Spatial analysis to evaluate the effects of soil sand content on the progress of the invasive process of G. triacanthos in riparian forests

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Abstract

Riparian systems are highly threatened by alterations in its hydrological regimen and biological invasions. To guide its conservation is important to understand the relationships established between biological invasions and abiotic conditions affected by the hydrological regimen. We analyze the relationship between the distribution pattern of soil sand content and the invasive process of the woody invasive *Gleditsia triacanthos* in riparian forests of the Esteros de Farrapos and Islands of Uruguay River National Park, zoning the study area according to the type of relationship between both variables. We integrate the use of regression trees and geographic information systems to zone this relationship. This is a novel approach to study the relationships between an invasive species and its environment. Areas with lower sand content were found to be favorable for the development of the invasive species, and areas with higher sand content were found to limit its spread. No relationship was found between the intermediate sand content and the progress of the invasive process. This work highlights the complexity inherent to the definition of causal relationships in highly heterogeneous systems such as riparian ecosystems. Spatial analysis techniques are a useful tool for this approach.

Introduction

Riparian systems are highly threatened by various factors that modify their water regime, such as canalization, dredging, dam construction, irrigation systems and water extraction (EEM 2005). In a context of global change, biological invasions are added as another of its main threats (Richardson et al. 2007), being in turn facilitated by the alteration of ecosystems (Moreno et al. 2015). Poff et al. (2011) reported that the most successful invasive processes in riparian systems develop in areas where the hydrological regime has been previously modified. In order to guide the conservation of these vulnerable systems, it is important to understand the relationships established between ecological processes and abiotic conditions (Vaughan 2009).

Riparian systems are characterized by their spatial and temporal heterogeneity resulting from the redistribution of sediments, organic matter and other materials. Deposition and erosion processes are key drivers of vegetation development (Naiman and Décamps 1997). These processes operate at the local scale (Politti et al. 2018) and spatially arrange soil texture (Schaaf et al. 2011). Changes in soil texture in fluvial systems are associated with environmental conditions and water dynamics; there being a direct relationship between the size of deposited material and the carrying capacity of water flow, thus smaller materials (light textures) will be deposited in areas with lower flow rate (Bornette et al. 2008). In these situations, plants are exposed to longer periods of flooding due to the lower flow rate and a lower infiltration capacity in the soil as the size of the soil's constituent mineral fraction decreases. On the other hand, coarse-textured soils indicate areas of high energy, with higher flow rate and therefore greater entrainment and shorter flooding periods due to greater soil infiltration. The effects of sedimentation on vegetation development in riparian systems are not yet clear. In riparian forests associated with intermittent watercourses, Jolley et al. (2010) reported a negative relationship between deposition processes and the richness, diversity and occurrence of woody species. Similarly, in Nigerian wetlands, Festus and Zakaria (2021) reported that the sand content of the soil limits the development of invasive processes. On the other hand, the existence of a positive relationship between sediment supply and vegetation growth was reported for saline wetlands where sediment supply increases soil aeration, nutrient content and substrate height reducing the effects of flooding (Mendelssohn and Kuhn, 2003). This positive relationship was also reported in temperate flooded grasslands as a facilitator of the invasive process of the herbaceous *Phalaris arundinacea* (Zedler and Kercher 2004). These differences could be explained by the fact that different species respond differently to these conditions. However, in fluvial forests of the Uruguay River it was detected, using spatial analysis techniques, that the invasive woody *Gleditsia triacanthos* shows a complex response to variations in soil sand content (Sosa et al. 2018) indicating that despite its wide tolerance to modifications in environmental conditions, changes in soil texture affect its spread.

Gleditsia triacanthos is a woody species belonging to the Fabaceae family native to North America, and has been described for Uruguay as one of the two woody species with the greatest potential to displace native forest (Nebel 2006). In particular, in the riparian forests of the Esteros de Farrapos National Park, the invasive process of *G. triacanthos* has displaced almost all native species in some areas. This work was carried out with the objective of zoning the relationship between the distribution pattern of soil sand content and the invasive process of *G. triacanthos* in the riparian forests of Esteros de Farrapos and Islands of the Uruguay River National Park, using regression trees and geographic information systems. Although the integration of these tools has been used in a wide variety of environmental problems, groundwater mapping (Naghibi et al. 2016), heavy metal distribution in soil (Cheng et al. 2009; Kheir et al. 2010), erosion risk zones (Kheir et al. 2008) vegetation mapping (Lees and Ritman 1991), their use for zonation of ecological processes has been less explored. Further development of methodologies for zonation of the relationships between species and their environment is critical to determine which aspects of the heterogeneity of these systems affect invasive species.

Methodology

Study area-

It is located in the riparian forest of the Esteros de Farrapos and Islands of the Uruguay River National Park in the department of Rio Negro (32°37'36.308" S -58°09'40.920" W) Uruguay (Fig, 1).

The National Park comprises a fluvial wetland located in the final section of the Uruguay River where the flow rate decreases forming a zone of active deposition with fluvial islands and formation of sandbanks. It covers an area of 5,760 ha, including lakes, sandy beaches, floodable grasslands, and riparian forests (Achkar et al. 2003).

The fluvial bank on which the riparian forest develops is characterized by a landform that presents different shapes that can be described as ridge, spur, valley, hollow and flat (Jasiewicz and Stepinski 2013). In this area the riparian forest is of biogeographic importance due to the intrusions through the

Uruguay River of the subtropical forests of the Paranaense region, which have their southern limit of distribution in this area (Cabrera and Willink 1973; Grela 2004). The mean annual temperature and precipitation in this area are 18°C and 1244 mm (DMN 1996) respectively. Among the main native species in the study area are *Phyllanthus sellowianus* Müll., *Sebastiania schottiana* (Müll. Arg), *Ruprechtia laxiflora* Meisn., *Sapium haematospermum* Müll. Arg., *Pouteria gardneriana* (A.DC.), *Guettarda uruguensis* Cha & Schltdl., *Combretum fruticosum* Stuntz, *Terminalia australis* Cambess., *Salix sp*, Inga vera Wild., *Eugenia mansonii* O. Berg. and *Eugenia uruguayensis* Cambess (MVOTMA 2017). The main human activities carried out in the study area are cattle ranching and beekeeping; logging and hunting are less frequent (DINAMA 2014). The main threats to biodiversity conservation are the invasion of *G. triacanthos* and erosion of the seasonal island (DINAMA 2014).

