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How are riparian plants distributed along the riverbank topographic gradient in Mediterranean rivers? Application to minimally altered river stretches in Southern Spain

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ABSTRACT

How are riparian plants distributed along the riverbank topographic gradient in Mediterranean rivers? Application to minimally altered river stretches in Southern Spain

Species structure and composition in Mediterranean riparian forests are determined by hydrological features, longitudinal zonation, and riverbank topography. This study assesses the distribution of four native riparian plants along the riverbank topographic gradient in three river stretches in southern Spain, with special emphasis on the occupation of adult and young feet of each species. The studied stretches suffered minimal human disturbances, displayed semi-arid conditions, and had wide riparian areas to allow the development of the target species: black alder (*Alnus glutinosa*), salvia leaf willow (*Salix salviifolia*), narrow-leafed ash (*Fraxinus angustifolia*), and oleander (*Nerium oleander*). Thalweg height was used to define the riverbank topographic gradient. The results showed a preferential zone for black alder and salvia leaf willow in the range of 0-150 cm from the channel thalweg, with adult alders and willows being more common between 51 and 150 cm and young alders being more common under 50 cm. Conversely, narrow-leafed ash and oleander were much more frequent, and showed greater development, in the ranges of 151-200 cm and 201-250 cm, respectively, whereas the young feet of both species covered the entire topographic range. Adult feet of the four species were spatially segregated along the riverbank topographic gradient, indicating their differential ability to cope with water stress from the non-tolerant alders and willows to more tolerant narrow-leafed ash trees and oleanders. Young feet, however, showed a strategy more closely linked to the initial availability of colonisation sites within riparian areas to the dispersion strategy of each species and to the distribution of adult feet. In Mediterranean areas, where riparian management has traditionally faced great challenges, the incorporation of species preferences along riverbank gradients could improve the performance of restoration projects.

Key words: Riparian forests, topography, river morphology, vegetation, restoration.

RESUMEN

¿Cómo se distribuyen las especies vegetales de ribera a lo largo del gradiente topográfico ribereño en ríos mediterráneos? Aplicación a tramos fluviales mínimamente alterados en el sur de España

*La composición y estructura de la vegetación ribereña mediterránea guarda una relación directa con las características del régimen hidrológico, la zonación longitudinal y la topografía de las zonas de ribera. En este estudio se evalúa la distribución de cuatro especies ribereñas nativas, a lo largo de un gradiente topográfico en las riberas fluviales de tres tramos del Sur de España, haciéndose énfasis en las pautas de ocupación de los ejemplares adultos y jóvenes de cada especie. Los tramos de estudio contaban con una escasa alteración por parte del hombre, estaban asociados a condiciones de semi-aridez, y presentaban una amplia anchura en sus zonas ribereñas, que permite el desarrollo de las especies objetivo: aliso (*Alnus glutinosa*), sauce salvifolio (*Salix salviifolia*), fresno común (*Fraxinus angustifolia*), y adelfa (*Nerium oleander*). La altura sobre la línea de vaguada fue la variable utilizada como descriptor del gradiente topográfico. Los resultados mostraron* *una zona preferente para alisos y sauces salvifolios en el rango 0-150 cm desde la línea de vaguada, siendo los ejemplares adultos de ambas especies más frecuentes entre los 51 y 150 cm, y los ejemplares jóvenes de aliso más habituales por debajo de los 50 cm. Por el contrario, fresnos y adelfas aparecían con mucha mayor frecuencia y con mayor desarrollo en los rangos 151-200 y 201-250 cm, respectivamente, mientras que los ejemplares inmaduros de ambas especies se repartían por la totalidad del gradiente topográfico. Los ejemplares adultos de las cuatro especies se encontraban espacialmente segregados a lo largo de dicho gradiente topográfico, indicando su capacidad diferenciada para tolerar el estrés hídrico, desde los poco tolerantes alisos y sauces hasta los más tolerantes fresnos y adelfas. Los pies jóvenes mostraron, sin embargo, una estrategia de ocupación más asociada a las posibilidades iniciales de establecimiento en las zonas ribereñas, a la estrategia de dispersión propia de cada especie y a la distribución de los ejemplares adultos. En las zonas mediterráneas, en las que la gestión de las riberas fluviales se ha enfrentado históricamente a grandes desafíos, la incorporación de las preferencias de las especies a lo largo de los gradientes ribereños podría contribuir a la mejora de las actuaciones de restauración de este tipo de ambientes.*

