Heterogeneity of the inland water–land palm ecotones (morichals) in the Orinoco lowlands, South America

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Abstract We analyzed the distributional pattern of species and environmental gradients across inland water–land palm ecotones (morichals) of the Orinoco lowlands to increase comprehension of the nature of ecotone heterogeneity. A total of 91 species (53 genera and 45 families) with aboveground phytomass > 0.1 g dry mass were recorded. Detrented canonical correspondence analysis (DCCA) indicated that vegetation phytomass was related strongly to soil properties, including gradients of silt (14.5–4.7%), exchangeable Al (1.05–3.10 cmole kg^{-1}), K (0.03–0.30 cmole kg^{-1}), Na (0.01–0.08 cmole kg^{-1}), Mg (0.03–0.54 cmole kg^{-1}) concentrations, pH (3.7–5.0 units), and soil organic matter. Cluster analysis allowed the definition of four types of ecotones on the basis of hydrogeomorphic processes. The first major group (1) encompassing the sites from Venezuelan lowlands (i.e., 3V, 4V, 5V, 6V, and 7V) was related to less acidic soils with high organic matter content. The second group (II) from Eastern Colombian llanos (i.e., sites 8C, 9C, 11C, 12C, 13C, 14C, and 15C) was located in acidic soils (3.9–4.5 units) with high Mg concentration. The third group (III) (i.e., sites IV and 10C) was located in soils with high Na content, whereas the fourth group (IV) (i.e., site 2V) was characterized by species growing in soils with low exchangeable aluminum. The results evidenced the interactive role of valley constraint, landforms, hydrological regime, and soil feature in structuring the plant community. Biogeographic and floristic considerations were also taken into account to explain differences in species composition.

Keywords Detrented canonical correspondence analysis · TWINSPAN · Savanna · Vegetation–environment relationship

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Introduction

In a landscape context, natural drainage networks are often fringed by transitional areas of riparian zones (Malanson 1993; Naiman et al. 2005). These areas are characterized by productive vegetation and animal populations (Beard 1953, 1955; Askew et al. 1970, 1971; Eiten 1983; Oliveira-Filho and Martins 1986; Haaser and Beck 1989; Oliveira-Filho et al. 1990; Catterall 1993; Eamus and Farrer 2006) as well as diverse flora and fauna assemblages (Catterall

et al. 2001). The highly dynamic ecotones and expansive alluvial floodplains are characterized by marked environmental gradients across groundwater–surface water exchange pathways. As a response to gradient in material and disturbance ecotones, species are adapted to spatial and temporal dynamic mosaic. Such gradients have been related to topography and soil features (Kalliola and Puhakka 1988; McGarigal and McComb 1992). Studies on spatial and biotic patterning in ecotones as a function of physical attributes of the environment have frequently focused on major taxa with different scales, fluvial environments, and edaphic factors. At the landscape scale, stream landforms, channel bedforms, and habitat features are the characteristics shaped by hydrogeomorphic processes, climate, sediments, and vegetation debris (Montgomery and Butfington 1997; Rot et al. 2000). At the patch scale, ambient hydrogeomorphic processes have the most influence on species distribution, interaction, and life histories (Wharton et al. 1982; Malanson 1993; Hupp and Osterkamp 1996; Rot et al. 2000). On a particular landform, the distributional pattern has been related to plant strategies, tolerance of severe stress and disturbance gradients, and biotic interactions (Levine 2000). Separation of these factors that influence fluvial-species distribution is difficult to achieve because most are interdependent. This article synthesizes research regarding environmental factors and vegetation pattern across a regional transect of ecotones throughout the Orinoco lowlands.

This paper focuses on one dimension of inland water–land ecotones, namely, vegetation pattern. Understanding community features in ecotones could be crucial for delineating community heterogeneity at different scales. In this sense, there is a vast pattern of ecotones ranging from open water-dominated vegetation to those where available water is controlled by vegetation (Montes and San José 1995). Accurate estimates are required for the study of a variety of ecological, hydrological, and climatic conditions, yet are difficult to obtain. In order to achieve this task, multivariate analysis of the data (Ter Braak and Prentice 1988) can provide adequate and suitable research means to assess the pattern of ecotones as a function of edaphic and climatic features. This analysis approach has been used to delineate plant communities and ecotones at different scales (Rochow 1972; Robertson et al. 1984; Collins et al.

1981; Hardin et al. 1989; Hupp 1992; Nilsson et al. 1994; Catterall et al. 2001; Lyon and Sager 2002; Veneklaas et al. 2005). As a consequence, although an increasing number of studies on inland water–land ecotones are being undertaken, the results are inconclusive.