Invasive Species-

Gleditsia triacanthos is a woody species belonging to the Fabaceae family native to North America, particularly in the Mississippi River basin, southern plains, and Texas (USDA 2016). It has a tolerance to a wide range of environmental conditions (USDA 2017). However, it shows moderate tolerance to flooding, (Hook 1984) and low regeneration when canopy is dense (Grime 1965). Its invasive potential is high; it has asexual and sexual reproduction, a high rate of fructification, seed production and germination and short juvenile stages (Marco and Páez 2000). It is dispersed by hydrocory and zoochory, mainly cattle (Henderson 2007).

It is recognized as an invasive species in a wide variety of regions and environments (USDA 2016). Its invasive status has been reported in Spain (Rivas and Bellot 1948), Australia (Csurhes and Kriticos 1994), Serbia and Ukraine (Nikolic et al. 2010). In South America it has been reported as invasive in Argentina (Ghersa et al. 2002; Fernández et al. 2017). In Uruguay it is recognized as one of the two woody species with the greatest potential to displace native forest (Nebel 2006), with the southwestern region of the country being the most vulnerable to this invasive process (Romero et al. 2021).

Sampling design-

In the invasive process of *G. triacanthos* on the riparian forest of the Uruguay River, Sosa et al. (2018) identified two spatial zones according to its status: a consolidated invasion area close to the area where it was initially planted, and a propagation area located south of Arroyo Farrapos. In this study, the effect of sand content in the propagation area was analyzed.

In December 2017, a total of 11 transects were marked between Farrapos Creek and De las Ovejas Gully, perpendicular to the coast, 5 and 10 m long depending on the width of the river bank. The average distance between transects was 550 m, with the aim of detecting variations in the distribution pattern of *G. triacanthos* (Sosa et al. 2018). A total of three 4 m x 20 m plots were established on each transect, whose major axis was aligned parallel to the coastline. The first plot was located on the coast edge, the second in the center of the forest and the third on the transition edge between forest and grassland (Fig. 2). All individuals of *G. triacanthos* recorded within each plot were counted. The spatial position of each plot was recorded using a Garmin 60CSx GPS.

Soil sampling was carried out using the composite method (Sosa 2012). Within each plot a zig-zag path was delimited where the point of extraction of the sample was marked at regular intervals of 1.30 m starting at one of its ends. Prior to the extraction of each subsample, the vegetation cover or leaf litter was removed from each point (Sosa 2012). Within each plot, a total of 15 subsamples were taken from the first 10 centimeters of soil. The different subsamples were deposited together in a container where they were mixed. A 500 g sample was collected from this mixture in a polyethylene bag. As a result, a total of 31 samples were collected (one sample per plot). The samples were processed at the Soil, Plant and Water Analysis Laboratory at the Alberto Boerger Experimental Station, La Estanzuela, of the National Institute of Agricultural Research (January 2018), using the Bouyoucos method by which sand content was quantified.

Spatial variability of G. triacanthos and soil sand content along the study area-

The most commonly used quantitative methods to characterize spatial variability include geostatistics, spectral analysis, wavelet analysis, and multifractal (Si 2008). Wavelets analysis is especially useful for spatial variations that are nonstationary (where the pattern itself changes with direction) (Perry et al. 2002 Camarero and Rozas 2006)

More often soil properties and ecological data are nonstationary, these trends may reflect important processes. The spatial variability of soil properties represents the interactions among soil physical, chemical, and biological processes that operate on a wide range of spatial and temporal scales (Si 2008). Spatial autocorrelation in ecological data is driven by exogenous causes such as autocorrelated environment, or disturbance and/or by endogenous factors (e.g., conspecific attraction, dispersal limitation, demography (Lichstein et al 2002).

Wavelet analysis is robust to non-stationarity and the presence of data anisotropy (Perry et al. 2002), thus, it is recommended in ecological (Cho and Chon 2006) and soil properties analysis (Si 2003). In the study site the spatial distribution pattern of soil sand content and the abundance of *G. triacanthos* is not stationary since spatial autocorrelation was detected (Sosa et al 2018) therefore, wavelets analysis was used to describe the spatial variability of these variables.

Wavelets analysis quantifies data structure as a function of position (Dale and Mah 1998) its basic tool is the wavelet transform that transforms a function **y(x)** where y is the measurement of the analyzed variable and x is its spatial location into a function W(x, s) of continuous location x and scale s (Si 2008).

It focuses on the "decomposition" of the data into repeated patterns that are compared to the shape of the wave function (Perry et al. 2002). The fundamental property of the wavelet variance is that it breaks up the process variance into pieces, each of which represents the contribution to the overall variance due to variability on a particular scale (Mondal 2010).

Wavelets analysis can be used to detect locations in the study area that may drive the overall pattern (Liebhold et al. 2002). In this work, we used the wavelets analysis to detect locations with abrupt changes in the abundance of *G. triacanthos* and locations with abrupt changes in soil sand content. To perform the wavelets analysis, we used the mean abundance value of *G. triacanthos* and the mean value of soil sand content of the plots located in each transect. In this sense, fluctuations in the variance represent sharp changes in the abundance of *G. triacanthos* and changes in sand content throughout the study area.

Different wavelet functions can be selected; to detect abrupt changes a nonsymmetrical wavelet such as the Harr wavelet should be used (Si 2008; Gamage 1990). We used the Haar function due to its ability to detect these changes. Wavelet analysis was performed using Passage 2. PASSaGE: Pattern Analysis, Spatial Statistics and Geographic Exegesis (Rosenberg and Anderson 2011).

A comprehensive nonmathematical overview in the development of wavelet transforms is given by Hubbard (1998), a toolkit use of wavelet analysis is provided by Torrence and Gilbert (1997); an illustration of how these methodologies can be applied in soil science is developed in Si (2004 and 2008), a framework to using this method with ecological data is presented in Perry (2002).

Detection of the spatial relationship between G. triacanthos abundance and soil sand content-

Local measures provide a more explicit consideration of space when spatial relationships are important (Fotheringham and Brunsdon 1999). These authors recommend its use when data are no stationary because these measures focus on the identification of variations in the pattern of spatial dependence within the study region. Therefore, to analyze the spatial relationship between the abundance of *G. triacanthos* and soil sand content we use local measurements.

