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MODELING SPATIAL PATTERNS OF PLANT DISTRIBUTION AS A CONSEQUENCE OF HYDROLOGICAL DYNAMIC PROCESSES IN A VENEZUELAN FLOODING SAVANNA

MODELO ESPACIAL DE DISTRIBUCIÓN DE PLANTAS COMO CONSECUENCIA DE LA DINÁMICA HIDROLÓGICA EN UNA SABANA INUNDABLE VENEZOLANA

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ABSTRACT

This study presents the main results of the analysis and integration of ecological ordination and spatially explicit relationships into an ecological-spatial model. This allows understanding, evaluating and predicting the distribution of dominant plant species in a changing flooding savanna landscape affected by embankments in the plains of the Orinoco river (Llanos del Orinoco), Venezuela. An ecological analysis of the relationship between plant species and environmental factors (relative altitude and soil water content), and species response using Gaussian logistic models was carried out. These ecological responses are integrated into a spatial model using a Digital Elevation Model (DEM) providing elevation as a spatial variable. Plant distributions of the dominant species were mapped based on the ecological knowledge generated from the Gaussian responses and DEM. Plant species community composition gradually changes with flooding conditions and the dominant species have a strong relation to subtle soil water content variations. *Leersia hexandra* and *Panicum laxum* are the main dominant species, and present a complementary relation without niche overlapping, whereas *Eleocharis intersticnta* and *Paspalum chaffanjonii* are dominant in small areas with medium-low frequency and cover values. The model allows prediction of changes in savanna species diversity as a result of modified flooding regimes within the landscape.

Keywords: vegetation-environment relationship, savanna ecosystems, Digital Elevation Model (DEM), Geographical Information System (GIS), embankment

RESUMEN

Este estudio presenta los principales resultados del análisis e integración de ordenación ecológica y modelos espacialmente explícitos dentro de un modelo ecológico-espacial. Este modelo permite entender, evaluar y predecir la distribución de especies dominantes de plantas en un paisaje de sabana inundable afectado por la construcción de diques en los Llanos del Orinoco, Venezuela. Como datos ecológicos de entrada usamos los análisis y resultados sobre la relación entre las especies de plantas y los factores ambientales (contenido de agua en el suelo y altitud relativa), y la respuesta de las especies utilizando modelos logísticos Gaussianos. Estas respuestas ecológicas son integradas dentro de un modelo espacial usando un Modelo Digital de Elevación como variable espacial. Se produjeron mapas de las distribuciones de plantas de las especies dominantes con base en el conocimiento ecológico generado en la respuesta Gaussiana y el Modelo Digital de Elevación. La comunidad de plantas cambia gradualmente con la condición de inundación y las especies dominantes presentan una fuerte relación con sutiles variaciones del contenido de agua en el suelo. *Leersia hexandra* y *Panicum laxum* son las principales especies dominantes y presentan una relación de complementariedad sin sobreposición de nicho, mientras que *Eleocharis intersticnta* y *Paspalum chaffanjonii* son plantas dominantes en pequeñas áreas con valores medios-bajos de frecuencia y cobertura. El modelo permite la predicción de cambios en la diversidad de especies de plantas como un resultado de los regímenes de inundación modificados dentro del paisaje.

Palabras clave: relación entre vegetación y ambiente, ecosistema de sabana, Modelo Digital de Elevación (DEM[1]), Sistema de Información Geográfica (SIG), embalse. [1] DEM por sus siglas en Inglés

INTRODUCTION

A dynamic process of ecosystem transformation has been occurring in the Venezuelan savannas. Particularly, in the flooding savannas of Southern Venezuela, this transformation involves changes in the hydrological dynamics of the area. Climatic conditions, with a pronounced dry season between November and March, and a rainy season between April and October generate a marked seasonality in the soil water availability with areas completely dry during the dry period and flooded during the rainy period. In 1971, the project *Módulos de Apure* started in the Mantecal area. This project was based on gated dike construction to control the surface water runoff by using gates. The idea was to store water which accumulates during the wet season in order to increase grass biomass production during the dry season and, thus, raise the forage capacity of the area (Sarmiento and Monasterio 1975, López-Hernández and Ojeda 1996). These transformations have lead to changes in the composition and distribution of savanna ecosystems (Chacón-Moreno 2001) and savanna species adapted to hydrological deficits have been replaced by species adapted to wet environments which have a greater palatability (López-Hernández and Ojeda 1996).

Much research on species distribution is focused on animal species, especially the mapping of animal habitats and the inference of the localization of the animal (Atkinson 1985, Crosby 1994, Skidmore and Gauld 1996, Dettmers and Bart 1999, Mauro 1999, Corsi *et al.* 2000, Tamisier and Dehorter 2000). Knowledge on spatial distribution of plant species contributes to an understanding of ecosystem dynamics in spatial context, and how environmental conditions determine the change in composition and abundance of species. Consequently, it is possible to model species composition of different areas.

In Landscape Ecology, modelling is an important tool to understand and analyze the relationship between spatial heterogeneity of the landscape and ecological resources (Goodchild 1994, Turner *et al.* 2001). Models are useful tools for analysing and evaluating plant species distribution in a spatial context. In addition, they allow the exploration and analysis of ecological processes in changing environments induced by natural dynamics or by human activity (Neilson and Marks 1994, Neilson and Drapek 1998, Aber *et al.* 2001, Bachelet *et al.* 2001, Hansen *et al.* 2001, Malcolm *et al.* 2002).

At least, two different general modelling approaches have been used to study spatial ecology. One, is the direct analysis of ecological processes in the spatial context without deep knowledge of the environmental factors, using autocorrelation techniques or so-called 'surface pattern methods' (such as interpolation, variograms and kriging) (Varekamp *et al.* 1996, Fortin 1999, van Horssen *et al.* 1999). Another approach is to include, , ecological processes in relation to the environmental factors and associated to the spatial heterogeneity and distribution of those factors (Skidmore 1989, Austin *et al.* 1994, Goodchild 1994, Neilson 1995, Skidmore *et al.* 1996, Toxopeus 1996, van de Rijt *et al.* 1996, Guisan *et al.* 1998, Zimmermann and Kienast 1999, Guisan and Zimmermann 2000). This approach uses ecological knowledge on the processes and dynamics of the species, populations, communities or ecosystems, and the spatial patterns of the environment.

In this study, ecological ordenation is developed and applied to understand the plant species distribution in a changing seasonally-flooded savanna landscape affected by embankments in the plains of the Orinoco river, Venezuela. This objective is achieved by combining two methodological approaches. The first approach, (Chacón-Moreno et al. 2004), studies the relationships between the environmental factors and plant species by using ecological ordination techniques. In the above study the hydrological gradients resulted to be the principal factor in determining species distribution. In the second approach, spatial information is used to determine hydrological gradients, using the Digital Elevation Model (DEM) of the study area (Smith et al. 2006) and, the correlation between the DEM and the relative soil water content derived from field data. The results are integrated and analysed in a Geographic Information System (GIS), and future changes in species composition are simulated as a result of continuing modifications to the flood regime.

STUDY AREA

The study was carried out in the seasonally-flooded savanna in the plains of the Orinoco river, Apure state, Venezuela (Llanos del Orinoco), specifically in an area of about 10000 ha at the El Frío Biological

Station. This area is boarded by tributaries of the Apure river and the landscape is very flat (3 m height difference over 12 km) causing large areas to flood during the rainy season, between April and November. During the dry season the majority of the area dries out completely and at the end of the dry season, fires are common (Figure 1).

Four main ecosystems dominate the area (Figure 2), three of which correspond to savanna ecosystems differentiated by soil water availability during the year and the seasonal pattern of phenology: seasonal, hyperseasonal and semiseasonal savannas (Sarmiento 1984, 1990, Chacón-Moreno 2004) and the gallery forest associated to water courses. These savanna ecosystems are associated to the different geomorphological units of the area.

