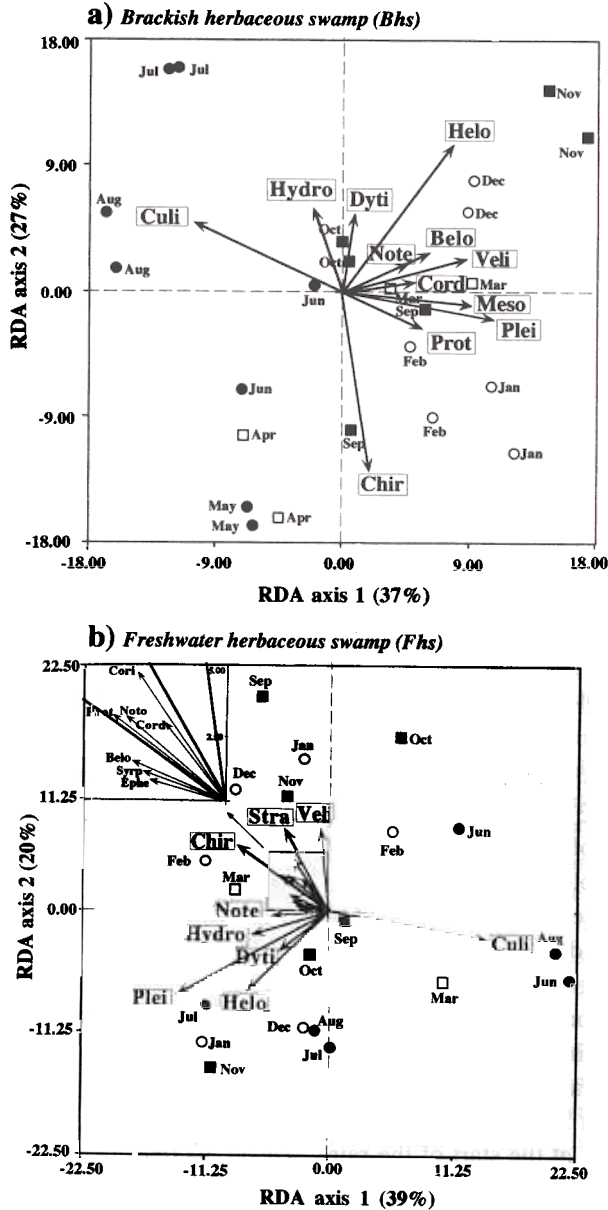
Fig. 1. a + b. Legend see page 422.