The Orinoco lowlands (0.4×10^{12} m^2) of northern South America are extensively covered by ecotones, which are connecting aquatic and land phases in vegetational toposequences (Montes and San José 1995). These areas provide an opportunity to study a wide range of inland water–land ecotones. The regional pattern of ecotone composition across the environmental heterogeneity of the Orinoco basin has not been interpreted. Specifically, we considered the following. If elucidating the vegetation pattern of the ecotones constitutes a major challenge in vegetation science (Naiman et al. 2005), then the wide range of vegetation community should capture the behavior inherent to ecotones. This focus can identify environmental heterogeneity and predict the implications of ecotones for conservation. In contrast, if heterogeneity does not limit vegetation pattern, then we can expect similar specific compositions. This study was undertaken to establish the environmental gradient responsible for the vegetation patterns of the palm inland water–land ecotones in the Orinoco lowlands using the multivariate approach.

Materials and methods

General view of the ecotones

This research was conducted across the Orinoco lowlands. In the landscape, alluvial plains are formed from detrital material accumulated during the lower Pleistocene (Malagon 1987). The geological formation of these highlands has been defined as "Mesa" (Hedberg and Pyre 1944). Here, the deposited material has been eroded, mainly by wind and water, and to a lesser extent by orogenic movement. The annual rainfall increases from the Orinoco Delta (900–1,300 mm) toward southwestern latitudes (1,800–2,800 mm). At the same time, the length of the dry season decreases from 5 to 2 months as determined by the South Atlantic anticyclone and the Equatorial Trough (Cochrane et al. 1985). In these plains, toposequences have been considered as an

ecological factor, determining vegetational patterns associated with ecotones where the superficial plains of the valleys and geofractural plains provide substantial groundwater surface exchange (Fig. 1) (Pérez 1981; San José et al. 2001). These conditions lead to the presence of the inland water–land palm ecotones (i.e., Morichals) (Pérez 1981; Montes and San José 1995; San José et al. 2001). The ecotone soils involve Entisols and Histosols (Gonzalez 1987; Montes and San José 1995) with high soil aluminum saturation, which reaches up to 90% and deficiencies in K, Ca, Mg, and P (Mazorra et al. 1987).

Study sites: ordination and classification of inland water–land palm ecotones across the Orinoco lowlands

Site selection was based on a survey covering the heterogeneity of ecotones found throughout the Orinoco lowlands (0.4×10^{12} m^2; Fig. 1). The diversity of morichals is largely controlled by topographic conditions, which affect surface groundwater and drainages. These ecotones are commonly found in the river headlands of the Orinoco basin. The groundwater-fed streams are ranked as first order (Strahler 1957, 1964) (i.e., streams fed only by groundwater exfiltration and receiving no tributary inputs). In the

lowlands, there is a vast array of landforms ranging from flat-floored to V-shaped valleys. The flat-floored valleys correspond to endogenous depression with hemispheric shapes characterizing the surface of the topography, where the relief is underlined by herbaceous ecotones with scattered individuals of *Mauritia flexuosa* and associated trees and shrubs. The pattern of the V-shaped valleys takes the form of permanent flooded woody ecotone in humid gley soils. This ecotone was characterized by *M. flexuosa*, which makes up a conspicuous element of the emergent woody layer. Across the Orinoco lowlands, the first set of sites (Fig. 1) was located in the northern region of the Orinoco llanos (V = Venezuela) (San José and Montes 1991) as delimited by the foothills of the Coastal Caribbean Range in the north (9°42′N; 67°25′W) and the Orinoco River in the south (7°46′N; 63°25′W). The second set of sites (Fig. 1) was placed in the western region of the Orinoco llanos (C = Colombia) between latitude 3° and 6°N to the east of the Andes mountains, and between longitude 71° and 68°W at the western margin of the Orinoco river. The study sites were selected on the basis of maps and aerial photographs as well as on the basis of field trips throughout the Orinoco lowlands. Therefore, the full range of structural diversity types, bioclimatic conditions, and different degrees of