These geomorphological units originate from the river dynamics and are named locally: *banco, bajío,* and *estero* (Figure 2). *Bancos* are natural levees along the edge of streams and rivers where sandy soils predominate as well as seasonal savanna ecosystems and gallery forest. *Bajíos* are extended areas with medium topographic relative elevation,

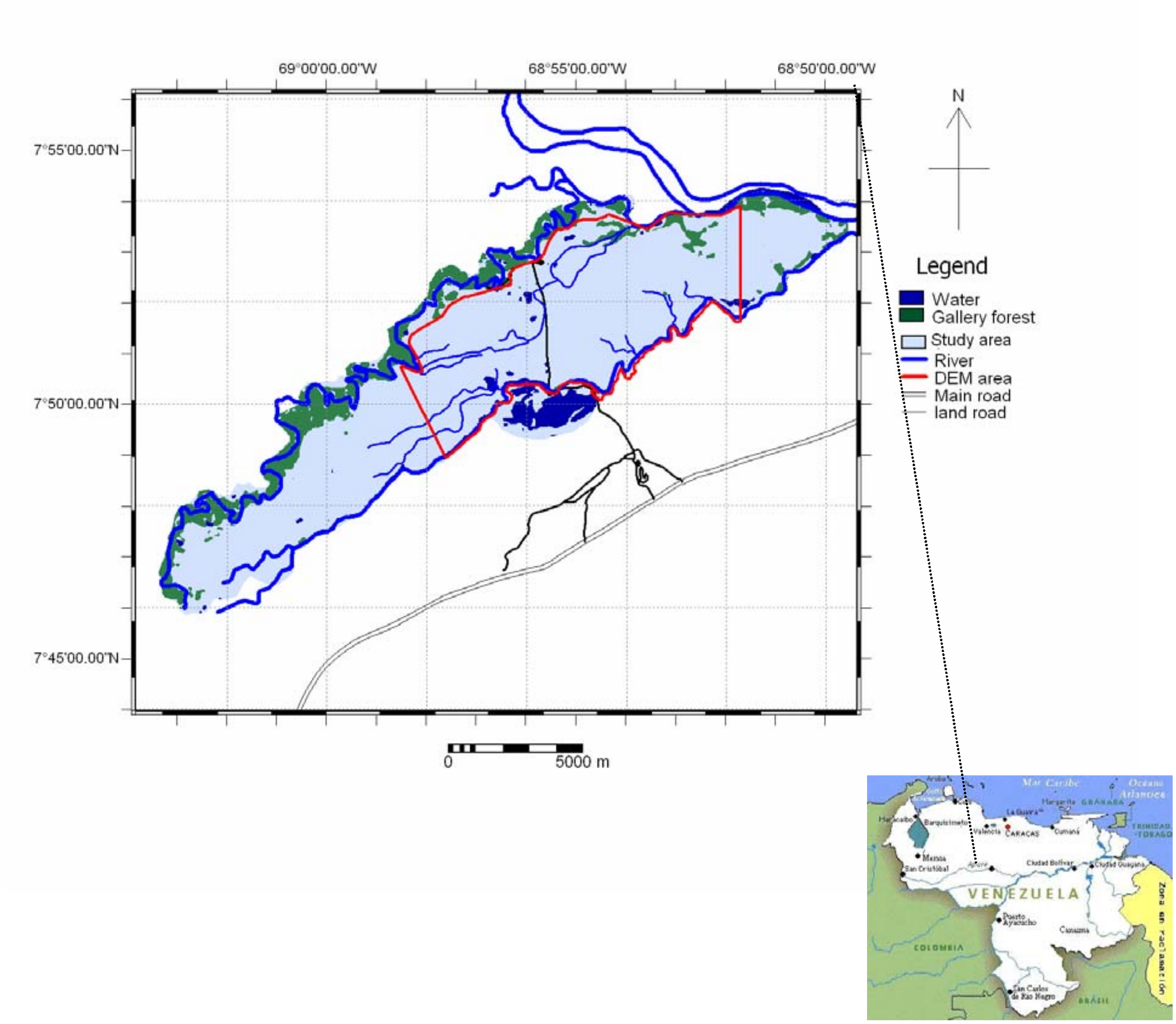

Figure 1. Geographical location of the study area in the flooded savanna of El Frío Biological Station, Venezuela. The sample sites and dike are indicated.

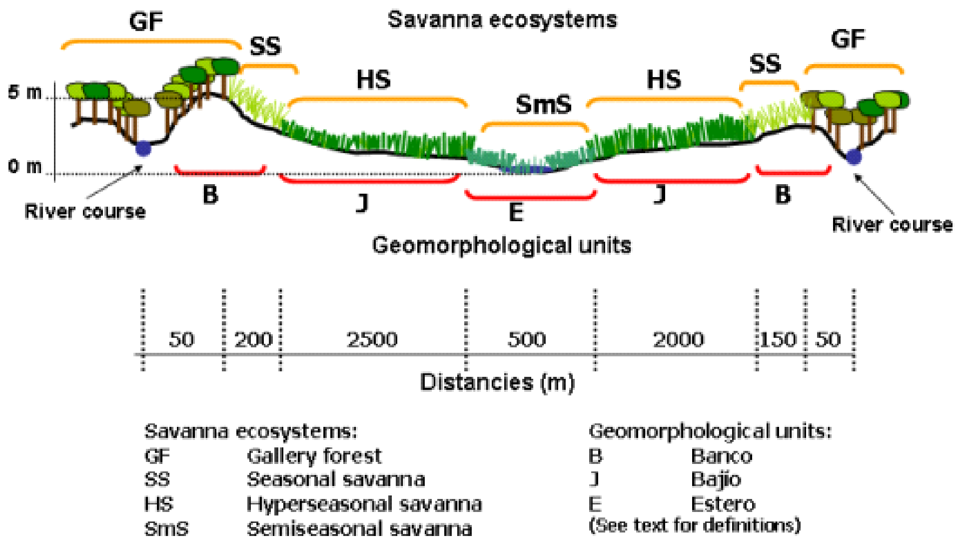

Figure 2. Idealized profile showing the ecosystem distribution in the study area in relation to the geomorphological units in the topographical gradient. Approximate distances between different units and relative altitude are shown.

where soils are of silty texture. On this kind of unit, the hyperseasonal savanna ecosystem is dominant. The third unit is *estero* which is the lowest unit of the topographic catena with a predominance of clay textured soil. Semiseasonal savanna and swamp ecosystems predominate in this unit. These geomorphological units highly influence the water distribution and soil humidity during the year and, consequently, the spatial distribution of plant species and ecosystems associated with them. Because of the construction of dikes, large areas of the *bajío* are almost permanently flooded and increasingly dominated by the semiseasonal savanna ecosystem.

Extensive grazing is the main land use activity in the area and in 1960 an earth dike was built to manage and store water during the rainy period and supply water in the dry period in order to maintain forage availability. The main change that has taken place as a result of dike construction is the replacement of hyperseasonal savanna by the semiseasonal savanna, reducing hyperseasonal vegetation from 45% to 21% in area (Chacón-Moreno 2001).

Previous studies concerning the ecology, soil and geomorphology of the study area have been presented by Castroviejo and López (1985), Pereira da Silva and Sarmiento (1997), Pinillos (1999), Sarmiento and Pinillos (2001), Sarmiento *at al.* 2004, Chacón-Moreno (2007).

METHODS

Three phases were followed: ecological analysis of species distribution, spatially explicit model of hydrological dynamics, and the integration of the species distribution in a spatial model.

Ecological analysis of species distribution

The direct and indirect response of vegetation species to environmental factors was analysed using canonical correspondence analysis (CCA) as a direct gradient analysis technique and path analysis as an indirect statistical technique(Figure 3). Vegetation data contained information on plant species presence/absence, frequency and cover of 57 sampling sites. The sites were sampled with 100 m^2 (10m x 10m) quadrats according to a stratified random sampling design. At each site, 10 plots of 1 m^2 were selected at random, species were listed and cover % of each species was estimated. For each of these sites, environmental and management characteristics were recorded, and for 37 sample sites relative soil water content was analyzed by collecting soil samples and measuring the percentage of water content in the laboratory. Additional information from maps created from remote sensing data (radar and Landsat images) was incorporated in the analysis. Detailed description of the results and analysis were presented in Chacón-Moreno *et al.* (2004).

Using a Generalized Linear Models (GLM) procedure for presence/absence data, the presence probability model of a species related to an environmental parameter or variable can be calculated using the Gaussian logit curves as the predictor model (Ter Braak 1995, Ter Braak and Looman 1995). The procedures to create the Generalized Linear Model are presented in CanoDraw software (Smilauer 1992).