tidae and Libellulidae, had high abundances mostly during the rainy season, whereas the remaining taxa (except in *Ccmf*) were mainly associated with the dry season (Fig. 1 a–d). Moreover, Ceratopogonidae (Pond *habitat*) and Helodidae (*Pond* and *Mang* wetlands) were also associated with the dry season.
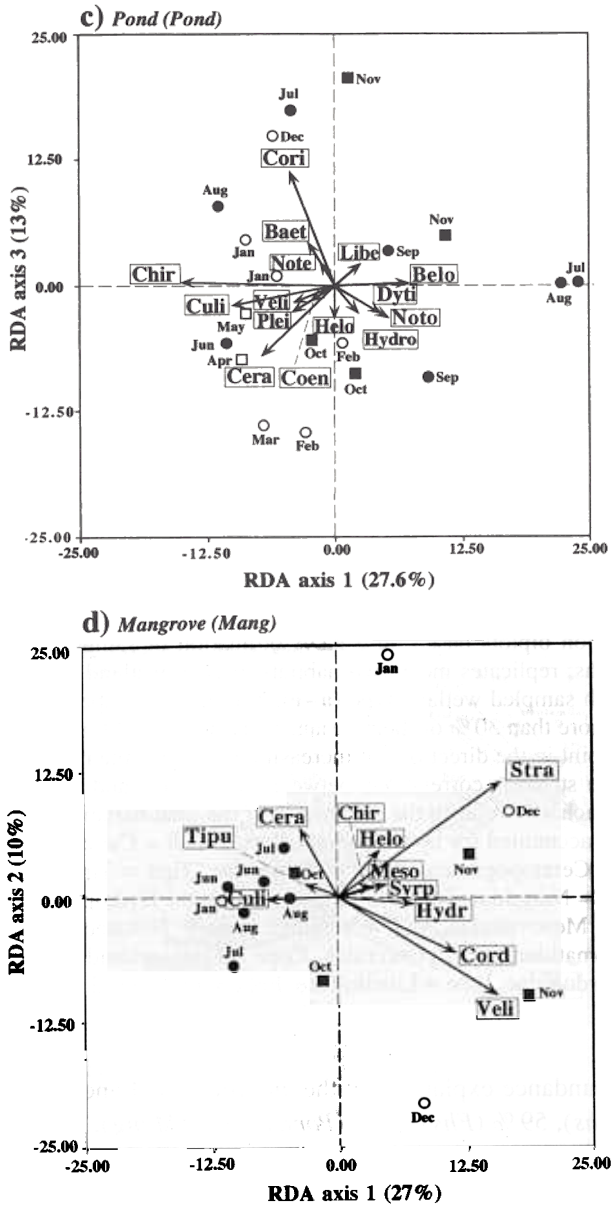
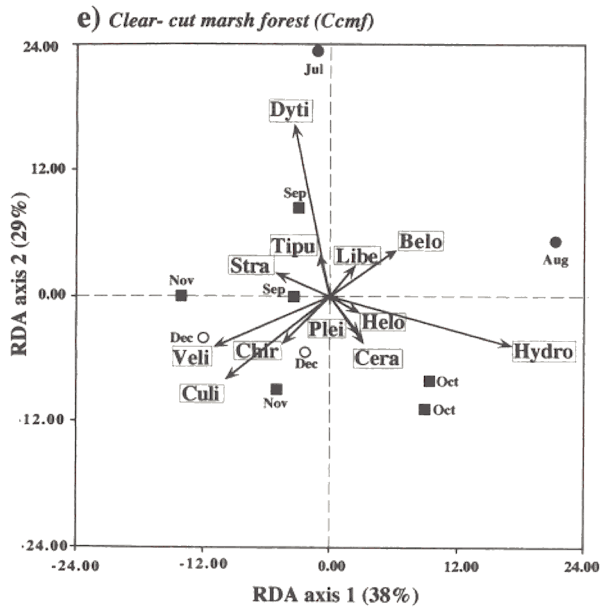**c)** *Pond (Pond)*

d) *Mangrove (Mang)*

Fig. 1. c + d. Legend see page 422.

An overall permutation test of significance based on the sum of all canonical eigenvalues showed that the relationship between insect abundance and the environmental and temporal factors was highly significant (all $P<0.001$) in the five wetlands (Fig. 2). For each of these analyses, the amount of variation

Fig. 1. Correlation biplots based on a RDA ordination of sampling sites (symbols = sampling months; replicates mean two habitats of each wetland type) and insect taxa (arrows) in each sampled wetland type (a–e). The displayed species were selected on the basis that more than 30 % of their variance was accounted for by the diagram. Vectors (arrows) point in the directions of increasing values for the respective taxa; longer vectors indicate stronger correlations between taxa scores and axes. The percentage reported with each axis refer to the percentage of the total variation in the insect abundance which is accounted for by the canonical axis. Culi = Culicidae, Chir = Chironomidae, Cera = Ceratopogonidae, Syrp = Syrphidae, Tipu = Tipulidae, Stra = Stratiomyidae, Note = Noteridae, Dyti = Dytiscidae, Hydro = Hydrophilidae, Helo = Helodidae, Meso = Mesoveliidae, Veli = Veliidae, Noto = Notonectidae, Plei = Pleidae, Belo = Belostomatidae, Cori = Corixidae, Coen = Coenagrionidae, Prot = Protoneuridae, Cord = Corduliidae, Libe = Libellulidae, Ephe = Ephemeridae.