Palabras clave: *Bosques ribereños, topografía, morfología fluvial, vegetación, restauración.*

INTRODUCTION

Riparian vegetation plays a vital role in river ecosystems. Riparian species help supply matter and energy and regulate fluxes in aquatic and riparian ecosystems. They provide the main food sources for in-channel organisms (Naiman *et al.*, 1993; Bodie & Semlitsch, 2000) and influence many geomorphological processes by reducing the erosion of river margins, supplying woody debris, enhancing sediment retention, and creating new habitats (Gregory *et al.*, 2003). Riparian stands also mitigate water temperature increases (Quinn *et al.*, 1992; Jobling, 1995) and improve water quality by preventing pollutants and nutrients from entering channels through direct runoff or subsurface flow (Lowrance *et al.*, 1984). The influence of riparian vegetation on the conservation of biodiversity and on landscape structure has been also extensively documented. For example, Gregory *et al.* (1991) and Malanson (1993) showed that well-vegetated riparian areas have higher biodiversity and landscape value than adjacent areas. Furthermore, these areas can act as natural corridors, connecting ecologically distant areas for different species (Fischer & Fischenich, 2000), including many species of birds (Peak & Thompson, 2006; Seavy *et al.*, 2009).

The functions and services provided by riparian stands are centrally defined by their structure and specific composition, which are mainly determined by hydrological features, longitudinal zonation, and riverbank topography (e.g., Auble & Friedman, 1994; Hupp & Osterkamp, 1996; Angiolini *et al.*, 2011). On the one hand, the influence exerted by flow regimes and water availability on riparian stands has been extensively described in different areas, especially in semi-arid and Mediterranean regions, where high and low flows are very important for explaining riparian structure and composition (Camporeale & Ridolfi, 2006; Stromberg *et al.*, 2007; Merritt *et al.*, 2010; Rodríguez-González *et al.*, 2010; González *et al.*, 2012). On the other hand, longitudinal zonation is a key factor in explaining riparian patterns at the basin scale (Thorp *et al.*, 2006). The importance of environmental factors in the structure of riparian vegetation has been addressed in several Mediterranean rivers in the Iberian Peninsula. Salinas *et al.* (2000a, 2000b) and Salinas & Casas (2007) showed that the richness and cover of woody species declined with increasing water salinity and human impacts, and this suggested remarkable changes in riparian structure and composition from upper to middle-lower segments due to changes in water chemistry. González-Muñoz *et al.* (2011) suggested irradiation capability as a factor exerting a strong influence on species richness, distribution patterns, and the establishment success of riparian plants along riverine areas. Moreover, specific environmental factors (climate, elevation, river hierarchy) could be more related to compositional groups of species in the riparian stands than to functional groups of the same species (Nucci *et al.*, 2012; Aguiar *et al.*, 2013). These examples highlight the relationship between riparian vegetation and longitudinal zonation in rivers. Finally, different authors have shown that riverbank topography and riparian vegetation are strongly related (Szaro, 1990; Stromberg & Patten, 1990, 1996; Hupp & Osterkamp, 1996; van Coller *et al.*, 2000; Disalvo & Hart, 2002; Stella *et al.*, 2013a). In particular, significant positive relationships have been observed between tree species richness, width of the riparian zone, and topographic riverbank complexity, while adjacent land use and bedrock geology appeared to show a much smaller influence on this attribute (Everson & Boucher, 1998).

Some recent studies have attempted to describe the interactions between riparian vegetation and riverbank topography in Spanish basins (e.g., Corbacho *et al.*, 2003; Fernández-Aláez *et al.*, 2005; Garófano-Gómez *et al.*, 2011, 2013; Bejarano *et al.*, 2012, 2013; Magdaleno & Fernández-Yuste, 2013). These descriptions are essential for compliance with the recent amendments to the Spanish National Water Law (L. 11/2005), which recognise native riparian vegetation and autochthonous fish as the main target species that must be protected downstream of dams and other hydraulic infrastructures. Although several studies have focused on the influence of hydrology and longitudinal zonation in Spain (see above), they have mostly been conducted in greatly altered rivers. Therefore, detailed studies that assess the relationship between riparian species and riverbank topography in minimally altered sites are still scarce, but they are necessary to ensure their protection and management.