Three kinds of analysis were carried out for each group of data previously mentioned. The first type of analysis corresponds with the presence-absence vegetation data, the second type is related to the frequency vegetation data, and the third type is carried out with cover vegetation data. The predictor model used for presence/absence data is the "logit" predictor (equation 1) where γ = linear predictor. The final equation solutions for the model of species probability, and frequency and cover distribution are presented in equations 1 and 2. In these equations the quadratic term is modified including ecological terms as *tolerance* and *optimum* (Ter Braak and Prentice 1988, Ter Braak and Looman 1995).

Equation 1

$$\gamma = \frac{\mathrm{ae}^{-0.5\left[\frac{(\chi - \mu)^2}{t^2}\right]}}{1 + \mathrm{ae}^{-0.5\left[\frac{(\chi - \mu)^2}{t^2}\right]}}$$

Equation 2

$$\gamma = \mathrm{ae}^{-0.5\left[\frac{(\chi - \mu)^2}{t^2}\right]}$$

Where $\boldsymbol{\gamma}$ is the probability (equation 1) and abundance (relative frequency) or the percentage of cover (equation 2) estimated by the model, $\boldsymbol{\chi}$ is the environmental factor, $\boldsymbol{\mu}$ is the species' optimum for this environmental factor, $\boldsymbol{t}$ is the tolerance, and $\boldsymbol{a}$ is a coefficient related to the height of the peak. Ecological definitions of this parameter are described in Ter Braak and Prentice (1988), and Ter Braak and Looman (1995). Further description of the statistical methods and procedures to analyze the data are found in Smilauer (1992), Jongman *et al.* (1995), Ter Braak (1996) and Ter Braak and Smilauer (1998).

Spatially explicit model of hydrological dynamics

To determine and understand the flooding spatial pattern of the savanna ecosystems, a Digital Elevation Model (DEM) was created from 5500 height points measured with GPS (precision <15 cm) and additional information from aerial photograph interpretation. As the height data was in form of points and lines and not homogeneously distributed a Triangular Irregular Network (TIN) was calculated and late a raster map of a resolution of 5 m and a height precision of centimeters, was derived (Smith *et al.* 2006).

A modification of the DEM (Smith *et al.* 2006) was constructed in order to obtain a raster map where elevation points are relative to a virtual plane. The result of this modification is a relative elevation model (Figure 4) where each point in the area is relative to an inclination plane described by a simple equation, taking the maximum elevation point at the beginning of the slope and the minimum elevation point at the end of it (Figure 5). This simple model was created because the area represents a large plane with a minimal gradient, derived from the natural course of the rivers from west to east in the Apure-Arauca river basin. Using regression analysis between relative elevation model and the relative soil water content based on data collected in the field (Chacón-Moreno *et al.* 2004), the hydrology-topography relationship was established and raster maps of the relative soil water content (SWRC) were elaborated. The regression coefficients derived from the regression analysis were used to calculate the relative soil water content for each pixel or cell of the relative elevation model raster map. Regression analyses were made under two different scenarios considering the field data with and without the influence of the dike.

Ecological and spatial integrated model of species distribution

The spatial distribution of the plant species was obtained by integrating the main results of the ecological analysis and plant species distribution models with the spatial models. The spatial model for the topographical gradient is represented by the

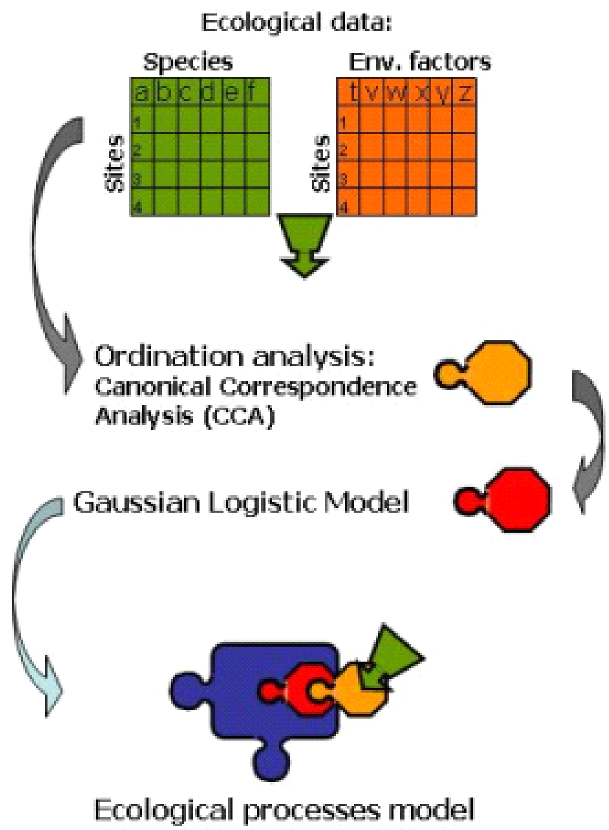

Figure 3. Scheme of the methodological approach for the ecological analysis of species distribution. Integration of species and environmental data into the ecological analysis (ordination and Gaussian models) is indicated.

relative altitude model and the spatial model of soil water availability is represented by the SWRC model, which was derived from a regression between relative soil water content from field data and the relative altitude (Chacón-Moreno et al. 2004). The integration of ecological and spatial models was developed using GIS (ILWIS).

Models of species distribution were elaborated considering the different hydrological scenarios and maps of present/absence, frequency and cover of the main species were elaborated (See methodological scheme in Figure 6).

Validation of the species distribution models

To validate the accuracy of the species distribution models, a sample set of 43 ground data points was collected to confirm species presence/absence. The size of the sampled ground data control was 10 x 10 m and the data were compared to species distribution maps and error matrices. Kappa analysis and descriptive technique analysis were used to measure the accuracy of the models (Congalton *et al.* 1983, Congalton 1991, Janssen and van der Wel 1994).

RESULTS

Selected species

Table 1 lists the frequency and cover of the dominant species for each savanna ecosystem of El Frío Biological Station. *Leersia hexandra, Panicum laxum* and *Ipomoea fistulosa* are the most common species found in the whole area. However, for each particular ecosystem class, the species dominance changes; in the seasonal savanna, *P. laxum* is the most frequent species observed, *Paspalum chaffanjonii* shows an important value of frequency and *L. hexandra* is

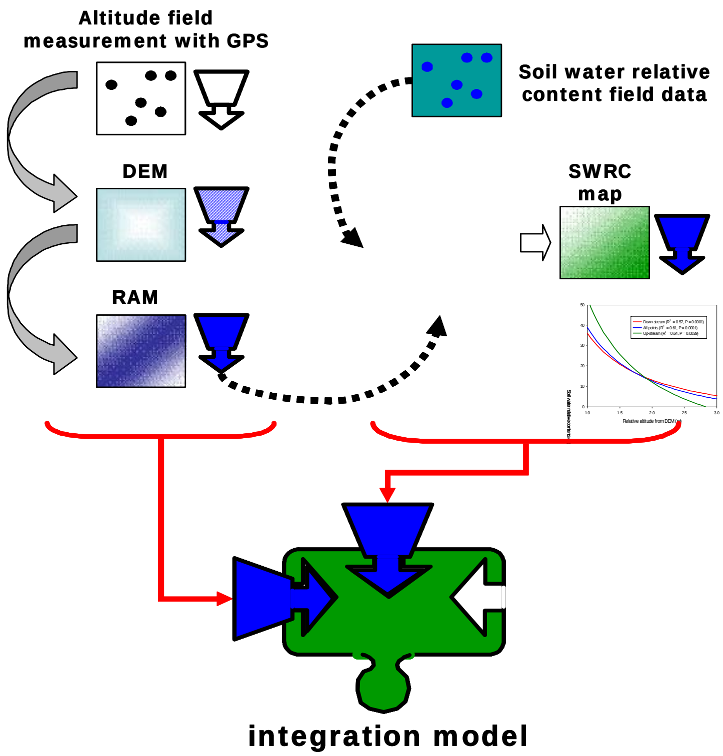

Figure 4. Scheme of the elaboration of the spatially explicit integrated model. Digital Elevation Model (DEM) derived from GPS measurements, and relative elevation model (RAM) derived from DEM. Relative soil water content (SWRC) map derived from regression between field data of relative soil water content and relative elevation model.

Calculation model of the relative elevation:

The diagram shows a representation of the slope in the area and the relation with the real situation (blue line) where the hmax and hmin are the maximun and minimum elevation, dmax is the length of the gradient, dx is the distance from the point of maximun elevation, and y is the elevation value in the model.