Fig. 1 Study sites of inland water–land palm ecotones in the Orinoco River basin: (1V) El Recreo, (2V) La Chinea, (3V) Hato Becerra, (4V) Morichal Redondo, (5V) Maturin, (6V) Hicacal, (7V) Las Babas, (8C) El Porvenir, (9C) Pachaquiaro II, (10C) Mozambique, (11C) Alto Menegua, (12C) La Bonga, (13C) Caño Porfia, (14C) Alto Neblinas, and (15C) Cabecera Río Muco
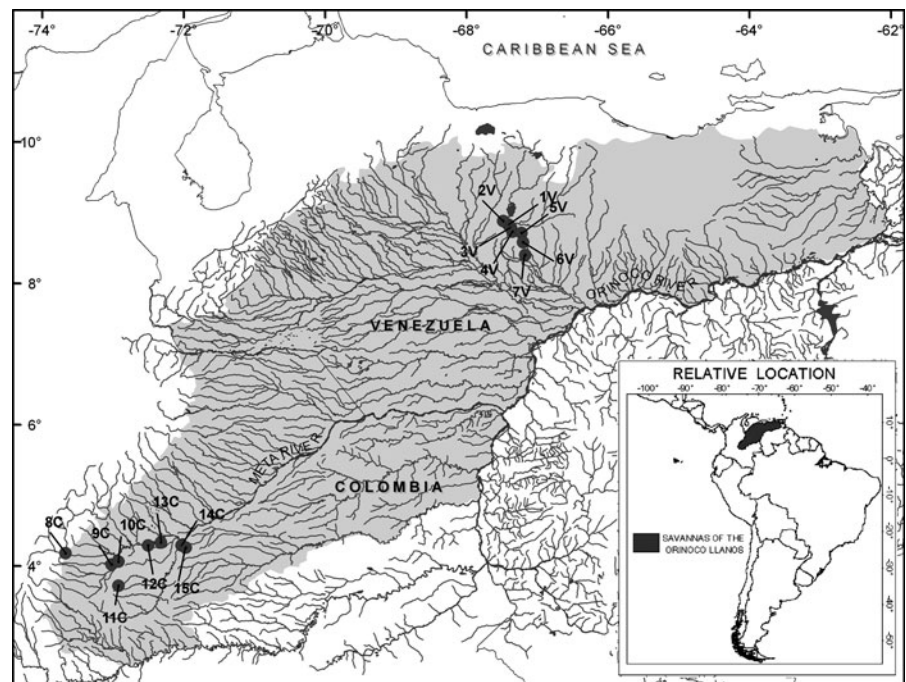
landscape dissection were taken into account. The sites were characterized by the absence of agricultural practices and severe cattle grazing effects according to information over the past 10 years provided by local farmers. The vegetation is burned occasionally during the dry season.

Voucher specimens of the observed taxas were deposited at the National Herbarium (Caracas); the Ecology Center Herbarium (IVIC, Caracas) and the Missouri Botanical Garden. Plant names follow the nomenclature used in the Venezuelan National Herbarium.

Sample design: quadrat size and spacing

In the presence of changes in the floodplain reach of each study-site, we expected differentiation in the ecotone to be related to a slight gradient on the basis of the interaction of stream channel configuration and landform. At each selected study-site, the area consisted of a measured distance along the channel length (i.e., corresponding to 100 channel width) by the total ecotone width. This reach length would allow for at least the annual flooding frequency, magnitude, and duration. In this area, most of the flora of the ecotone was sampled as indicated by species-area curve. At each study-site, three transects were selected at right angles to the stream. At each transect, contiguous quadrats were established. In the flat-floored valleys with dominant herbaceous species and scattered individuals of *M. flexuosa* and associated shrubs, the dimension of the quadrats was 1.0 m × 1.0 m. In the V-shaped valleys with permanent flooded woody ecotone, the dimension was 5.0 m × 5.0 m. At each transect, the total length was equal to the total ecotone. At each quadrat, maximum aboveground dry matter accumulated by the herbaceous vegetation (August–September) was harvested. Phytomass was separated by species into green and non-green material, and surface litter was also collected. Samples were oven-dried at 80°C to a contrast dry mass. For each quadrat, the height/biomass relationship was determined for each tree species found in the ecotone as outlined in San José et al. (1998). The full range of tree heights represented in quadrats was sampled for 0.5 m height increments by felling 40 trees per height class. Leaves, branches, and stems were weighed and subsamples were oven-dried at 80°C until constant

dry mass. Whole tree fresh mass were then converted to dry based on these fresh/dry mass ratios from subsamples. Phytomass was appropriate for our purposes because it defines the species' use of resources for growth and allows comparisons of different sizes on a single-scale (Whittaker 1975; Kent and Coker 1992).

The phytomass as a function of position along the transect was used to elaborate semivariograms (Clark 1979). From slope m of the double logarithmic plot of the semivariogram was calculated the fractal dimension D by the function $D = (4 - m)/2$ (Burrough 1983). The fractal dimension plotted as a function of scale (i.e., fractograms) allowed fixing quadrat size and spacing (Palmer 1988). Thus, the fractograms for the ecotones corresponding to the flat-floored (PFV) and V-shaped (VSV) valleys showed sections with U-shaped limbs resting on the value of $D = 2$. Therefore, the quadrat size (i.e., left limb of the U) was close to 4 m × 4 m and 20 m × 20 m, for the ecotones in the PFV and VSV, respectively. The quadrats were separated (i.e., at a distance of at least the right limb of the U) by a distance of 12 and 32 m, for the interface of PFV and VSV, respectively. On the basis of these results, a maximum of three positions were selected along the gradient (i.e., close to the channel bed, middle of the floodplain and the flood-prone area). At each position in the gradient, a minimum of four quadrats were selected and a total of 33,600 and 1,536 m^2 were sampled in the PFV and VSV, respectively. At each quadrat, above-ground phytomass per species was measured as described in the preceding section. A total of 180 quadrats were selected at the 15 sites.