This study attempts to address some of the aforementioned gaps by focusing on the relationship between species distribution and riverbank topography in minimally altered sites in three Mediterranean rivers in southern Spain. Our main hypothesis is that riverbank topography greatly influences the relative locations of riparian species in minimally altered river stretches, as is the case in altered river sites. In addition, our study aims to determine whether riverbank topography affects the adult and young feet of riparian species differently. We will also provide insights on how to integrate riverbank characteristics into management and restoration strategies for riparian habitats in Mediterranean areas.

Figure 1. Location of the study river stretches in southern Spain (Guadalquivir and Guadiana Basins). *Localización de los tramos fluviales muestreados en el sur de España (cuencas del Guadalquivir y Guadiana).*

MATERIALS AND METHODS

Study area

The study was carried out in three river stretches located in the Guadalquivir (Robledillo River) and Guadiana basins (Estena and Ruecas Rivers) in southern Spain (Fig. 1 and Table 1). These river stretches display typical Mediterranean climate characteristics, with a rainfall period between autumn and spring and a drought period in summer and with frequent intermittent flow conditions (Gasith & Resh, 1999; Bonada & Resh, 2013). These climatic characteristics generate a high intra- and inter-annual variability in flow regimes. The mean annual rainfall of the entire study area is approximately 550 mm, with a mean annual air temperature of 15.4 °C.

The studied river stretches drain an area with a siliceous geology (schist and quartzite), which is

Table 1. Main characteristics of the study river stretches and cross-section features. Flow occurrence was typified according to the Basin Authorities of Guadalquivir (CH Guadalquivir, 2010) and Guadiana (CH Guadiana, 2011). *Características de los tramos estudiados y de los transectos de muestreo realizados en cada uno de ellos. La información sobre caudales se extrajo de la Confederación Hidrográfica del Guadalquivir (CH Guadalquivir, 2010) y del Guadiana (CH Guadiana, 2011).*

River	Basin, municipality and province	Typology according to flow occurrence	Average bank-to-bank width (m)	Transect	Length (m)	Number of plots	River margin	Dominant species
Robledillo	Guadalquivir-Solana del Pino (Ciudad Real)	Intermittent (flows 100-300 days per year). Minimum flows: June, July, August and September.	6.5	1	9.50	10	Right	Black alder (*Alnus glutinosa*) Oleander (*Nerium oleander*) and Tamujo (*Flueggea tinctoria*)
				2	5.50	6	Right	
				3	3.50	4	Right	
				4	21.20	15	Right	
				5	30.45	24	Right	
				Total	70.15	59		
Estena	Guadiana-Helechosa de los Montes (Badajoz)	Temporary (flows over 300 days per year). Minimum flows: July and August.	8.0	1	69.60	21	Left	Narrow-leafed ash (*Fraxinus angustifolia*) and Salvia leaf willow (*Salix salviifolia*)
				2	46.50	12	Left	
				3	22.80	7	Left	
				4	7.80	6	Left	
				5	4.65	5	Left	
				6	3.00	4	Right	
				7	11.50	10	Right	
				Total	166.15	65		
Ruecas	Guadiana-Cañamero (Cáceres)	Temporary (flows over 300 days per year). Minimum flows: July and August.	7.0	1	4.00	5	Left	Black alder (*Alnus glutinosa*)
				2	3.00	4	Left	
				3	2.00	3	Left	
				4	4.00	5	Left	
				5	3.00	4	Left	
				6	2.00	3	Left	
				Total	18.00	34		