The relative elevation is the difference between y and the real elevation derived from field measurement.

$$y = d_{max} + ((h_{min} - h_{max}) \div d_{max}) \times d_x$$

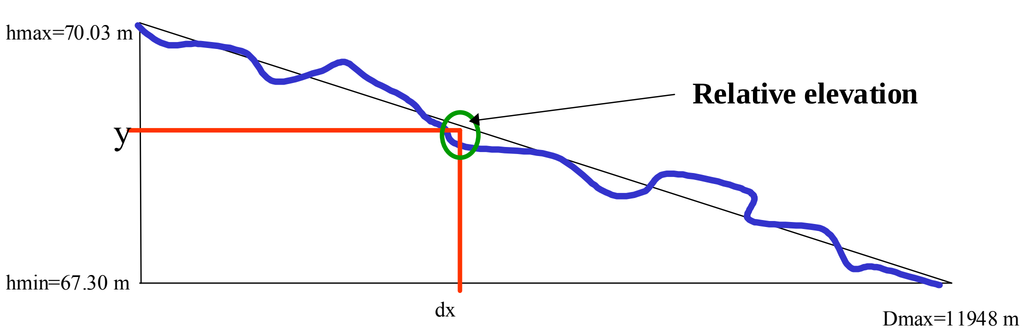

Figure 5. Representative diagram of slope calculation from the Digital Elevation Model (DEM) described in Smith *et al*. (2006), in order to obtain raster map values of relative elevation.

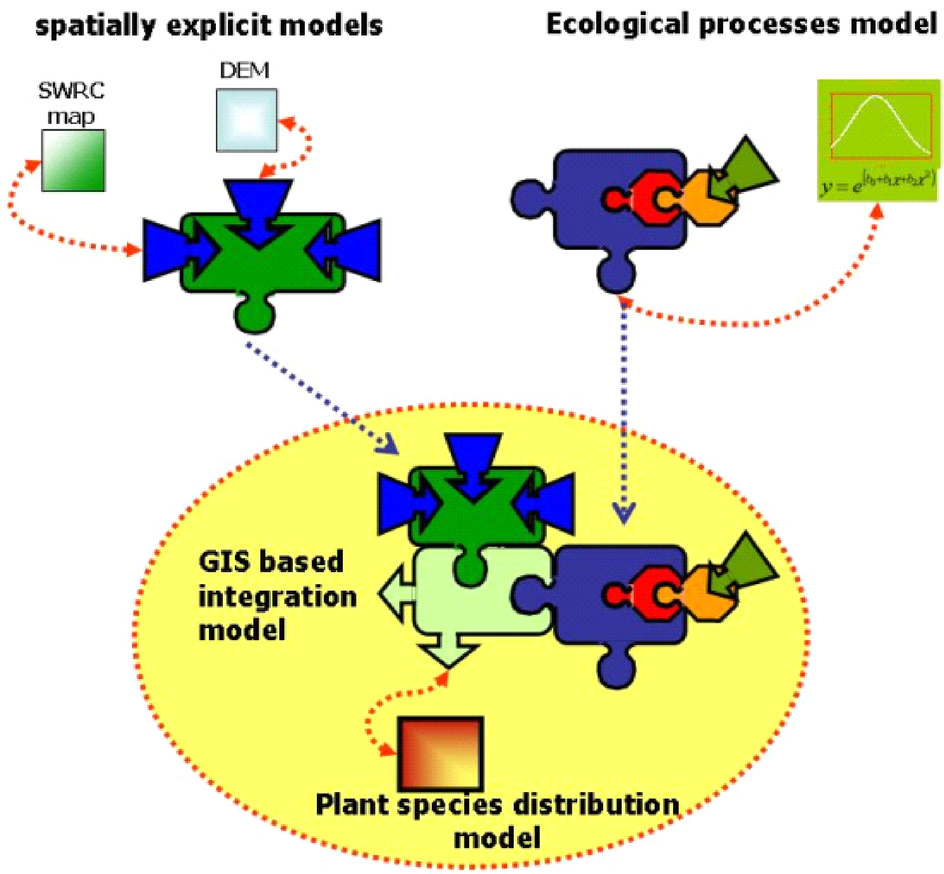

Figure 6. General methodological scheme of the pattern of species distribution and spatial models. The ecological processes and spatially explicit models are integrated using a GIS.

the third most important species showing values lower than those for the whole area. In the hyperseasonal savanna ecosystem *P. laxum* remains the most important species, and *L. hexandra* increases its importance related to the other ecosystem classes. In the semiseasonal savanna ecosystem class, *L. hexandra* predominates over the other species and *Hymenachne amplexicaulis* and *Eleocharis interstincta*, which were not important in the other ecosystems, now present high values of frequency.

For cover data, the results are similar to those of frequency, where *P. laxum* and *L. hexandra* present the major cover values with dominance of over 25% in comparison to the total list, while the other species does not reach 10% cover.

Gaussian distribution model of plant species

Figure 7 shows the Gaussian distribution models according to presence-absence, frequency and cover data in relation to relative elevation in catena (Fig. 7a, 7c, 7e) and the relative soil water content (Fig. 7b, 7d, 7f). The probability model of species distribution in relation to relative elevation (Fig. 7a) shows a clear division between the two groups of species. At the lowest topographical position, *H. amplexicaulis* and *E. interstincta* have the highest probability; however, when the relative elevation increases above 1.5 m, the probability of occurrence of these species decreases immediately to 0. *L. hexandra* remains with the highest probability values until 2.0 m, when it begins to decrease to minimum values at 3.0 m. On the other hand *P. laxum* and *P. chaffanjonii* present the highest probability values at the highest topographic position (2-3 m), nevertheless, the probability decreases when the elevation is lower than 1.5 m. The model represents a clear niche separation

Table 1. List of the most frequent species and species with the highest cover for each savanna ecosystem and the total area in the flooding savanna of El Frío Biological Station. Frequency and cover values are in brackets.

Major frequency	Major cover
From the whole area:	**From the whole area:**
Leersia hexandra Swartz (0.81)	*Panicum laxum* Swartz (32.3%)
Panicum laxum Swartz (0.72)	*Leersia hexandra* Swartz (26.1%)
Ipomoea fistulosa Mart. Ex Choisy (0.52)	*Paspalum chaffanjonii* Maury (5.0%)
	Hymenachne amplexicaulis (Rudge) Nees (2.5%)
From seasonal savanna	**From seasonal savanna**
Panicum laxum Swartz (0.94)	*Panicum laxum* Swartz (43.0%)
Paspalum chaffanjonii Maury (0.79)	*Leersia hexandra* Swartz (14.2%)
Leersia hexandra Swartz (0.68)	*Paspalum chaffanjonii* Maury (9.0%)
	Axonopus purpusii (Mez) Chase (5.0%)
From hyperseasonal savanna	**From hyperseasonal savanna**
Panicum laxum Swartz (0.90)	*Panicum laxum* Swartz (48.1%)
Leersia hexandra Swartz (0.80)	*Leersia hexandra* Swartz (15.1%)
Ipomoea fistulosa Mart. Ex Choisy (0.70)	*Paspalum chaffanjonii* Maury (5.8%)
	Ipomoea fistulosa Mart. Ex Choisy (1.3%)
From semiseasonal savanna	**From semiseasonal savanna**
Leersia hexandra Swartz (0.94)	*Leersia hexandra* Swartz (49.6%)
Hymenachne amplexicaulis (Rudge) Nees (0.74)	*Hymenachne amplexicaulis* (Rudge) Nees (7.4%)
Eleocharis interstincta (Vahl) Roem. & Schult. (0.47)	*Eleocharis interstincta* (Vahl) Roem. & Schult. (6.8%)
	Panicum laxum Swartz (4.8%)

among the species. The patterns of species distribution along the relative soil water content variable (Fig. 7b) show a bell-form curve for all the species, except *P. laxum* which has the highest probability at the lowest water relative content value. *L. hexandra* and *I. fistulosa* present similar patterns and amplitude at the medium-high values of relative soil water content (optimum between 15 and 30 %). Conversely, *P. chaffanjonii* was restricted to a narrow range of relative soil water content (5-13%), and *H. amplexicaulis* was restricted to the highest range of relative soil water content (> 25%).