Selected variables for the gradient analysis

At each selected quadrat, edaphic variables were ascertained. Thus, triplicate soil samples down to 0.3 m at 0.1 m-depth increments were taken in the ecotones. Plant residues on the soil surface were not included in the samples. For the edaphic variable, the samples were analyzed as follows: pH using a glass electrode in a 2:5 soil:water slurry, exchangeable acidity and aluminum using the procedure outlined by Yuan and Fiskell (1959), total nitrogen (N) using Kjeldahl procedures (Bremner 1965) and ammonium colorimetrically (Technicon Auto-Analyzer 1978), available phosphorus colorimetrically (Olsen and

Dean 1965), and exchangeable cations extracted with 1 N NH_4Cl, measuring their concentrations by atomic absorption spectrophotometry. The soil bulk density was determined from the volume occupied by ten soil samples of 1 m^2 using the method proposed by Pla Sentis (1977). Soil texture was evaluated using the Bouyoucos method (Day 1965). Soil organic matter percentage was determined using the Walkley and Black method (Jackson 1958).

An edaphic variable analysis was performed to decrease the redundancy of the variables. Thus, the variables were subject to a preliminary analysis using the variance inflation factor of a variable in a multiple regression equation (Montgomery and Peck 1982). Collinear variables were deleted from the variable set, and 18 original variables were reduced to 7. The vegetation structural data based on the total above-ground phytomass per species were ordinated using a detrented canonical correspondence analysis (CA-NOCO: Ter Braak 1988; Ter Braak and Prentice 1988), a direct gradient analysis technique. As the ecotone community was dominated by only a few abundant species, the raw data was transformed using the logarithmic approach before analyzing (Ludwig and Reynolds 1988). The minimal species abundance (i.e., aboveground phytomass) for DCCA analysis was 0.1 g. The rare species were not underweighted since the ecological interpretation was not improved (Kent and Coker 1992).

The data set was classified by two-way indicator species analysis (TWINSPAN) (Hill 1979), a divisive method which produces grouping of both sites and species.

Results and discussion

The morichal pattern for a given set of conditions is of particular significance in identifying the environmental range within which the ecotones are occurring. Thus, the ordination predicts how morichal vegetation changes as a function of a given set of conditions. In the extreme heterogeneous environment of the Orinoco lowlands, we found that the eigenvalues of the first four DCCA axes of the ordination were 0.56, 0.33, 0.12, and 0.08, respectively. The first axis of the species–environment relationship accounted for 71% of the cumulative variance in the 91 species in relation to seven

environmental variables. The sum of all canonical eigenvalues was 1.77. The species–environment correlations measuring the strength of the relationship between species and the environment for the first two axes were 0.93 and 0.94, respectively. The Monte Carlo test carried out to analyze the significance of the eigen values for the first two canonical axes (Hope 1968) indicated that species were significantly related to the environmental variables at the 5% significance level. In this study, contrast in structure and species composition was related to the effect of edaphic differences within the ecotones. The findings of the DCCA were displayed in an ordination diagram (Fig. 2). The dominant pattern in species composition was delineated in ordination Fig. 3. Thus, we infer that the first axis for the ecotones represents soil chemical and physical gradients, in which the silt proportion ranges from 14.5 to 34.7% and exchangeable aluminum from 1.05 to 3.10 cmole kg^{-1} in the layer of 0.0–0.3 m in depth. They explained the major variation among the sites, where extreme soils with the higher silt proportion might lead to low water movement and reduced hydraulic conductivity. It was found that the aluminum saturation was a collinear variable. However, a remarkable feature of the ecotone soils was the very high aluminum saturation, which reaches up to 90%. Comparatively in the adjacent savannas with Ultisols and Oxisols, aluminum saturation ranged from 40 to 50% (San José and Garcia-Miragaya 1979). The high aluminum saturation in the ecotones could be related weathering processes, occurring in alternation between reducing and oxidizing conditions in poorly drained soils (Buol et al. 1993). Here, the edaphic attributes were highly variable indicating the pressure of broad soil gradients. This variability is associated with the diversity in parent material, landforms, and hydrological features in the ecotones. Thus, sampling was effective in assessing across environmental gradients in the ecotone landscape. The range in quadrats indicates that vegetation sampling occurred across a topographic gradient that include flooded and flood-prone areas.