Getis and Ord (1992) introduced the local statistics Gi and G* to detect pockets of spatial association. Using these statistics, it is possible to identify spatial clusters of large and small attribute values (Nelson 2008). Lately, these statistics were redefined as a standard variate by taking the statistic minus its expectation, divided by the square root of its variance; this new form increases the statistics' flexibility, and, therefore, their usefulness (Getis and Ord 1995).

The standardized G* is essentially a Z-value and can be associated with statistical significance in this sense positive and negative G* statistic with high absolute values correspond to clusters with high and low value events; a G* value close to zero implies a random distribution of events (Manepalli 2011).

In this study high values of G* refers to areas where the high abundance of G. triacanthos are surrounded by other areas of high abundance, alternatively low values of G* are identified in areas where low values of abundance are close to each other. To detect the spatial relationship between *G. triacanthos* abundance and soil sand content we used the standardized G* statistic obtained from the hotspot analysis for the variables sand content and abundance of *G. triacanthos*.

Hot Spot Analysis (Getis-Ord Gi*) was performed using the fixed distance band. A distance band is appropriate when data sites are regularly spaced (Nelson 2008). We used the default distance threshold, this threshold is the minimal distance that ensures every feature has at least one neighbor (ArcGisPro, 2023). As we are interested in identifying where high/low values for our variables cluster spatially we run hot spot analysis using raw values (ArcGisPro 2023).

A mosaic structure is formed as the simplest way to represent the spatial heterogeneity of ecological processes (Turner et al. 2001). Thus, to map the spatial relationship between *G. triacanthos* abundance and soil sand content we built a mosaic with 10 m x 10 m cells.

Spatial interpolation is a widely applied method which uses sample values of known geographical points (or area units) to estimate (or predict) values at other unknown points (or area units) (Comber and Zeng 2019). The values assigned to each cell in the mosaic resulted from the application of interpolation techniques of the G* standardized values obtained from records on the sand content and abundance of *G. triacanthos* (Fig. 3). We used the Inverse Distance Weighted (IDW) an interpolation method widely used in geographic analysis (Wong 2017). This is a suitable method when the data are regularly distributed in space (Li and Heap 2014).

Interpolation (IDW) and Hot Spot analysis were performed with the geoprocessing tools available in ArcGIS Version 10 software. Copyright ESRI Inc., Redlands, CA, USA.

Finally, to detect the spatial relationship between the abundance of *G. triacanthos* and soil sand content we used the regression tree technique, this method is commonly used to analyze relationships between variables in mosaic structures (Turner and Chapin 2005; Strobl et al. 2009). G* standardized values for soil sand content were entered as the independent variable and G* standardized values for *G. triacanthos* abundance as the dependent variable (Fig. 3). This technique is based on identifying increasingly homogeneous configurations, nodes, of predictor variables that should lead to increasingly homogeneous configurations of response variables (Cheng 2009). For this purpose, the space defined by the data is recursively partitioned; once a partition is defined it is not considered in subsequent partitions (Berk 2005). The partitioning culminates when the nodes do not accept further subdivisions or when a previously defined criterion is reached as the end of the partition (Simpson and Birks 2012). The CRT (classification and regression tree) growth method was used to obtain the simplest possible tree the tree growth was limited to 5 levels. The tree was created and tested with the entire data set. SPSS V.9 software was used for this analysis.

In this work each node of the classification tree groups a similar set of values that have their geographic coordinates associated with them, therefore it is possible to identify the spatial location of each node (Fig. 3). When the node comprised two or more geographic zones, it was subdivided according to the number of zones it represented (Fig. 5). At each node or sub-node, the relationship between the variables was analyzed using scatterplots and their fit to a line or a second-order polynomial was evaluated (Fig. 3). The results were classified into positive relationships (lines with positive slope); negative (lines with negative slope), polynomial relationships and no relationship (when no linear or polynomial relationship was detected). This is the simplest possible categorization and is also the one with the greatest interpretative potential. These categories were spatialized, generating a map in which the study area is zoned according to the type of relationship detected between soil sand content and the abundance of *G. triacanthos* in the study area (Fig. 3).

Results

Spatial variability of G. triacanthos and soil sand content along the study area-

The sand content of the soil varied throughout the study area. Haar wave function analysis recorded two peaks of variance that correspond to points of high soil sand content (Fig. 4A). The first peak is located over transect 2 which is close to an area of active deposition. The variance and sand content increases again from transect 4 and begins to decrease from transect 5, presenting a sharp decrease around transect 7. It is worth noting that between transects 4 and 6 active deposition processes are also identified. The reduction in sand content at transect 7 is explained by the presence of an area of active deposition found in the transverse island (of recent formation) Banco Grande in front of this transect. A further increase was recorded around transect 8 located in the vicinity of the spit sand bar, an area of active deposition (see Fig. 2; Fig. 4a). The sand content decreases gradually along transects 9, 10 and 11. Transects 9 and 10 are located in an area of lower flow due to the barrier generated by the spit (Fig. 2); in front of transect 11, De la Paloma transect island is located, which concentrates deposition in that area (Fig. 4a).

The distribution and abundance pattern of *G. triacanthos* is more stable, with a peak of high abundance at transect 4, 550 m north of the peak of high sand content in the soil (Fig. 4b).

Detection of the spatial relationship between G. triacanthos abundance and soil sand content-

The classification tree detected a total of 36 nodes (Annex 1) with a risk estimate (within-node variance = 0.22). The spatialization of the two main nodes (into three sub-nodes) allowed a first zonation of the study area that is consistent with the geomorphological structure of the area (Fig. 5). The first zone, located to the north of the study area, constitutes a floodplain connected to the Uruguay River by a discontinuity in the seasonal island where active deposition processes are identified in the coast area. The second zone is the narrowest area of the seasonal island, which develops without relevant discontinuities in direct contact with the main riverbed. The beginning of the last zone matches the presence of Banco Grande Island. This zone is also characterized by the presence of the spit. The presence of these two structures affects the sediment supply of the continental seasonal island.