in the taxa abundance explained by the environmental and temporal variables were 42 % (*Bhs*), 59 % (*Fhs*), 57 % (*Pond*), 48 % (*Mang*), and 58 % (*Ccmf*) of the total variation of these taxa. RDA analyses with forward selection of the selected predictor variables indicated that nine environmental factors (rainfall, water depth, phytoplankton, alkalinity, oxygen, CO_2, conductivity, temperature, and macrophyte cover) and several months influenced significantly the insect community structure in all the wetlands (Fig. 2). Likewise, the first two canonical axes (and the third one for the *Pond* habitat) in each model were all significant (Fig. 2, all $P < 0.05$). Overall, taxa that dominated the ordination were Culicidae, Chironomidae, Ceratopogonidae, Stratiomyidae, Helodidae, Pleidae, Dytiscidae, Hydrophilidae, Corixidae, Veliidae, and Corduliidae.
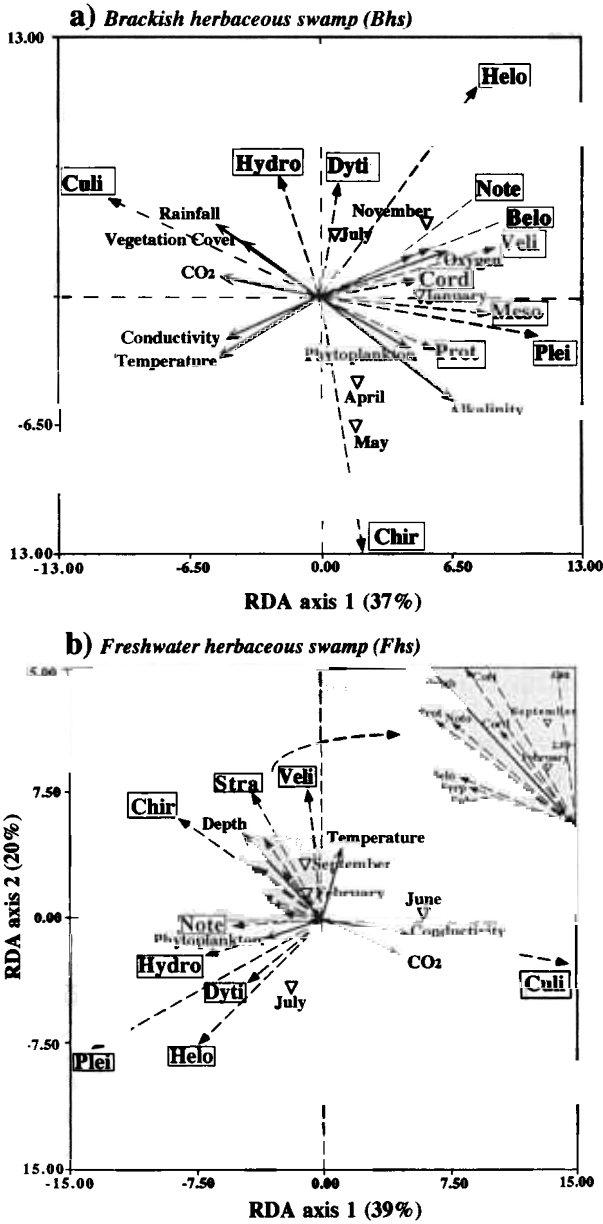
Fig. 2. a + b. Legend see page 425.