The second DDCA axis (Fig. 2) accounted for 28% of the variance in the weighted average of the species with respect to the environmental variables. Thus, we infer that species distribution along this axis is related to variation in K (0.03–0.30 cmole kg^{-1}), Na (0.01–0.08 cmole kg^{-1}), and Mg (0.03–0.54 cmole kg^{-1})

Fig. 2 Ordination triplot of axes one and two of a detrented canonical correspondence analysis (CANOCO) of inland water–land palm ecotones (Morichales) with respect to environmental variables of the Orinoco lowlands. The major explanatory environmental variables are shown by *arrows*. *Longer vector lines* represent inter-set correlations (after Ter Braak 1986). Localities of study sites (*closed squares*) are given in Fig. 1. Groups of morichals (I, II, III, and IV) were classified by TWINSPAN
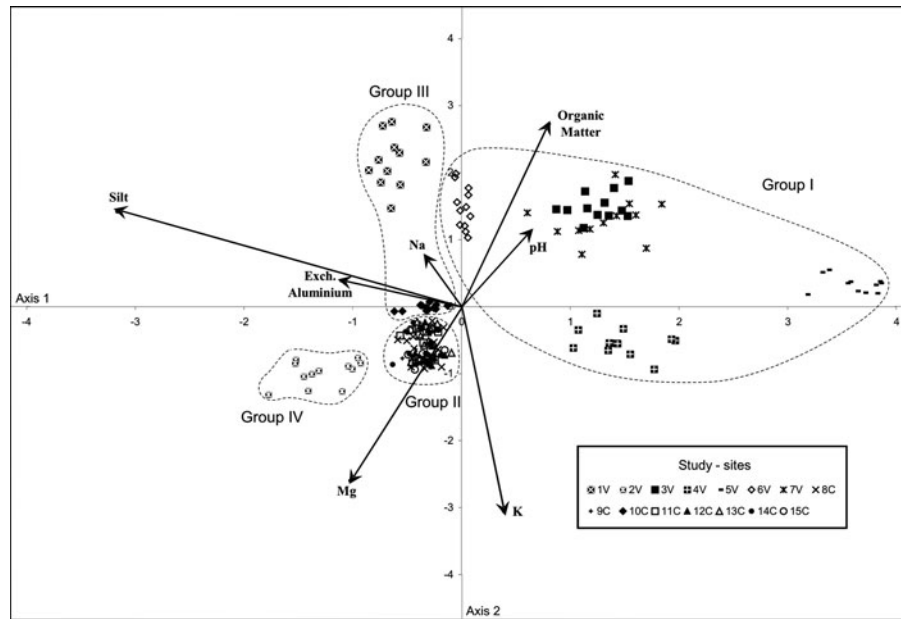
concentrations, as well as pH (3.7–5.0 units) and organic matter (1.5–12.3%). These variables are probably related to variation in the decomposition rates and inundation regime. Therefore, a contrast between sites based on a difference in soil chemistry was evident. In the Venezuelan Guayana, the floristic composition of the palm ecotones was defined by soil exchangeable acidity, exchangeable Al, effective exchange capacity, sum of bases, and exchangeable H^+ (Teran and Duno 1988). Similarly, canonical correspondence analysis of riverine wetland vegetations in the Haut–Saint–Laurent region and riparian forest in the Colombia savanna landscape suggested that soil fertility and organic matter accumulation were driving abiotic variables correlated with plant community composition (Martin and Andre 1993; Veneklaas et al. 2005). However, cation concentrations in the Colombian and Brazilian gallery forests (Felfili 1994; Oliveira-Filho et al. 1994, 1997) were comparatively higher than those in the inland water–land palm ecotones. Comparatively, the range of base saturation in the herbaceous layer (i.e., 44–60%) and woody layer soil (i.e., 94%) of the adjacent savannas (San José and Garcia-Miragaya 1979) was lower as compared to that in the ecotones (i.e., 5.3–26.4%). In addition to the aforementioned tropical riparian forests, the response to these edaphic gradients has been reported for high latitude ecotones (Dollar et al. 1992; Lyon and Sager 2002).