By spatializing the nodes of the classification tree, a total of 6 subnodes with a negative linear relationship, 24 subnodes with a positive linear relationship, 20 subnodes in which no relationship was detected and 2 subnodes that fitted a polynomial curve of order 2 with negative coefficient were identified (Annex 2). Consistent with the spatial location of these subnodes, it was possible to identify a total of 12 main zones (Fig. 6). The average value of soil sand content in the plots located in areas where a positive linear relationship was detected was 24.5%; this value doubles (47%) in the plots located in areas where no relationship was detected. The area where a negative linear relationship was detected had the highest sand levels (87.6%).

Discussion

The methodology used allowed zoning the study area based on the relationship established between the invasive process of *G. triacanthos* and the sand content of the soil. Specifically, areas with linear relationships (positive and negative), areas with quadratic relationships and areas with no relationship were identified, highlighting the inherent complexity of defining causal relationships in heterogeneous systems. These results also indicate that, despite the wide tolerance of the invasive to variation in environmental conditions (USDA 2016), the environmental heterogeneity of this system may modulate its spread. This modulation is linked to the extremes of the environmental gradient, with areas that showed lower sand content being areas where positive linear relationships were detected and areas with higher content areas with negative linear relationships. No relationship was detected in areas with intermediate sand content. These results contrast with the literature that analyzes these relationships in riparian ecosystems where only positive relationships were detected (Mendelssohn and Kuhn 2003; Zedler and Kercher 2004) or only negative relationships (Jolley 2010; Festus and Zakaria 2021). Of note, unlike the present work, the aforementioned studies did not use spatially explicit methodologies; the difference in methodological approach could explain these differences and should be further analyzed.

Abiotic stress occurs when environmental conditions limit resource availability, growth or reproduction of resident plants (Grime 1989), so that environments under abiotic stress decrease the invasive potential of alien species (Zefferman 2015). The negative relationships detected for *G. triacanthos* in areas with high sand content could be explained by "abiotic stress" in relation to coverage and/or high energy entrainment limiting the survival of early stages of this species. On the other hand, the areas in which a positive relationship was detected have the lowest sand content, being the areas with the lowest abiotic stress related to coverage. These areas with lower energy could present a higher nutrient content due to the deposition of organic matter (Johnson 1994; Schwarz et al. 1996) facilitating the development of the invader in accordance with the nutrient release hypothesis (Davis et al. 2000). In this work, the absence of relationships is detected in the areas that recorded intermediate sand contents. It is possible that due to tolerance to variation in environmental conditions, invasive species do not respond to abiotic conditions in the intermediate range of the gradient.

The identification of positive relationships in the southern end of the spit, whose formation corresponds to current sand deposits, differs from the results presented in the coastal seasonal island, where the areas of active deposits are associated with negative relationships. It should be noted that in these areas the invasive process takes place in qualitatively different environments; on the coastal seasonal island the invasion is established and gradually excludes species from the existing native woody community. The invasive process in the southern area of the spit involves the colonization of a new environment together with the native species that must also establish in the area. The deposition processes in this area would facilitate the arrival of propagules and therefore the development of the invasive aspect in this area, in the absence of biotic resistance, this factor would explain the positive relationships detected. It is important to note that the detection of relationships between sand content and the abundance of *G. triacanthos* in this area is consistent with the biogeomorphological succession approach according to which hydrogeomorphological processes modulate the first two phases of plant succession (Cornebilt 2007). Analyzing the relationship between these newly formed areas and invasive processes is fundamental to understanding woody invasions in riparian systems.

The importance of defining transition zones has been proposed by Thorph (2006) and these authors also state that zones associated with the confluence of tributaries, convergence and divergence areas in rivers, islands with vegetation and parafluvial ponds constitute areas of ecological relevance. The area of polynomial relationships could be indicating a transition zone since immediately to the south of it begins a structurally different area defined by the presence of Banco Grande Island. On the other hand, in the area where the coastal seasonal island bifurcates and the formation of the spit associated with the mouth of Gully A begins, a zone is identified where small areas of positive and negative relationships alternate. The detection of this variation in a structurally complex area could also indicate the existence of a transition zone. In this context, the transition area would begin in the zone with polynomial relations and would culminate with the beginning of the spit. Field observations suggest that from the transition zone, the invasive process develops mainly on the spit, since the abundance of *G. triacanthos* would be higher in this area than on the seasonal island; thus, the transition zone would play a decisive role in directing the spatial pattern of this invasive process.

The core of high abundance of *G. triacanthos* is located in an area where no relationship between sand content and abundance of the invasive species were detected. Therefore, sand content is one of the factors that modulates, but does not determine the spread of this process. Cadotte and Tucker (2017) state that a single environmental factor is unlikely to determine community structure. The confluence of several environmental factors as determinants of vegetation composition has been suggested for coastal wetlands (Bantilan-Smith et al. 2009). In the study area, several factors, which have not been identified in this work, would be determining the spread of this invasive process. A total of 39 explanatory hypotheses are currently recognized, which are grouped into five clusters: resource availability, biotic interactions, propagules, strategies, and Darwin clusters (Enders 2018). We propose that one of the main challenges in understanding the development of invasive processes in riparian systems is to link the relative importance of these hypotheses to environmental heterogeneity. The results of this work show the potential of this methodology to detect ecologically relevant spatial heterogeneity in riparian systems. Its strengths and weaknesses should be further analyzed.

The importance of analyzing invasive processes at a local scale has been recognized in the study of biological invasions (Lembrechts 2017), so the spatial analysis of the relationships between *G.*

triacanthos and its environment at a local resolution in a changing riparian ecosystem constitutes a fundamental input to understand and control the invasive process. Specifically, with respect to the generation of information for management, the spatially explicit approach is relevant to detect areas at high risk of invasion (McGeoch et al. 2016) or priority areas for control and management (Wittenberg and Cock 2001). The results of this work provide a first orientation in this sense, the areas with high risk of invasion are located in areas with intermediate sand content, in areas where the sand content is low the invasive process is facilitated as well as in newly formed structures so they are areas that should be monitored carefully. In the areas of active deposits on the seasonal island, the spread of the invasion would be limited, so in low resource contexts these are the areas where the least control efforts should be made.