Using frequency data, figure 7c shows that , *H. amplexicaulis*, *L. hexandra* and *P. laxum* present a pattern distribution with optimums above 90% of frequency. *H. amplexicaulis* is located at low relative elevation and narrow distribution whereas *P. laxum* is located at high relative elevation. *L. hexandra* exhibits a wide distribution along the topographical gradient ranging from 0.5 m to 2.0 m with relative frequency above 40%. *I. fistulosa* presents a narrow distribution and the lowest frequency values (> 50%) as well as *P. chaffanjonii* with a distribution located at the highest elevation. Figure 7d presents the pattern of species distribution for frequency data in relation to relative soil water contents. *L. hexandra* and *P. laxum* are the species that present major relative frequencies values, almost 1, in the optimum of the gradient, and occupy different places along the gradient. *P. laxum* has a gradient optimum at low water contents; nevertheless, *L. hexandra* shows an optimum of 26.8 % in the other extreme of the gradient. *P. Chaffanjonii* has a similar pattern to that of *P. laxum*, but the range amplitude of distribution is narrow, and the optimum is located at 9.45 %. In contrast, *I. Fistulosa* has a similar distribution pattern to *L. hexandra*, but with lower frequency and amplitude values. *H. Amplexicaulis* and *E. interstincta* present a singular pattern with a narrow amplitude or tolerance (3.42 and 0.83 %), but with the highest frequency values at the optimum, which occur at 28.7 and 22.81 % respectively.

Figure 7e shows the species cover model according to relative elevation and figure 7f shows

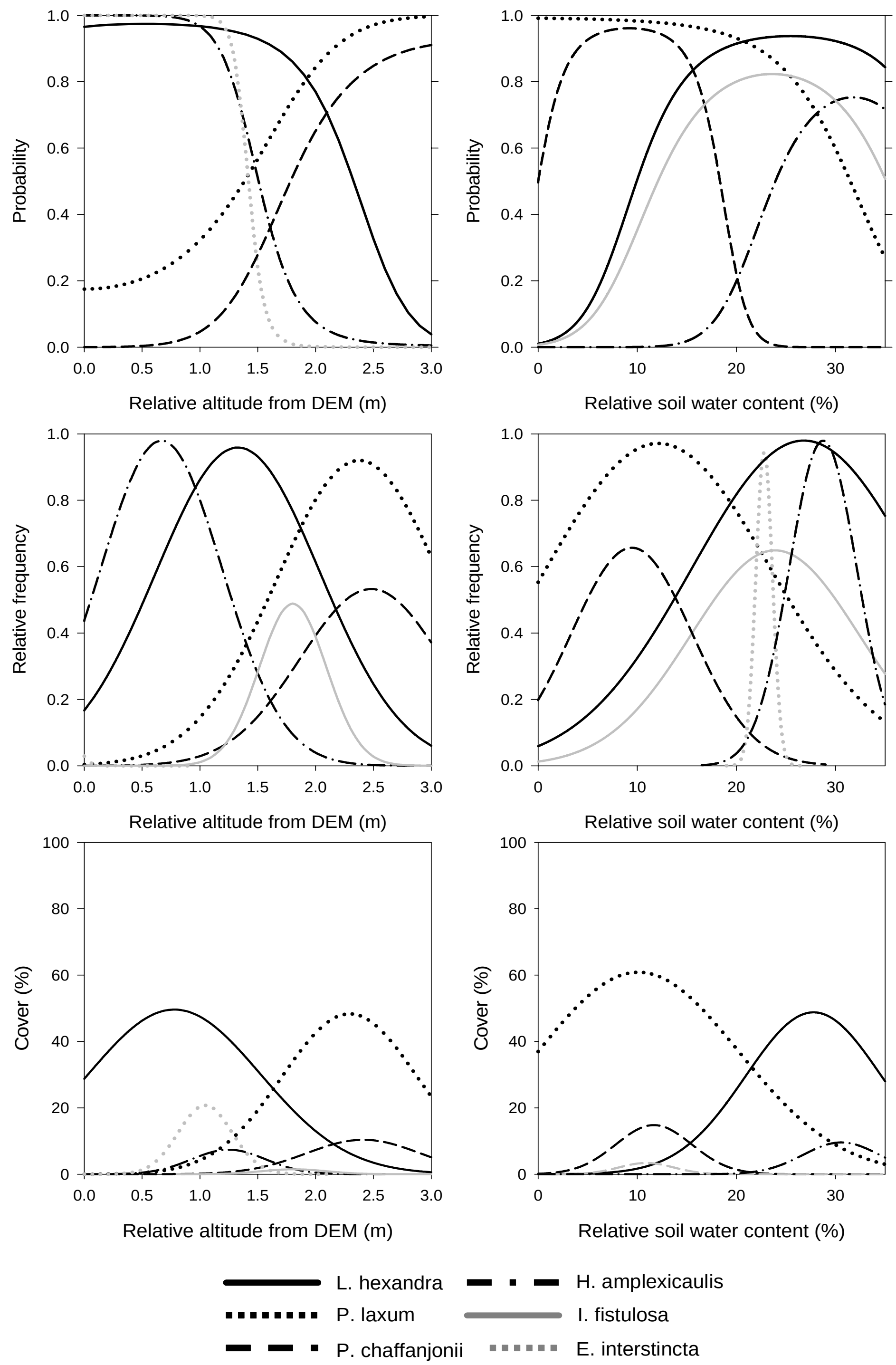

Figure 7. Gaussian distribution models of *P. laxum, L. hexandra, H. amplexicaulis, E. interstincta* and *P. chaffanjonii* according to presence/absence (7a and 7b), frequency (7c and 7d) and cover (7e and 7f) data in relation to the relative elevation in catena derived from DEM (7a, 7c and 7e) and relative soil water content (7b, 7d and 7f) of El Frío Biological Station, Venezuela.

the species cover model in relation to relative soil water content. Only *P. laxum* and *L. hexandra* present cover values above 40% and a wide distribution (Fig. 7e); moreover, these species occupy different niche or position into the gradient, *P. laxum* grows on areas above 1.0m high whereas *L. hexandra* grows on areas under 2.0m high. On the other hand, *E. interstincta* presents a narrow distribution on low areas with a comparative high cover value around 20%. *P. chaffanjonii*, *H. amplexicaulis* and *I. fistulosa* present cover values under 5%. The percentage of cover vegetation of *P. laxum* was the largest with respect to the relative soil water content showed in figure 7f, reaching 60% of cover and ranging between 20 and 60% for water content between 0 and 22 %. Besides *L. hexandra* presented a maximum cover of 50 % with a wide range distribution along the gradient on the wet side. These two species occupy the whole gradient with maximum covers and overlapping. *P. chaffanjonii* and *H. amplexicaulis* presented cover values above 8%, and they were restricted to dry and wet areas respectively, without any overlapping between them.

Spatial model of relative elevation from DEM

Figure 8 shows the relative elevation model derived from DEM for the study area (Smith *et al.* 2006) (the equation is explained in figure 5). This model shows that the basins areas are mainly located upstream from the dike and are associated to the Macanillal river on the south-west side. Higher zones are associated to the small banks of the small rivers inside the area and the highest area is associated with the Guaritico river bank in the confluence with the Apure river at the north-east side.