In the DCCA ordination diagram, the data set was classified into four major groups of ecotone type by the two-way indicator species analysis (TWIN-SPAN); Hill 1979). It allowed the classification of the data into four major ecotones groups (Kent and Coker 1992). The first major group (I) encompassing the sites from Venezuelan lowlands (i.e., sites 3V, 4V, 5V, 6V, and 7V) was delineated along the right upper side of the diagram. This group was related to high organic matter percentage in less acidic soils where litter decomposition seems to be low. It is notable that the soils of these particular morichals were extremely infertile with Mg and K concentrations below 0.04–0.13 and 0.03–0.30 cmole kg^{-1}, respectively. However, in these less silty soils, water movement is enhanced. These features are found in the herbaceous ecotones with scattered trees and palms (i.e., in flat-floored valleys). In this group, the hemispheric surface of the topography is underlain by scattered *Mauritia* palms. In this type of morichal, the herbaceous layer (Fig. 3) is dominated by the common species belonging to the Poaceae (*Acroceras zizanoides*, *Axonopus compressus*, *Isachne polygonoides*, *Panicum cayenensis*, and *P. parviflorum*), Cyperaceae (*Eleocharis interstinta*, *E. plicarhachis*, *Rhynchospora papilosa*), Melastomataceae (*Rhynchanthera serrulata*), Labiatae (*Hyptis conferta*), Xyridaceae (*Xyris savanensis*), and Eriocaulaceae (*Syngonanthus caulencens*). The second major group
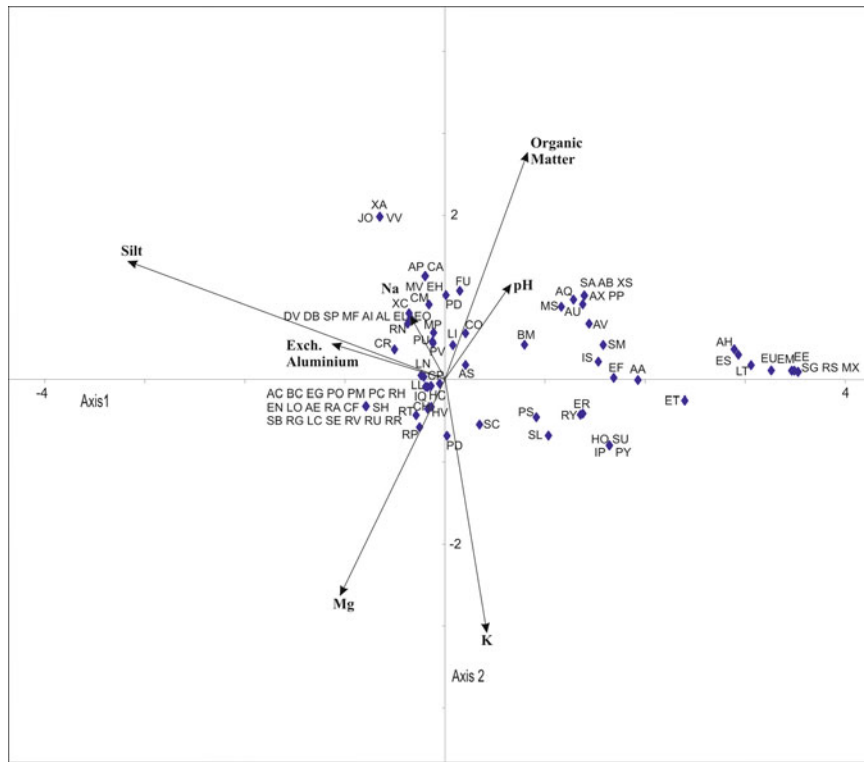
Fig. 3 Ordination of axes one and two of the canonical correspondence analysis of the species in the inland water–land palm ecotones (Morichales) of the Colombia and Venezuelan lowlands. Composition quantified by aboveground phytomass. The *letters* refer to species: (AQ) *Acisanthera quadrata* Pers., (AB) *Acroceras zizanioides* (Kunth) Dandy, (AA) *Aeschynomene americana* L., (AP) *Aeschynomene pratensis* Small, (AI) *Andropogon bicornis* L., (AL) *Andropogon leucostachyus* Kunth, (AS) *Andropogon selloanus* (Hack.) Hack., (AV) *Andropogon virgatus* Desv. ex Ham., (AC) *Aristida capillacea* (Lam.), Chase, (AE) *Aristida setifolia* Kunth, (AH) *Arundinella hispida* (Humb. & Bonpl. ex Willd.) Kuntze, (AX) *Axonopus compressus* (Sw.) P. Beauv., (AU) *Axonopus purpusii* (Mez) Chase, (BM) *Bacopa monnieroides* (Cham.) Robinson, (BC) *Bulbostylis capillaris* (L.) Clarke, (CA) *Cassytha americana* Nees, (CP) *Cecropia peltata* L., (CM) *Croton trinitatis* Millsp., (CO) *Cuphea odonellii* Lourteig, (CF) *Cyperus flavescens* L., (CH) *Cyperus haspan* L., (CR) *Cuphea micrantha* Kunth, (CT) *Curatella americana* L., (DV) *Desmocelis