In the *Bhs* wetland (Fig. 2 a), the first axis arranged samples and insect families based on two gradients mostly related with water chemical and trophic conditions. Samples to the left end of the ordination were related to
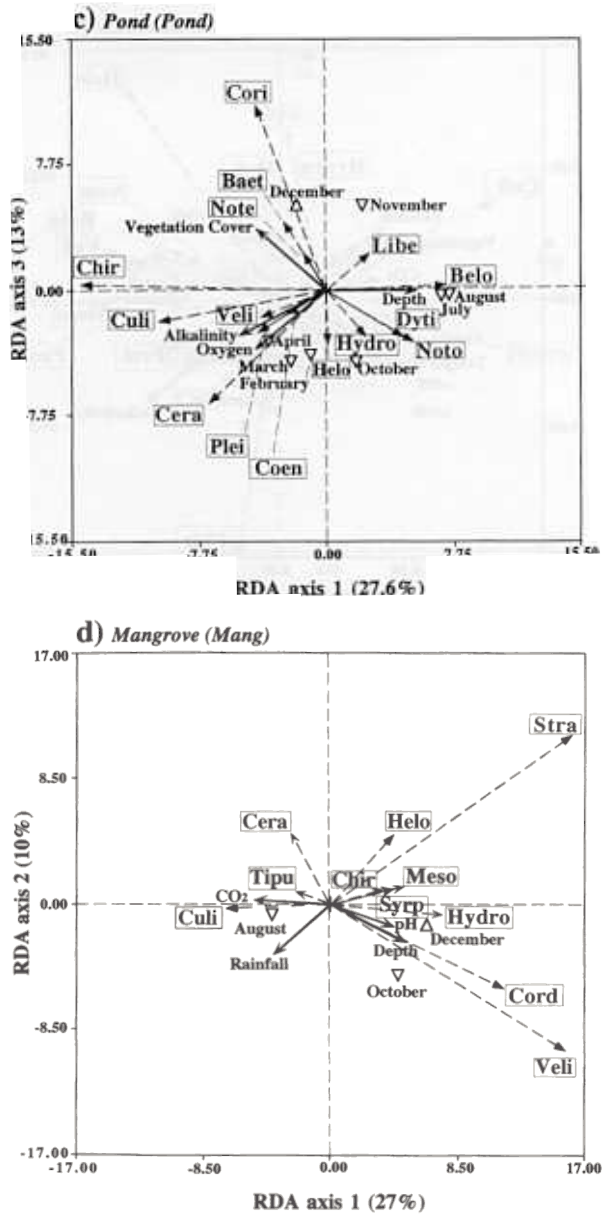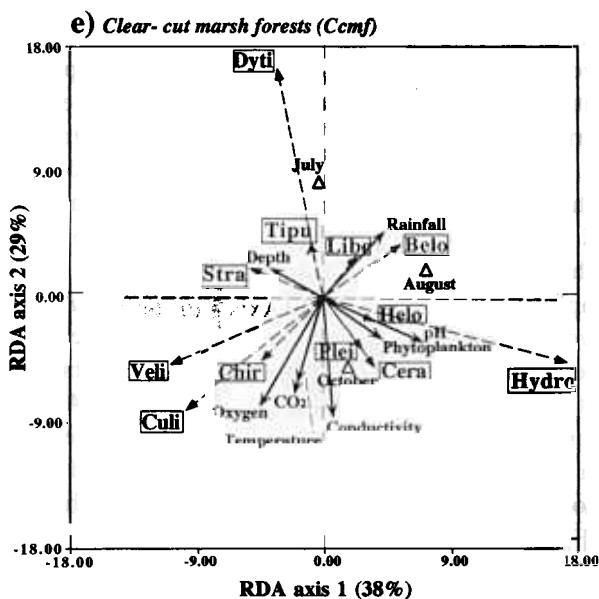
Fig. 2. c + d. Legend see page 425.

high levels of vegetation cover, CO_2, low values of phytoplankton and alkalinity during the rainy months. Culicidae were positively associated with this first wetland condition. Conversely, samples at the opposite end were more asso-

Fig. 2. Correlation biplots based on a RDA ordination of insect abundance (dashed arrows) and the environmental (solid arrows) and temporal factors (triangles) in each type of sampled wetland (a–e). Quantitative and qualitative variables are indicated by arrows and triangles, respectively. Only the environmental factors retained in each model by the forward selection procedure ($P < 0.05$) are shown. Vectors (arrows) point in the directions of increasing values for the respective variables; longer vectors indicate stronger correlations between variables scores and axes. By inspection of the angles between arrows, one may visualize the correlation between taxa abundance and environmental variables. Culi = Culicidae, Chir = Chironomidae, Cera = Ceratopogonidae, Syrp = Syrphidae, Tipu = Tipulidae, Stra = Stratiomyidae, Note = Noteridae, Dyti = Dytiscidae, Hydro = Hydrophilidae, Helo = Helodidae, Meso = Mesoveliidae, Veli = Veliidae, Noto = Notonectidae, Plei = Pleidae, Belo = Belostomatidae, Cori = Corixidae, Coen = Coenagrionidae, Prot = Protoneuridae, Cord = Corduliidae, Libe = Libellulidae, Ephe = Ephemeridae.

ciated with high levels of oxygen but low values of conductiviy and temperature during November and January, and a number of families belonging to the Coleptera, Hemiptera, and Odonata were positively correlated with this second habitat gradient. Along the RDA axis 2, Chironomidae grouped to the bottom of the diagram and were associated with the months of April and May, whereas the coleopterans (Hydrophilidae and Dytiscidae) were correlated with the month of July at the top of the ordination.