Conclusion

Riparian systems are highly threatened by alterations in its hydrological regimen and biological invasions. The sand content modulates, but does not determine, the spread of the invasive process of this species. This modulation is linked to the extremes of the environmental gradient (areas with high and low sand content). These results show that, despite the wide tolerance attributed to this invasive species to environmental conditions, edaphic heterogeneity in riparian ecosystems can modulate and limit its spread. In addition, the results of this work highlight the complexity inherent to the definition of causal relationships in highly heterogeneous systems such as riparian ecosystems. Spatial analysis techniques are a useful tool for this approach.

Declarations

STATEMENTS AND DECLARATIONS

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Competing interest

The authors have no relevant financial or non-financial interests to disclose.

AUTHOR CONTRIBUTION

Beatriz Sosa contributed to conception, design, data acquisition, data analysis and interpretation and draft writting.

David Romero contributed to drafting the manuscript and revising it critically.

Jose Guerrero contributed to critically revising the manuscript.

Federico Rodriguez contributed to drafting the manuscript.

Marcel Achkar contributed to conception, data analysis and interpretation and given the final approval of the version to be published

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Figures

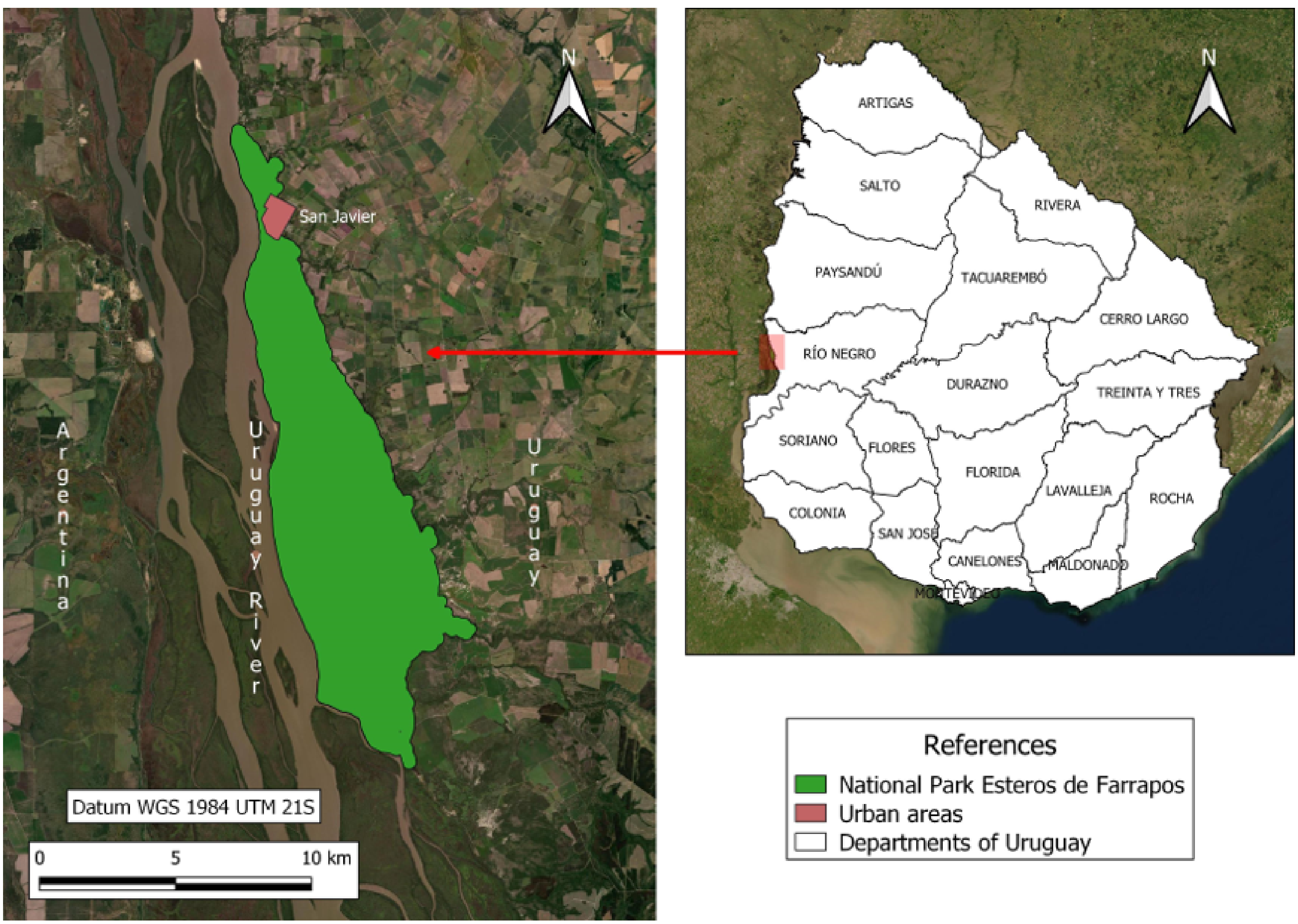

Figure 1

Location of the study area. The context of the study area in Uruguay, in Rio Negro, and the detail of the study area are indicated.