villosa* (Aubl.) Naud., (DB) *Desmodium barbatum* (L.) Benth., (ET) *Echinodorus tenellus* (Mart. ex Schult. & Schult. f.) Buchenau, (EG) *Echinolaena gracilis* Sw. Laena, (EF) *Eleocharis filiculmis* Kunth, (ES) *Eleocharis flavescens* (Poir.) Urb., (EE) *Eleocharis interstincta* (Vahl) Roemer & J.A. Schult., (EH) *Eleocharis minima* Kunth, (EM) *Eleocharis mutata* (L.) Roem. & Schult., (EU) *Eleocharis nuda* C.B. Clarke, (EP) *Eleocharis pachystyla* (C. Wright) C.B. Clarke, (ER) *Eleocharis plicarhachis* (Gris.) Svenson, (EL) *Elephantopus mollis* Kunth, (EN) *Eriocaulum humboldtii* Kunth, (EO) *Eupathorium odoratum* L., (FU) *Fiurena umbellata* Rottb., (HO) *Hyptis conferta* Pohl., (HV) *Hypoginium virgatum* Desv. H.V., (HC) *Hyptis dilatata* Benth., (IS) *Ipomoea schomburgkii* Choisy, (IQ) *Ipomoea squamosa* Choisy, (IP) *Isachne polygonoides* (Lam.) Döll, (JO) *Jacaranda obtusifolia* Bonpl., (LL) *Leptocoryphium lanatum* (H.B.K.) Nees, (LC) *Lisanthus cheloides* L.f., (LT) *Ludwigia decurrens* Walts., (LI) *Ludwigia lithospermifolia* (Micheli) H. Hara, (LN) *Ludwigia nervosa* (Poir.) H. Hara, (LO) *Ludwigia octovalvis* (Jacq.) P.H. Raven, (MX) *Mauritia flexuosa* L. f., (MF) *Mayaca fluviatilis* Aubl., (MS) *Mayaca sellowiana* Kunth, (MV) *Melochia villosa* (Mill.) Fawc. & Rendle, (MP) *Miconia stephananthera* H.B.K., (PV) *Otachyrium versicolor* Pipger, (PY) *Panicum cayennense* Lam., (PP) *Panicum parvifolium* Lam., (PS) *Panicum stenodoides* Hubb, (PM) *Paspalum multicaule* Poir., (PO) *Paspalum orbiculatum* Poir., (PD) *Phyllanthus stipulatus* (Raf.) G.L. Webster, (PC) *Polycarpae corymbosa* (L.) Lam., (PU) *Protium heptaphyllum* (Aubl.) March., (RY) *Rhynchanthera serrulata* (Rich.) D.C., (RU) *Rhynchospora globosa* (Kunth) Roem & Schult., (RH) *Rhynchospora hirsuta* Vahl, (RG) *Rhynchospora marisculus* Nees Roem. & Schult., (RR) *Rynchospora nervosa* (Vahl.) Boeck., (RS) *Rhynchospora papilosa* W.W. Thomas, (RP) *Rhynchospora podosperma* (C. Wright) Koyama, (RA) *Rhynchospora pubera* (Vahl) Boeck., (RN) *Rhynchospora tennerrima* Nees ex Spr., (RT) *Rhynchospora tenuis* Link, (RV) *Rhynchospora velutina* (Kunth) Boeck., (SM) *Sacciolepis myuros* (Lam.) Chase, (SG) *Sagittaria guyanensis* H.B.K., (SB) *Scleria bracteata* Cav., (SH) *Scleria hirtella* Sw., (SC) *Sesbania corniculata* Steud, (SE) *Setaria geniculata* P. Beauv., (SP) *Sorghastrum parviflorum* Desv., (SU) *Sporobolus cubensis* Hitchc., (SL) *Staurogyne leptocaulis* Bremek, (SA) *Syngonanthus caulescens* (Poir.) Ruhland, (VV) *Vochysia venezuelana* Stafleu, (XA) *Xylopia aromatica* (Lam.) Mart., (XC) *Xyris caroliniana* Walter, (XS) *Xyris savanensis* Miq