The first RDA axis in *Fhs* separated the samples with high levels of conductivity and CO_2 in the water during June from samples with increasing values of phytoplankton (Fig. 2 b). Culicidae were positively related to conductivity and CO_2, whereas a group of taxa (at the left side of the ordination) showed

a positive relationship with phytoplankton. A gradient related mainly with the depth of the wetland was described by the RDA axis 2, separating the deeper and warmer sites during September and February from the shallow and less warm sites during July. Abundances of Chironomidae, Stratiomyidae, Veliidae, Corixidae, Notonectidae, Protoneuridae, and Corduliidae were positively associated with the water depth and temperature, whereas the coleopterans Dytiscidae and Helodidae were associated with the month of July.

Water depth and the months of July and August were most important in separating samples and insect taxa along Axis 1 of the *Pond* wetland (Fig. 2 c). Vegetation cover, alkalinity, oxygen level, the rainy-dry season transition period (November and December), and the dry season (February–April) were most important in arranging samples and insect taxa along Axis 2.

In the seasonal *Mang* wetland (Fig. 2 d), ordination largely showed the difference in taxa composition between the more alkaline and deeper sites at the late rainy season and the sites with high levels of CO_2 at the beginning of the rainy season. Families belonging to the Diptera were positively associated to the high levels of CO_2 during August, whereas the remaining taxa were linked to high levels of depth and alkalinity during October and December.

The first axis, in the temporal *Ccmf* wetland (Fig. 2 e), arranged samples and taxa mostly along a trophic gradient. Abundances of some families belonging to the Coleoptera and the Ceratopogonidae characterized the more alkaline, shallow and eutrophic water conditions, whereas the Stratiomyidae and Veliidae showed a negative relationship with this gradient. Ordination axis 2 represented a physico-chemical and rainy gradient, where Culicidae, Chironomidae and Veliidae were positively linked to levels of oxygen, CO_2, temperature and conductivity at the late rainy season (October), whereas the abundances of Dytiscidae, Tipulidae, Libellulidae and Belostomatidae were negatively correlated with this chemical condition at the beginning of the rainy season (July).

Partial ordination and associated factors

The total environmental contribution (component $a + b$: 29 %, 30 %, 29 %, 29 %, and 58 % for *Bhs, Fhs, Pond, Mang*, and *Ccmf*, respectively) was significant ($P < 0.001$) and similar in all cases except by *Ccmf* (Fig. 3). The pure contribution of the environmental variables (component a) in the variation of insect data in each type of wetland also was significant ($P < 0.001$) and ranged from 12 % (*Bhs*) to 29 % (*Fhs*). Likewise, the pure temporal contribution (component c) was significant ($P < 0.001$); except for the non-permanent *Ccmf* habitat where component c was lacking, ranging from 12 % (*Bhs*) to 29 % (*Fhs*). Component b means the fraction of variation of insect taxa explained by the environmental variables, which is temporally structured. It may be
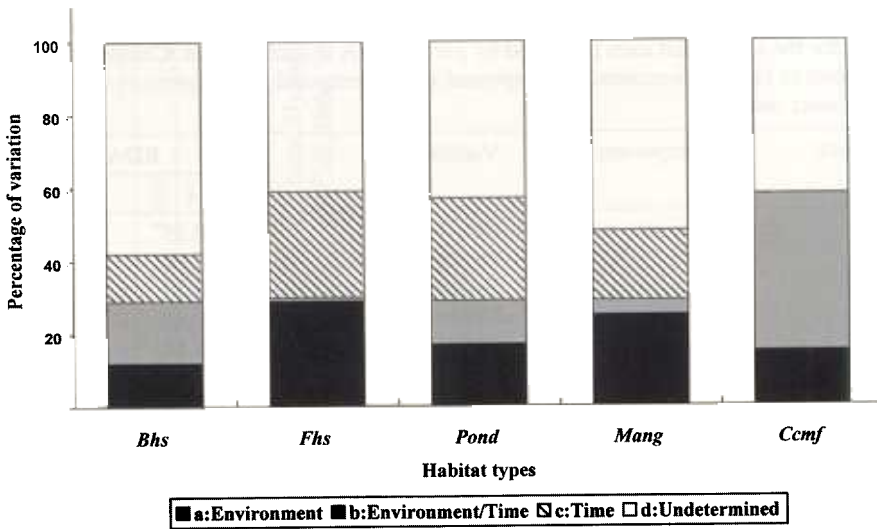
Fig. 3. Variation partition of the insect data matrix in the different wetland types studied in northern Venezuela. Environmental variation independent of any temporal structure (component a), temporal structuring in the insect data shared by the environmental factors (component b), temporal patterns not shared by the environmental data (component c), and unexplained variation (component d).