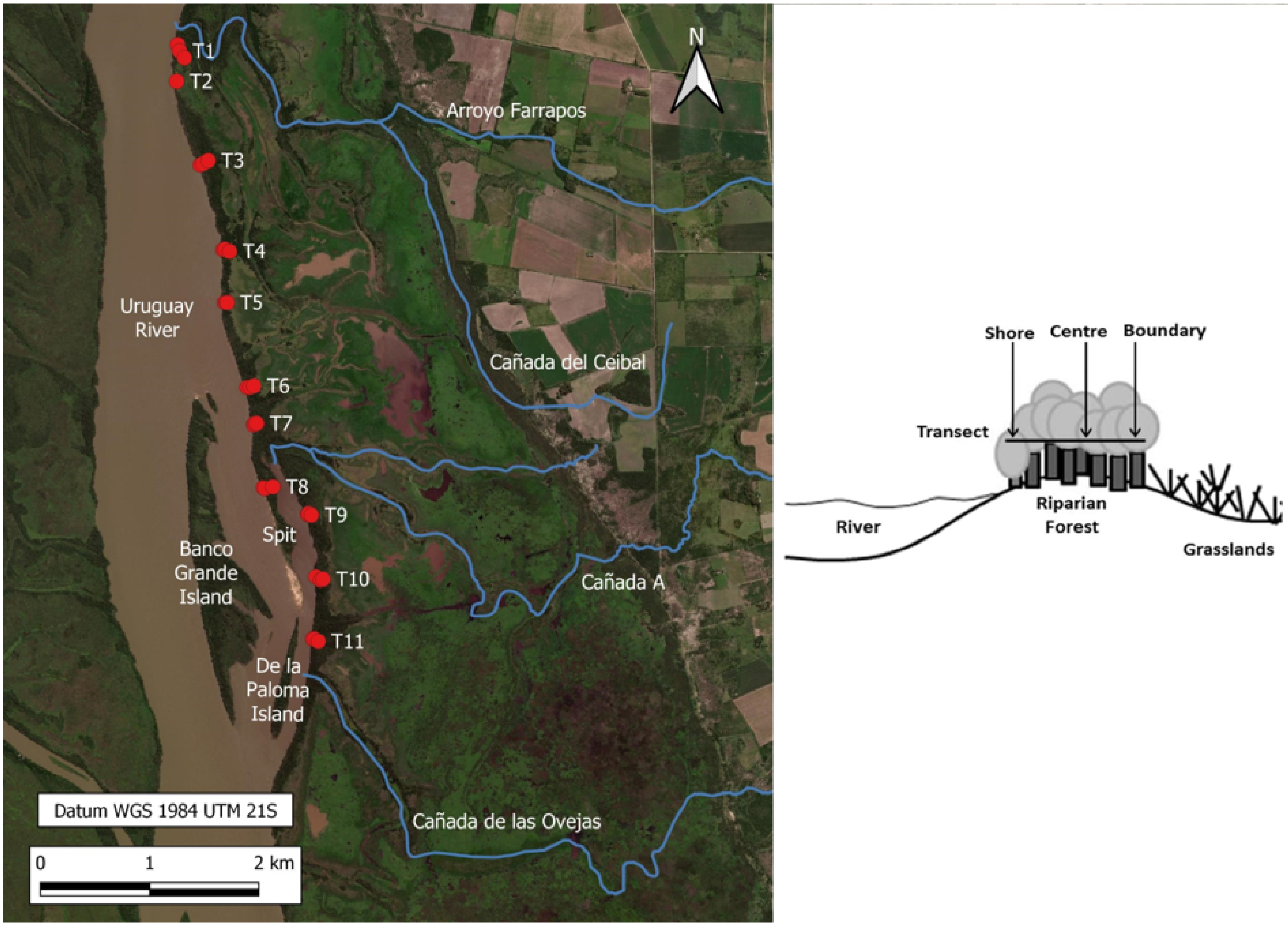

Figure 2

Sampling design. **Left.** Distribution of the sampling transects over the riparian forest is shown in red. **Right**. Arrangement of sampling plots over each transect: on the coastal edge on the left, forest center, and edge of forest-grassland transition on the right.

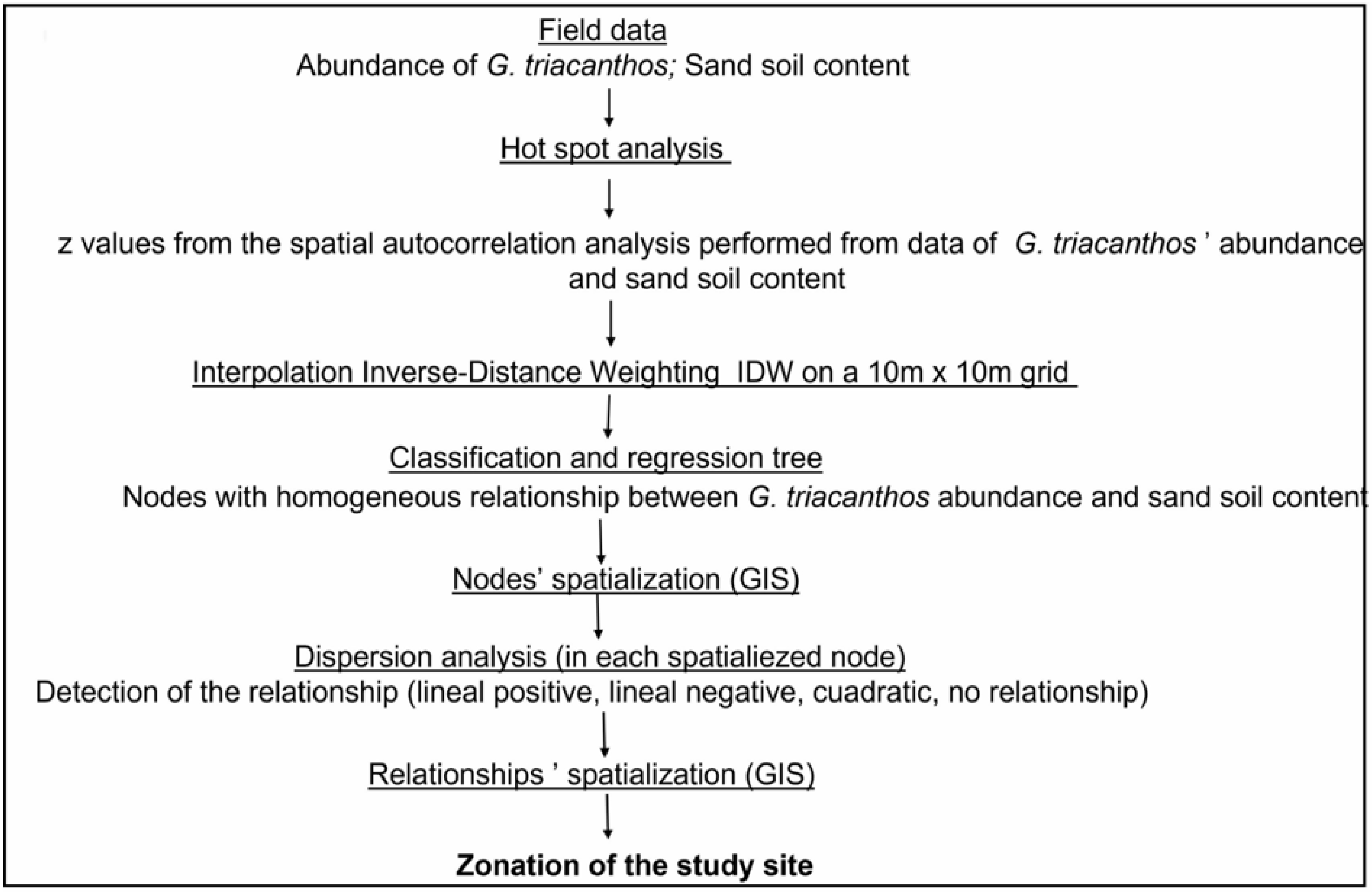

Figure 3

Flow chart to establish, in the invaded area, the relationship between the spatial structure of the abundance of *G. triacanthos* and the sand content of the soil.