of morichal types (i.e., II) was located in the lower left site of the second axis in the diagram (i.e., sites 8C, 9C, 11C, 12C, 13C, 14C, and 15C), where a soil acidity gradient with pH ranging from 3.9 to 4.5 unity is reinforced by poor nutrient status. However, the soils are characterized by a high Mg concentration spanning 0.16–0.54 cmole kg^{-1}. These characteristics are found in flat-floored valleys (i.e., 8C) and V-shaped valleys (i.e., sites 9C, 11C, 12C, 13C, 14C, and 15C). It is noted that ecotones from the Eastern Colombian llanos present different sediments with ferromagnesian minerals. The common species belong to the families Poaceae (*Hypoginium virgatum*, *Leptocoryphium lanatum*), Cyperaceae (*Cyperus haspan*, *Rhynchospora podosperma* and *R. tenuis*), Convolvulaceae (*Ipomoea squamosa*), and Labiatae (*Hytis dilatata*).

The third group (i.e., III) was ranked on the upper left side of the second axis and encompasses two sites with flat-floored valleys. These were 1V and 10C. Although low fertility is a trait common to all studied morichals, the soils of these particular ecotones were only moderately infertile with high Na content. Therefore, in these morichals, the environmental factors were the most potentially favorable for plant growth as compared to the other habitat conditions. The common species were characterized by the Poaceae (*Andropogon bicornis*, *A. leucostachyus*), Leguminosae (*Aeschynomena pratensis*, *Desmodium barbatum*), Cyperaceae (*Eleocharis minima*), Asteraceae (*Elephanthopus mollis*, *Eupathorium odoratum*), Melastomataceae (*Desmocelis villosa*), Euphorbiaceae (*Croton trinitatis*), Sterculiaceae (*Melochia villosa*), Bignionaceae (*Jacaranda obtusifolia*), Annonaceae (*Xylopia aromatica*), Vochysaceae (*Vochysia venezuelana*), and Lauraceae (*Cassytha americana*).

The fourth group (i.e., IV) was ranked in the lower left side of the second axis. It is represented by only one flat-floored valley (i.e., 2V), which is characterized by the abundant species belonging to the families Poaceae (*Echinolaena gracilis*, *Paspalum multicaulis*, *P. orbiculatum*), and Cyperaceae (*Bulbostylis capillaris*, *Rhynchospora hirsuta*, *R. globosa*, *R. pubera*). These species are growing in soils with low exchangeable aluminum. In this site, noticeable is the abundance of *Polycarpaea corymbosa* of the Caryophyllacea family, an annual herb characteristic of the nearby well-drained savannas. This site is a

particular ecotone with open canopy and abundance of the perennial sedge species *Scleria bracteata*. Herbaceous species belonging to the family Eriocaulaceae, such as *Syngonanthus caulens* and *Eriocalum humboldtii*, were commonly found. Comparatively, Dick and Gilliam (2007) have determined the spatial heterogeneity and dependence of soil resources and characteristics of plant communities within different vegetation types in a stream floodplain in southwestern West Virginia.

The inland water–land palm ecotones of the Orinoco landscape were a relatively species-poor ecosystem. Thus, we found 91 species belonging to 53 genera and 45 families. The families represented by most species were Cyperaceae and Poaceae. Comparatively, the collection of vascular plants in the ecotones was lower than that in the seasonal gallery forest (243 species), seasonally flooded palm savannas (213) and well-drained savannas (194) of the Orinoco toposequences (Montes and San José 1995). In the gallery forest of the Colombian savanna landscape, most of the 147 tree species were evergreen and belonging to 110 genera and 45 families (Veneklaas et al. 2005). In terms of the aboveground phytomass, 87 and 99% of total phytomass in the flat-floored and V-shaped valleys were accumulated by 17 and 11 species, respectively. All these species were evergreen.

In the survey of species along the Orinoco morichals, endemic species were not found such as had been reported by Aristeguieta (1968). The flora of the analyzed Orinoco ecotones showed scarce affinity with that of surrounding regions of the Andes, the coastal range, and the Guayana Shield (Montes and San José 1995). Aristeguieta (1968) reported that the flora of the Orinoco morichals had not evolved in the savannas because 80% of species occurring in the Orinoco physiographic province were found in the Guayana physiognomic province. This lack of inherent floristic composition in the morichals has also been reported for riparian forests occurring in Colombian savanna landscape, Nigerian wet savannas, Belize lowlands, and Brazilian cerrados (Keay 1959; Prance 1992; Meave and Kellman 1994; Montes and San José 1995; Oliveira-Filho and Ratter 1995). In the Orinoco ecotones, a possible reason for the floristic trend is the migrational strategies of taxa. They expanded or shrank to occupy a much larger or smaller area through time (Delcourt and Delcourt

1991). Palynological evidence shows a Paleocene environmental history for the *Mauritia* pollen from different sedimentary basins of South America (van der Hammen 1992). From the dispersion center in the Amazon basin (Muller 1970), *Mauritia* might have moved during the quaternary climatic fluctuations (Berrio et al. 2002) to the flooded areas of neotropical lowlands. Therefore, these ecotones constitute ecological corridors from the Guayana and Amazonian regions to the Orinoco lowlands.

The aforementioned results might provide information relevant to the formulation of effective conservation, restoration, and management approaches in the Orinoco ecotones to ensure that management practices maintain integrity. In summary, results showed that vegetation and ecotone types are related to valley constraints, land forms, and soil characteristics. These seem to be key factors for maintaining land uses that support function integrity. When these systems are properly managed, they make provision for climate, geological processes, soil development, community productivity, animal activities, and human health.

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