equally attributed to the environmental or the temporal variables (months). The amount of unexplained variation (41 % to 52 %) indicated that other external factors, not taken into account in our study, were also important in influencing the insect assemblages in these wetlands.

The main results of the partial ordination of the insect taxa in each type of wetland are shown in Tables 1, 2 and 3. The environmental and temporal variables retained in each model are in Table 1: for component (a) (after removing the temporal factors) and for component c (after partialling out the environmental variables). The insect taxa discriminated either in component a or c are shown in Tables 2 and 3, respectively. These results allowed us to identify: i) true ecological and seasonal gradients that remained even after partialling out the effect of time or habitat variables, and/or ii) new gradients that appeared when we removed either the environmental or seasonal effects. As an example, in *Bhs*, there were only three significant environmental variables (phytoplankton, CO_2, and temperature) retained in the model for obtaining component a (Table 1), compared with those seven variables included in the model for obtaining component $a + b + c$ (Fig. 2 a). However, the results corroborated the importance of the trophic-chemical gradient in explaining the taxa variation. Regarding the pure temporal variation in the *Bhs* wetland, the months and the insect families selected in the model for obtaining component

Table 1. Inter-set correlation coefficients of forwardly selected environmental variables for the significant axes produced by partial RDA in each habitat. Components correspond to pure environmental (component a) and temporal (component c) variation in the insect data.

Habitat	Component	Variables	RDA axis	
			I	II
Bhs	a	CO_2		
		Phytoplankton		
		Temperature		
	c	December		
		April		
		June		
		January		
		October		
		July		
Fhs	a	Vegetation Cover		
		Depth		
		Temperature		
		Phytoplankton		
		CO_2		
		Conductivity		
	c	July		
		August		
		September		
		October		
		February		
		June		
Pond	a	Depth		
		Conductivity		
		Alkalinity		
		Phytoplankton		
		Temperature		
		August		
		October		
		November		
		April		
		December		
		February		
Mang		Oxygen		
		Temperature		
		Depth		
		October		
		December		
		January		
		June		
Ccmf	a	Phytoplankton		
		Depth		

Bhs = Brackish herbaceous swamp; Fhs = Freshwater herbaceous swamp; $Pond$ = Pond; $Mang$ = Mangrove; $Ccmf$ = Clear-cut marsh forest.

Table 2. Summary of the insect families responding positively (+) or negatively (−) to the different environmental variables, as identified in the partial ordination of the taxa against environmental variables while controlling for the temporal (months) variables. This analysis extracts component (*a*) of the examined variation. For insect taxa codes see Fig. 1.

Variables	Bhs	Fhs	Pond	Mang	Ccmf
			Habitat		
CO$_2$	(+) Dyti, Culi (−) Veli, Plei, Chir	(+) Caen, Culi, Gerr			
Phytoplankton	(+) Hydro, Helo, Note, Coen, Cera, Syrp (−) Thau, Cord	+) Plei, Helo, Dyti, Thau, Coen, Hydro	(+) Culi, Ephe		(+) Plei, Cera, Chir Note, Hydro, Prot (−) Culi, Helo, Veli
Temperature	(+) Plei, Veli, Chir, Thau	(+) Chir, Noto, Veli Cori, Cord, Prot, Libe, Stra, Belo, Cera, Note	(+) Chir, Cord, Dyti Noto, Belo, Gerr, Prot, Helo, Cori	(+) Helo, Stra (−) Culi	
Veget. cover		(+) Caen, Culi, Gerr			
Depth		(+) Chir, Noto, Veli Cori, Cord, Prot, Libe, Stra, Belo, Cera, Note	(+) Culi, Ephe	(+) Meso, Syrp, Chir Hydro, Cera, Cord Veli	(+) Cord, Stra, Dyti (−) Cera
Conductivity		(+) Caen, Culi, Gerr	(+) Plei, Coen, Veli Stra, Cera, Prot		
Alkalinity			(+) Plei, Coen, Veli Stra, Cera, Prot		
Oxygen				(+) Culi (−) Helo, Stra	

Bhs = Brackish herbaceous swamp; Fhs = Freshwater herbaceous swamp; Pond = Pond; Mang = Mangrove; Ccmf = Clear-cut marsh forest.