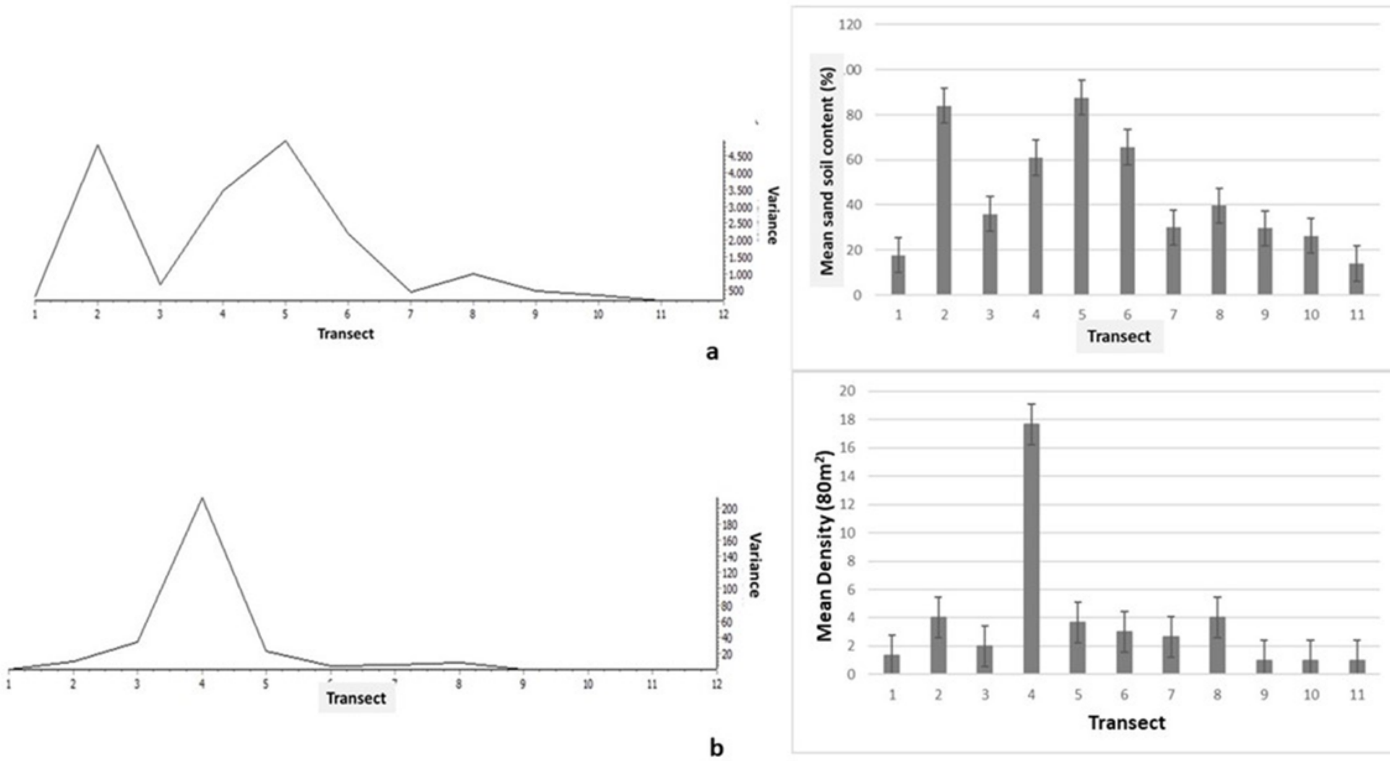

Figure 4

Detection of the pattern of variation along the 11 transects in the study area. The charts on the left represent the results of the Haar wave function analysis. The charts on the right represent the average values of the variables in each of the transects. **a**. Variations in soil sand content **b.**Variations in the density of *G. triacanthos*