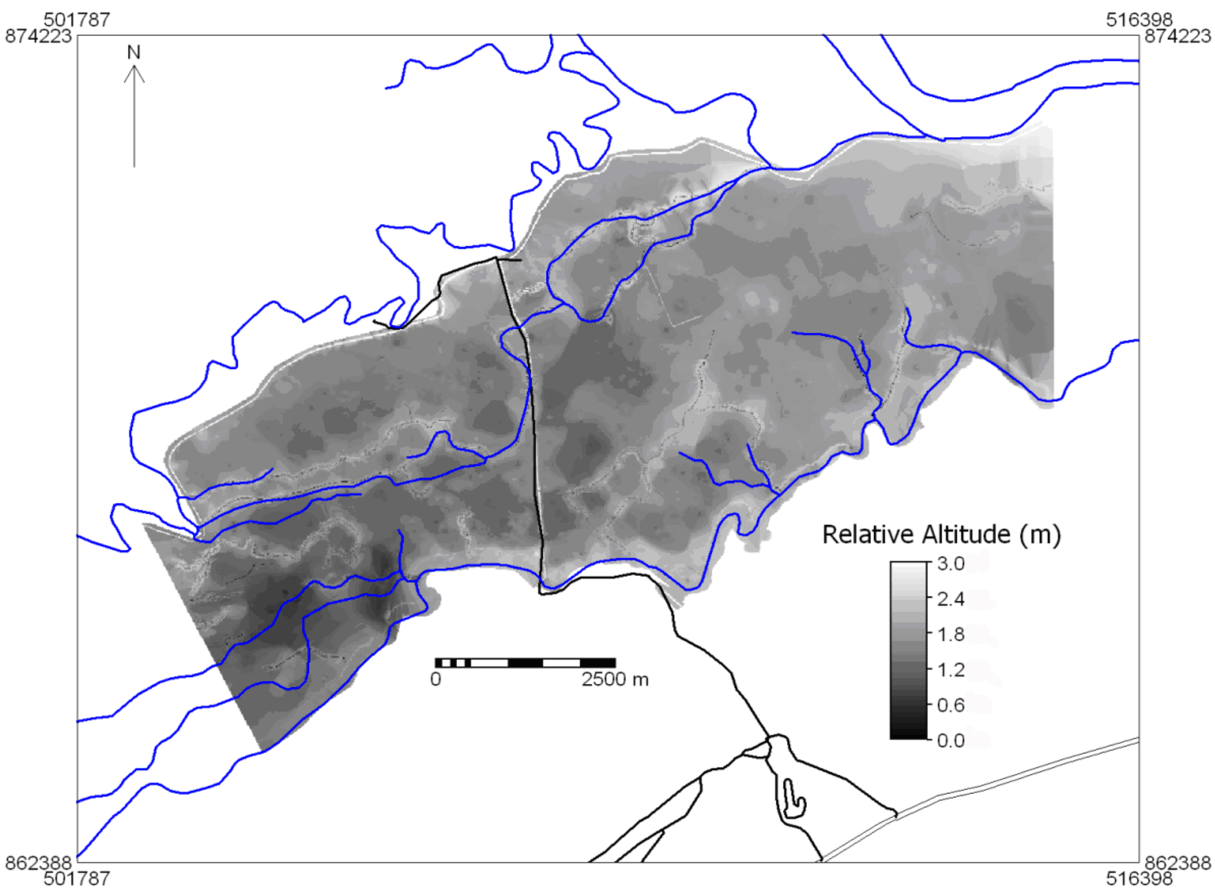

Figure 8. Relative Elevation Model (RAM) of the El Frío Biological Station study area, in the flooding savanna, Venezuela, derived from DEM (Smith *et al.,* 2006 and slope equation described in figure 5).

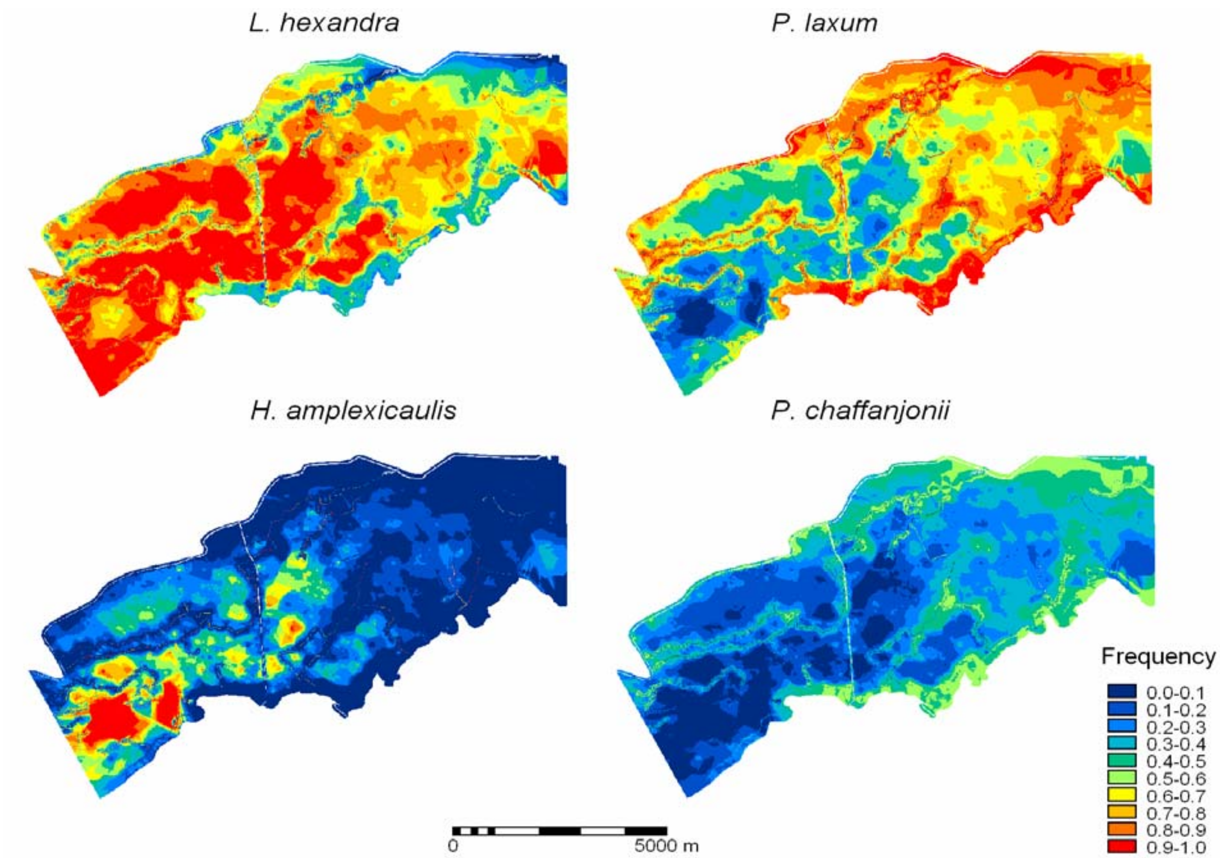

Figure 9. Model of species distribution of *P. laxum, L. hexandra, H. amplexicaulis* and *P. chaffanjonii* for frequency data based on Relative Elevation Model (RAM) in the flooding savanna of El Frío Biological Station, Venezuela.

Ecological and spatial model of species distribution based on relative elevation model

Figure 9 presents the frequency distribution model of the most common species in relation to the relative elevation in the catena. It is clear that the major frequency values of *L. hexandra* (> 0.75) are associated to the lowest areas in the west (upstream from the dike); however, higher frequency values are observed in the middle of the study area close to the east side of the dike. Medium frequency values for *L.hexandra* are observed in the rest of the study area. High frequency values of *P. laxum* are mainly distributed to the highest areas in the East (downstream from dike), but medium-low values are observed in the upstream dike area (West).

H. amplexicaulis presents a similar distribution to *L. hexandra*, but the frequency values are lower, except for the basin zones on the west side where the frequency values reach over 0.70. *H. amplexicaulis* is absent in areas associated to higher zones in the east. *P. chaffanjonii* presents lower frequency values and distribution similar to *P. laxum*; however, this species is present in almost all the area, except in the lowest part of the west side.

Figure 10 shows the coverage model for the most important species is presented in relation to relative elevation model. *P. laxum* presents the maximum cover with values above 15% for almost the whole area, but the cover values decrease to less than 5% in the lowest zones. *L. hexandra* presents the highest cover in areas upstream from the dike, medium cover values (10-25%) downstream from the dike and values < 5% in the highest areas on the river banks. *E. interstincta* and *P. chaffanjonii* present the lowest cover values (<5%). *E. interstincta* shows medium values in the lower zones, while *P. chaffanjonii* is confined to the river banks where it presents medium cover values.

Species distribution model validation

Table 2 presents the results of accuracy level and Kappa values derived from the error matrix analysis by comparing the result of species distribution models with the ground data collected. The values of producer accuracy obtained for the five studied species are high when presence/ absence data are considered, while producer accuracy values for frequency data are high for *L. hexandra*, and *P. laxum*,. For cover data *P. chaffanjonii* and *E. interstincta* present high values. Overall accuracy for *L. hexandra*, *P. laxum*, and *E. interstincta* was around 55 %. The producer accuracy is an evaluation of the map quality compared to the field measurements.

Ecological and spatial model of species distribution based on hydrological gradient

Figure 11 presents the regression models between the relative elevation derived from the DEM and the relative soil water content considering all downstream and upstream points. The regression model for data collected upstream presents a major slope due to the water accumulation through the dike. In contrast, the model for downstream data presents lower relative soil water content at the lowest relative elevation.