Table 3. Summary of the insect families responding positively (+) or negatively (-) to the different months, as identified in the partial ordination of the taxa against months while controlling for the environmental variables. This analysis extracted component (*c*) of the examined variation. There was no significant component (*c*) in the habitat *Ccmf* (see Fig. 3). For insect taxa codes see Fig. 1.

Habitat/ Month	*Bhs*	*Fhs*	*Pond*	*Mang*
January [1]				(+) Culi, Cera
February [1]		+) Chir, Plei, Belo Thau	+) Chir. Cera	
March [2]				
April [2]	(+) Prot, Coen		+) Cera, Chir	
May [3]				
June [3]	+) Plei, Nauc, Syrp	(−) Note, Plei		(+) Cera. Chir, Culi
July [3]	+) Note, Chir, Hydro Dyti	(+) Dyti, Helo, Hydro		
August		(+) Culi	·) Thau, Veli, Helo Prot. Cord	
September [4]		(+) Veli, Prot		
October [4]	+) Helo	(−) Dyti, Helo, Hydro Note, Plei	(+) Culi, Plei, Chir	+) Chir, Cord, Veli
November [4]			(+) Belo, Noto, Libe	
December [1]	+) Cord, Veli		(+) Cori. Stra	(+) Hydro, Helo, Meso Stra (−) Culi

Bhs = Brackish herbaceous swamp; *Fhs* = Freshwater herbaceous swamp; *Pond* = Pond; *Mang* = Mangrove; *Ccmf* = Clear-cut marsh forest.
[1] Early rainy season; [2] Late rainy season; [3] Early dry season; [4] Late dry season.

c (Table 1 and 3) confirmed, in general, the insect seasonal patterns observed in the total ordination (Fig. 2a), except by Culicidae, Chironomidae, and Pleidae.

Discussion

Insect distributions were non-random with respect to the measured environmental variables at the temporal (seasonal) scale and the taxonomic level examined. The fauna was dominated by few insect families during the early rainy season (Culicidae, Hydrophilidae, and Dytsicidae) and the late dry season (Chironomidae); high taxon richness was observed during the remaining periods. Although the seasonal changes of wetland macro-invertebrates has been widely documented in the temperate zones (e.g., WIGGINS et al. 1980, LAKE et al. 1989), it has only been reported in one study in the Neotropical region (Brazil: HECKMAN 1998).

In the present study, many of the measured environmental variables were temporally structured, as was revealed by the considerable fraction of environmental variation attributed to temporal variables (components $a + b$). The fraction of the total variation of the insect data that was attributed to both temporal and environmental variables (components $a + b + c$) showed that there was an overall similar response of the insect community to these variables, despite differences among wetland types, and supported the view that multiple factors, all of which are linked, determine the broad-scale differentiation of aquatic insects in these wetlands. Indeed, the observed pattern was partially the result of the well-defined and, in many ways, predictable seasonal changes in the physical, chemical, and biotic conditions of the wetlands. For instance, seasonal changes in precipitation (as a broad-scale factor) were reflected in local wetland conditions which, in turn, correlated well with seasonal differences in taxa distribution. The net effect of water inflow from rainfall could be a function of the interaction between physical processes (i.e., water depth and habitat size variation due to rainfall), chemical processes (i.e., nutrient enrichment due to rainfall and biotic activity), biological processes (i.e., enhanced productivity due to biotic activity), and heterogeneity of habitat (due to macrophyte growth). These results agree with previous studies that showed a strong association between Neotropical aquatic insect distribution patterns and water fluctuations in the habitat produced by rainfall (GRILLET & BARRERA 1997, HECKMAN 1998). In addition, our results provide support for the view that the hydrology or the water level fluctuation in wetlands represents one of the most important environmental component by which wetland insect communities are organized (WIGGINS et al. 1980, BATZER et al. 1999).