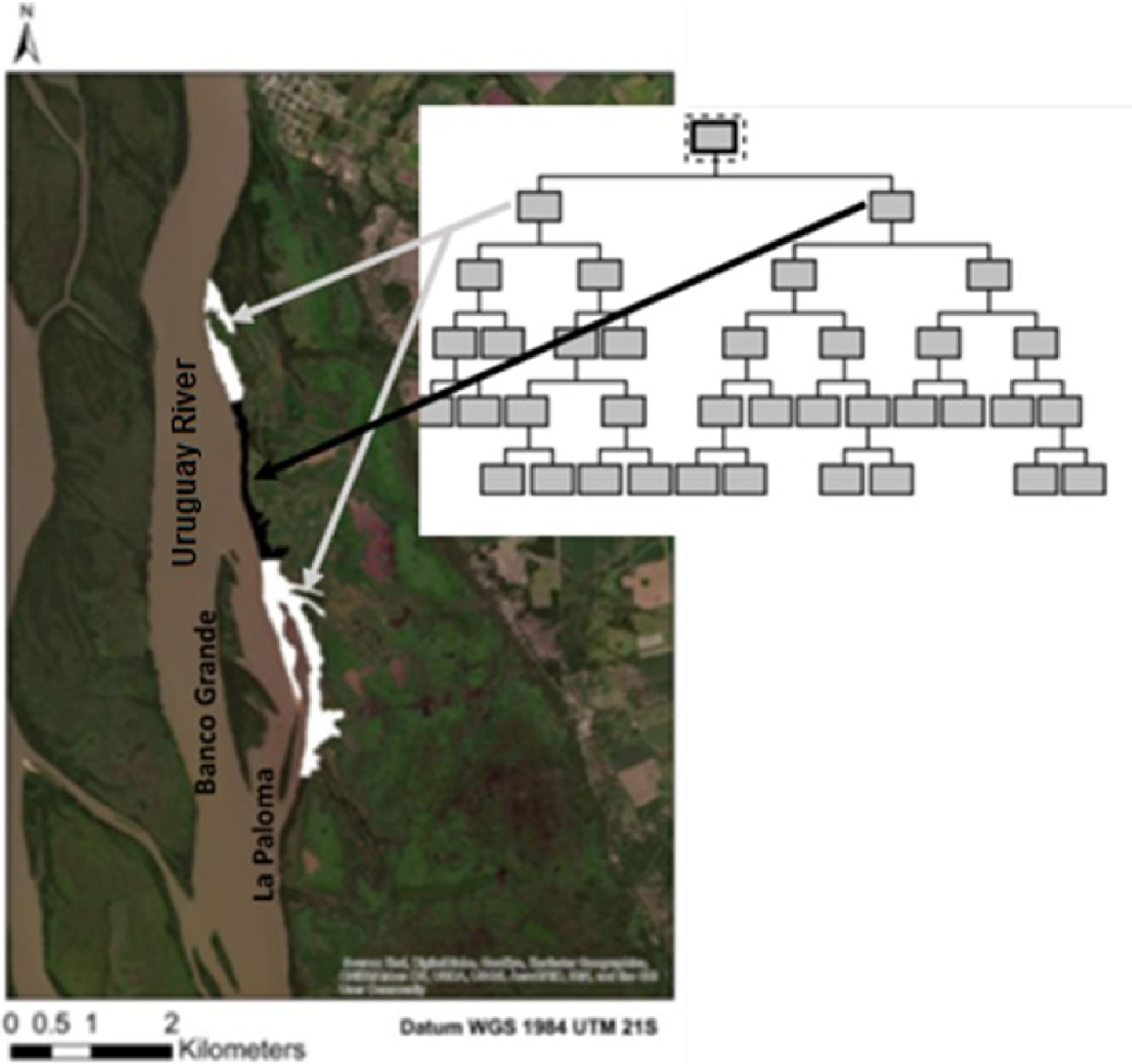

Figure 5

General scheme of the classification tree. The main nodes and the primary zonation made from them are indicated

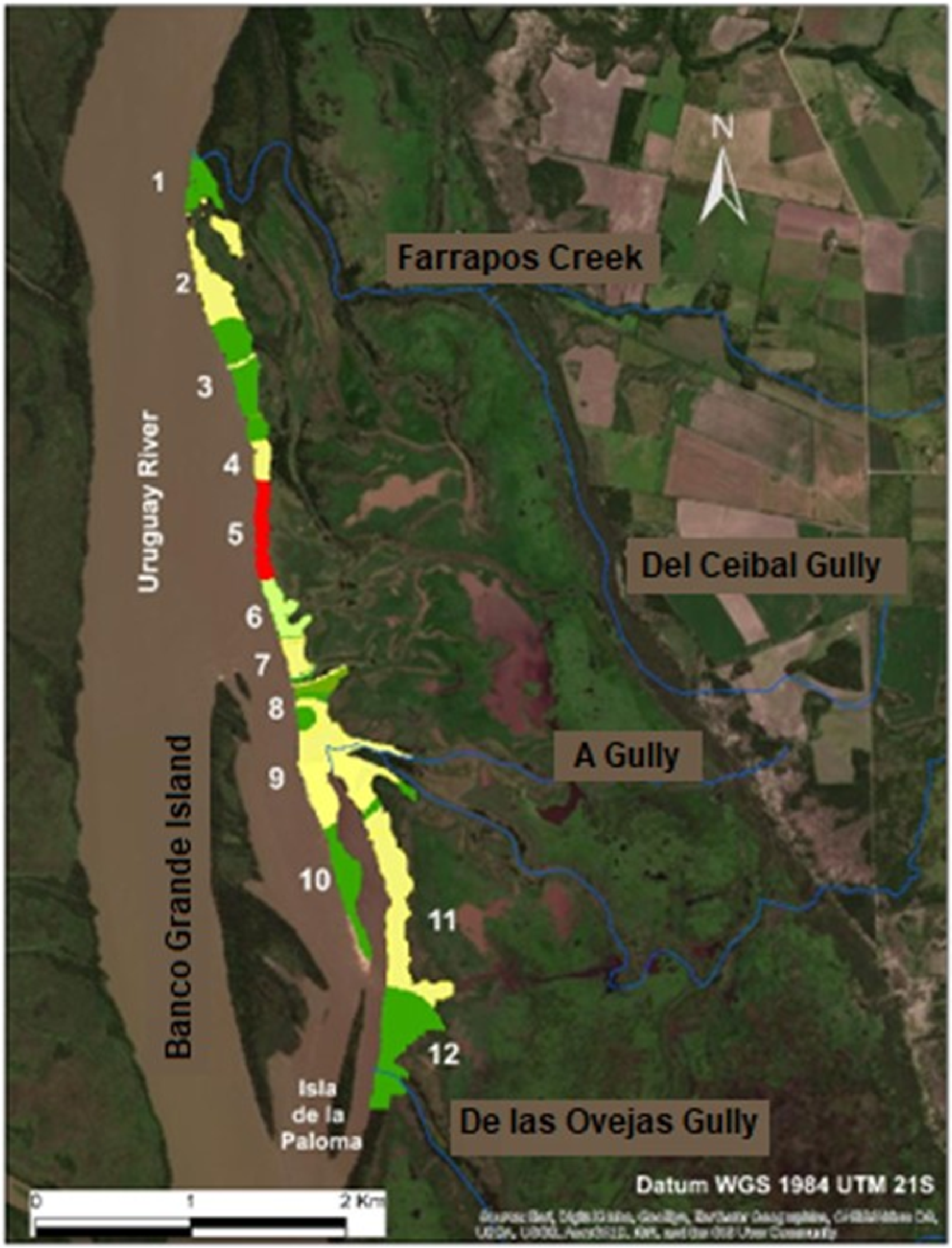

Figure 6

Relationship between soil sand content and abundance of *G. triacanthos* in the spreading area. Green: area with positive linear relationship; Light green: area with polynomial relationship; Yellow: area without linear relationship; Red: area with negative linear relationship.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- ANNEX12.docx