Figure 12 shows the cover distribution of the two most important species: *L. hexandra* and *P. laxum* in relation to the spatial hydrological gradients.

Three hydrological scenarios were modeled.

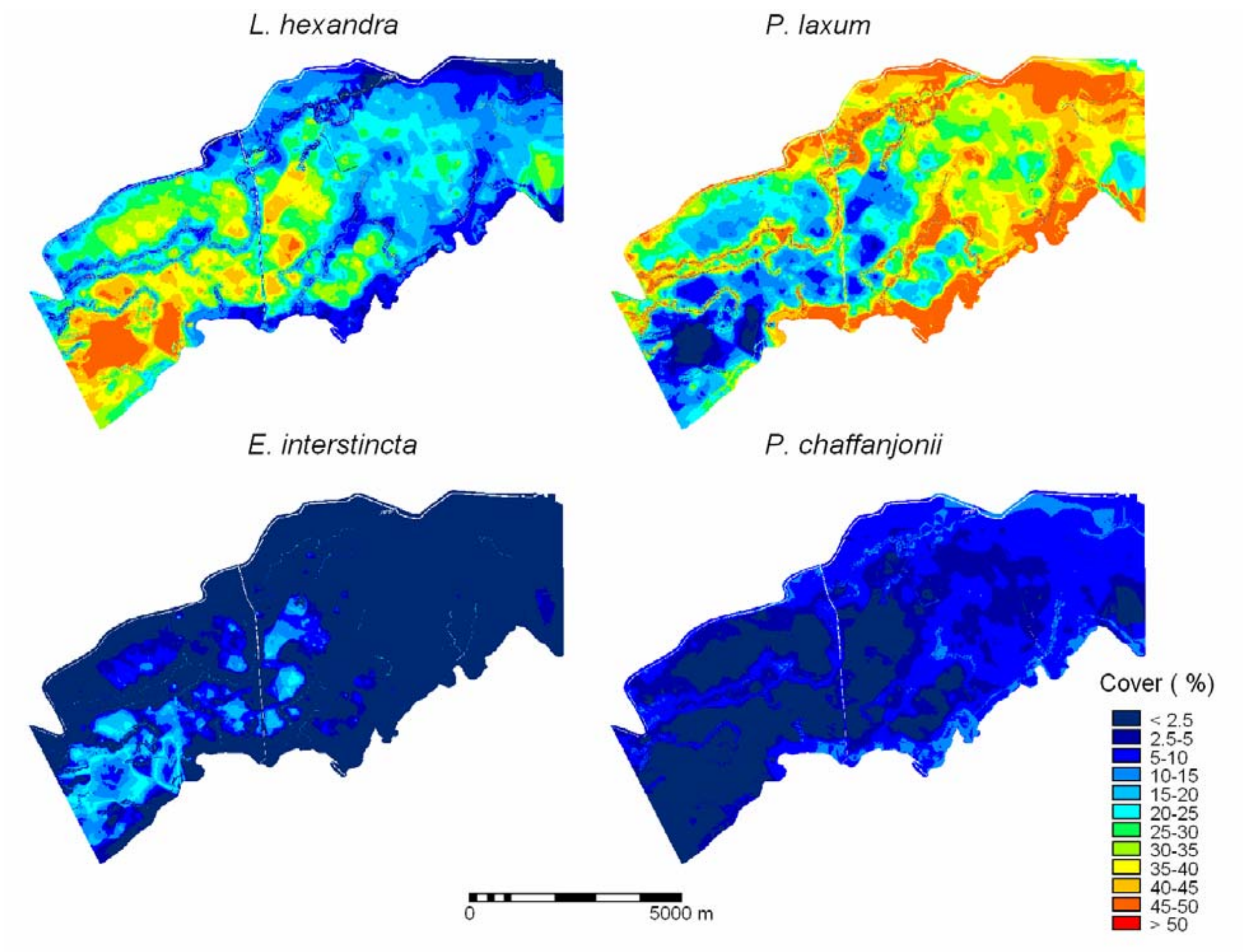

Figure 10. Model of species distribution of *P. laxum, L. hexandra, E. interstincta* and *P. chaffanjonii* for cover data based on the Relative Elevation Model (RAM) of the flooding savanna of El Frío Biological Station, Venezuela.

Table 2. Accuracy level and Kappa value derived from the analysis of error matrix of species distribution models versus independent collected ground data. For frequency, the data evaluated correspond to values larger than 0.5, and for cover, the data evaluated correspond to cover values larger than 25% and larger than 10%. For *H. amplexicaulis* data only is presented for frequency (0.5 and 0.25), and for *E. interstincta* only for cover (25% and 10%). NA = non applicable.

Species	Data type	Accuracy level			Kappa
		Producer	User	Overall	value
Leersia hexandra	Presence/absence	100	53	53	0
	Frequency	91	57	58	0.12
	Cover 25%	35	73	58	0.19
	Cover 10%	91	58	60	0.17
Panicum laxum	Presence/absence	100	60	60	0
	Frequency	77	57	51	-12
	Cover 25%	73	58	51	-0.1
	Cover 10%	96	60	58	-0.05
Paspalum chaffanjonii	Presence/absence	100	23	23	0
	Frequency	20	67	79	0.22
	Cover 25%	70	22	35	-0.03
	Cover 10%	100	24	26	0.01
Hymenachne amplexicaulis	Presence/absence	100	19	21	0.01
	Frequency (0.5)	0	0	67	-0.19
	Frequency (0.25)	25	25	72	0.08
Eleocharis interstincta	Presence/absence	83	20	51	0.13
	Cover 25%	0	NA	86	0
	Cover 10%	50	33	79	0.28

The first scenario is the actual situation where the dike controls the water distribution determining an accumulation on the west side (upstream from the dike) and a deficit on the east side (downstream from the dike). The two species show a clear niche differentiation. *P. laxum* presents major coverage downstream, where the hydrological conditions are drier than upstream.

The second scenario presents a hydrological condition without the dike and has a more uniform water distribution, leaving the upstream area less flooded. In this situation, *L. hexandra* shows a cover reduction and *P. laxum* increases its cover, especially upstream.

The third scenario shows a reduction of the relative soil water content of 5%, which could occur in a dry year. Here an almost absolute dominance of *P. laxum* and an important decrease of *L. hexandra* is observed. The areas where *L. hexandra* presents higher cover values are reduced to three sinks with the biggest depth.

DISCUSSION

The landscape of the flooding savanna is practically flat and the relative elevation differences are very subtle (not greater than three meters); however, direct observation shows that the species community gradually changes within the landscape and the dominant species have a strong relation to

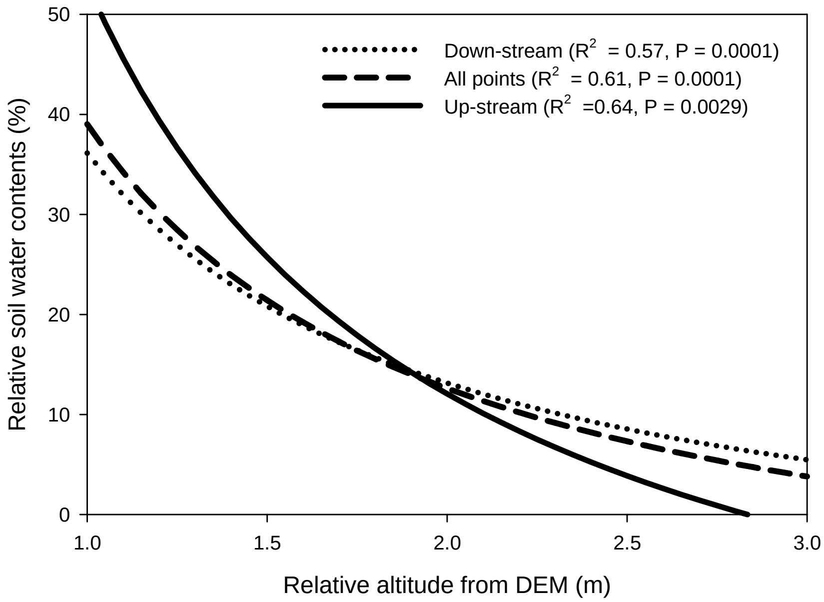

Figure 11. Regression curves between Relative Elevation Model values (RAM) derived from DEM (Smith *et al.* 2006) and Relative Soil Water Content values measured in the study area of the flooding savanna of El Frío Biological Station, Venezuela. Three sets of data were considered: all field observations, down stream of dike observations, and up-stream observations. Regression coefficients and significance values are indicated.

the small environmental gradients determined (Chacón-Moreno *et al.* 2004).