It has been suggested that the dynamic hydrology of wetlands has profound effects on the life cycles and colonization strategies of organisms as well as the species richness (WIGGINS et al. 1980, BATZER et al. 1999); hence temporal changes in community structure should be, in part, understood in terms of species strategies for coping with this seasonal variation in habitat. Thus, we hypothesized, following ARMITAGE et al. (1975), WIGGINS et al. (1980), MURKIN (1989), and BATZER et al. (1999), that the interplay of trophic conditions (food availability), related chemical conditions, wetland duration, and insect life history patterns, all of which are mediated by temporal variation in rainfall, could largely explain the temporal distribution of the insect taxa in these wetlands. Due to the taxonomic level examined here and the correlative nature of our study, this hypothesis only can be well addressed in future studies when a finer taxonomic level and a more experimental approach is carried out. However, some observations should be done to focus aspects for future research. First, Culicidae was the earliest taxon occurring in most of the wetlands, when flooding occurred during the early rainy season. Temporal distribution of mosquitoes could likely be related to the rich food resources provided by plant det-

ritus from the previous period since in this family most species are early colonizers with food habits of collectors-gatherers (MERRITT & CUMMINS 1984). Secondly, the taxa appearing later in the habitat (late rainy season or early dry season) were usually predators (such as Corixidae, Notonectidae, Belostomatidae, Pleidae, Mesoveliidae, Veliidae, Helodidae, Coenagrionidae, and Libellulidae) which in general are late habitat colonizers (WIGGINS et al. 1980), suggesting that their recruitment could be timed to coincide with abundant prey resources. Finally, taxon richness was maximal in moderately enriched conditions of the wetland (late rainy season and early dry season); then, it decreased with low (early rainy season) or excessive nutrient enrichment (late dry season), the latter condition possibly creating anoxic conditions (low water quality) which should adversely affect most invertebrates. Future studies are needed to explore the hypotheses mentioned above.

The fraction of insect taxa variation attributed to pure environmental variables emphasized and added to the evidence of the literature pointing out the importance of the physical, trophic and chemical conditions controlling insect abundances in wetlands (BATZER & WISSINGER 1996, BATZER et al. 1999). The effects of physical and chemical variables such as water depth (which is a function of habitat size), CO_2, pH, temperature, and conductivity (an indirect measure of nutrients) on wetland macro-invertebrate distribution have been well documented (BATZER & WISSINGER 1996). Most taxa belonging to the coleopterans, hemipterans and odonates showed positive relationships with depth, which agrees with the previous observations (e.g., BAZZANTI et al. 1996) suggesting that large water bodies could provide a greater diversity of prey to the predator taxa compared to small ones. By contrast, mosquitoes predominated in shallow water conditions but with high CO_2 and conductivity levels, indicating their relationship to detritus food (MERRITT & CUMMINS 1984). The relationship observed here between chironomids and temperature and pH has also been found in previous studies (BATZER & WISSINGER 1996, ENTREKIN et al. 2001).

The variance partitioning technique used in this paper permitted a quantification of the strictly temporal variation which cannot be related to the measured environmental variables. This suggests temporal trends that remain in the insect abundance data even after accounting for the effects attributed to our environmental variables. The temporal matrix could act partly as a synthetic descriptor of unmeasured underlying processes: e.g., species-specific life histories, habitat selection behavior, population dynamics, and/or dispersion events. Similarly, the fraction of unexplained variation found in this study may be due, on the one hand, to non-deterministic fluctuations, sampling errors, or scaling artifacts. On the other hand, it can be an indication that fine-scale factors (such as species-specific behavior, unmeasured abiotic and biotic variables, local community and population dynamics, or small-scale temporal and

spatial variation) are also important in the taxa-environment relationship. An experimental approach and a better insect taxonomic resolution are needed to account for these pure temporal and/or unexplained variation in the community.

We conclude that in northern Venezuela wetlands, local ecological factors (such as wetland hydroperiod, trophic state, and physical and chemical conditions) and their seasonality simultaneously explain much of the variation observed in the insect communities among wetlands. The relative importance of different factors varied markedly between habitats. This supports the hypothesis that purely local spatial variation related to the wetland type may also be important.

Acknowledgements

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