The dominance of *P. laxum* and *L. hexandra* over other species was remarkable when the cover values were considered; nevertheless, the frequency values are more realistic in relation to the species importance because the cover changes during the year due the seasonal climate patterns and phenological growing phases. Therefore, frequency is a vegetation parameter depending not on the extension or primary production but on the number of plants present, consequently it does not have as much variation as the cover parameter. So, high frequency species such as *H. amplexicaulis* in the semiseasonal savanna or *P. chaffanjonii* in the seasonal savanna characterize these ecosystem classes.

When the dominant 'natural' slope was eliminated from the digital elevation model, the relative elevation model showed an inverse slope direction, presenting the highest elevations in the West associated to the Apure river bank, which is the largest river in the area. The river banks of the Apure and Guaritico have higher elevations than the Macanillal river bank (where the deepest sink is found). The presence of lower areas in the West of the study area permits the accumulation of water along the dikes and result in a very wet environment where water in the soil can remain during lengthy periods.

The frequency distribution model of plant species based on the relative elevation model confirms the associations among the species and the hydrological conditions derived from the water availability and the flooding conditions expressed in the relative elevation model. *L. hexandra* is a species associated to medium-high values of soil water content, and the model shows a distribution associated to lower relative elevation values. On the other hand, *P. laxum* occupies these relatively higher areas associated with the hyperseasonal savanna conditions. *H. amplexicaulis* is mainly distributed in the lower areas, where water accumulation occurs over longer periods, while *P. chaffanjonii* presents a strong relation to the river and the stream banks, where a flooded condition is infrequent or absent throughout the year. The plant species distribution model for cover data confirm the dominance of the four main species considered in the study.

The higher producer accuracy values of the plant species distribution model indicate that the

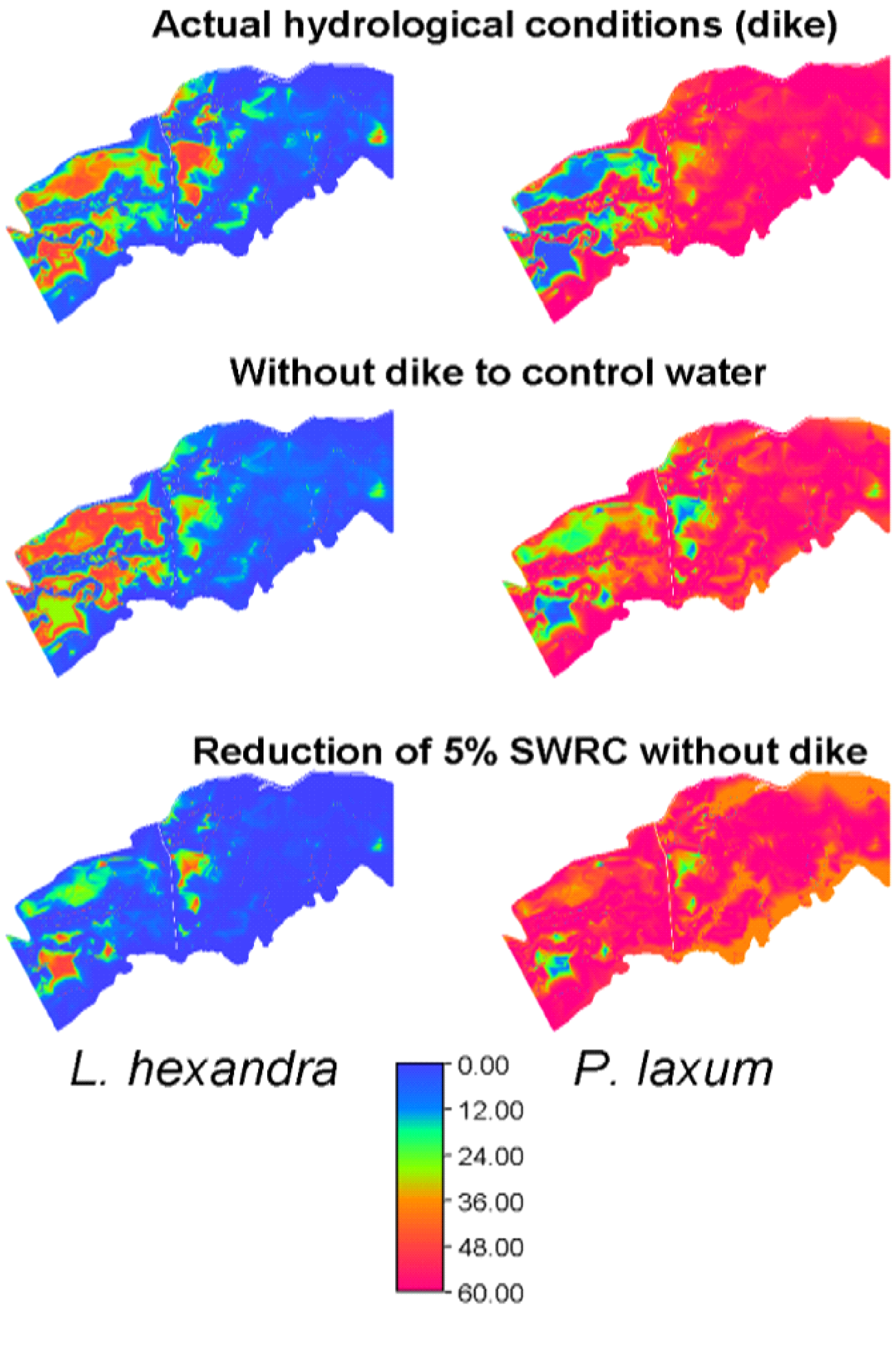

Figure 12. Distribution model of *P. laxum* and *L. hexandra* for cover data based on Relative Soil Water Content (SWRC) for three different hydrological scenarios: actual hydrological situation, without dike effect or control, and reduction of 5% of SWRC for the flooding savanna of El Frío Biological Station, Venezuela.

selection criterion considered in the analysis are satisfactory. The lowest Kappa values are explained because the number and selection of the sampled control data were not suitable, leaving some key areas without sampling.

A significant regression between the relative elevation model and the relative soil water content shows that relative elevation is the main environmental variable determining soil water availability (Chacón-Moreno *et al.* 2004). Also, the regression between relative elevation model and relative soil water content allows the possibility to estimate the soil water content in conditions dissociated to the dike effect, and even simulate the plant species distribution with different hydrological conditions.

The plant species distribution for frequency data in relation to relative soil water content of *P. laxum* and *L. hexandra* is similar to the distribution in relation to relative elevation model; however, the reduction of the dike effect causes drier conditions upstream. These conditions create favorable areas where the frequency values of *P.laxum* increase, while simultaneously the frequency values for *L. hexandra* decrease. *P. laxum* is a dominant species associated to the hyperseasonal savanna. When the simulation is directed towards diminishing the relative soil water content, the frequency values of *P. laxum* increase because the hydrological conditions are similar to the hyperseasonal savanna in areas where semiseasonal savanna ecosystem is dominant. This result shows the transformation derived from the embankment where the dominant species in the hyperseasonal savanna like *P. laxum*, and dominant species in the semiseasonal savanna like *L. hexandra*, are displaced in relation to new relative soil water content. These species displacement give origin to the landscape change described and analyzed in Chacón-Moreno (2001).

The results obtained from the ecological models confirm, through the high accuracy model producer, that the duration of water in the soil is the principal environmental factor that leads to plant species distribution in the flooding savannas and determines the ecological responses of the ecosystems. Furthermore, it is important that the plant distribution follows a gradual change where the main species do not overlap. Distribution and separation of dominant species along the gradient show a clear niche separation.

A product obtained from these models was the possibility to monitor the changes in species distribution derived from changes in the relative soil water content. Therefore, the distribution (cover and frequency) of the main plant species could be determined if changes in the hydrological balance are introduced and the plant communities and habitats could be quantified in order to understand the impact of ecosystem changes on diversity of the flooding savanna.

Finally, the application of this model could be useful to predict new changes in the plant species composition if hydrological conditions are modified. The innovation of the model described above resides in that it allows ecological aspects to be related to the spatial dimension.

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