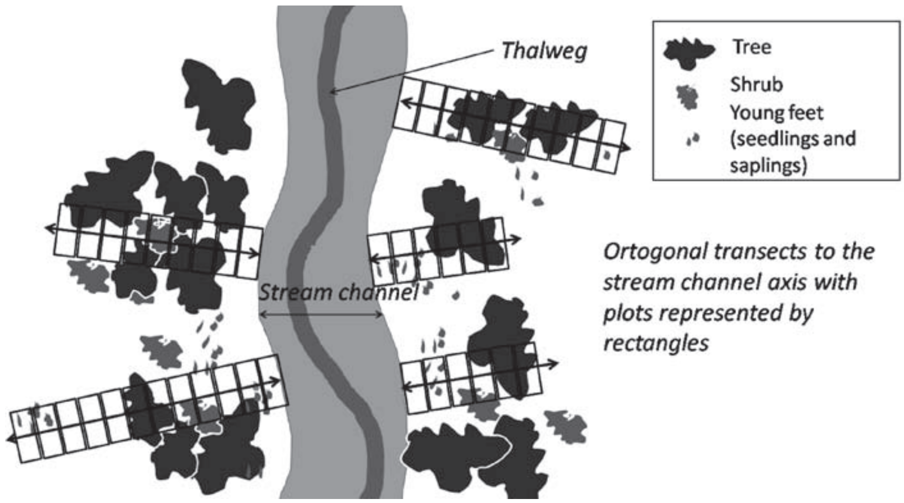

Figure 2. Schematic representation of the distribution of transects (represented by arrows) and plots (represented by rectangles). Transects comprised the total hydrological width occupied by riparian vegetation, so their length varied according to this width. *Representación esquemática de la distribución de los transectos (flechas) y cuadrículas (rectángulos). Los transectos se extendieron a lo largo de toda la banda hidrológica ocupada por vegetación ribereña, por tanto, su longitud varió en función de la anchura de esta banda.*

responsible for their low concentration of dissolved solids, with a mean conductivity of approximately 150 μS/cm. The study area has no significant reliefs, with a mean altitude over 600 m.a.s.l., although the sampling sites range from 450 to 550 m.a.s.l. All the studied stretches belong to the uppermost sections of their rivers and show a slope close to 4 %.

Riparian vegetation is well-conserved in all stretches (RFV index-Magdaleno *et al.*, 2010; Magdaleno & Martínez, 2014), with good longitudinal and transversal continuity and with high vegetation cover values (70-100 %). Furthermore, the three stretches present noticeable species recruitment (nearly 2 seedlings/m^2 on average). The dominant tree species in the Robledillo and Ruecas stretches is black alder (*Alnus glutinosa*), which, in Robledillo, is accompanied by a set of shrub species (*Nerium oleander*, *Flueggea tinctoria*, *Rubus ulmifolius* and *Vitis vinifera*) and ferns (*Pteridium aquilinum* and *Osmunda regalis*). Narrow-leafed ash (*Fraxinus angustifolia*) and salvia leaf willow (*Salix salvifolia*) are dominant in the Estena stretch, with *Rubus ulmifolius, Crataegus monogyna* and *Rosa* spp. as the main shrub species. The landscape surrounding the studied river stretches is covered by semi-natural forest (open forest composed by *Quercus ilex* subsp. *ballota* and/or *Q. suber*, which is referred to as *dehesas*).

Selection of river stretches and target species

The three river stretches were selected according to the following set of criteria: (I) absence of water regulation or extraction so as to reduce, as much as possible, any influence of these perturbations on the distribution patterns of riparian species; (II) similar habitat characteristics, such as stream order (all the stretches were order 2, according to Strahler, 1964), soil composition (gravel 3-8 cm and boulders 10-25 cm in all cases), channel width (6.5 to 8 m, Table 1), mean annual flow (< 4 m^3/s) and stretch position along the longitudinal river gradient (all stretches were located in the headwaters within 7 km of the source); (III) typology of surface water bodies classified as "rivers from low Mediterranean siliceous mountains", according to Toro *et al.* (2009); and (IV) broad riverbank areas with potential to support well-developed riparian vegetation (i.e., a defined topographic gradient from the thalweg to the upper zone of the riparian vegetation margin). These criteria allow analysis of the influence of riverbank topography on the distribution of riparian species, assuming a reduced effect of other potentially influential factors. Once the aforementioned criteria were applied, the three river stretches described above were selected (Fig. 1 and Table 1).

Four riparian species were analysed in this study: black alder, narrow-leafed ash, salvia leaf willow, and oleander (*Nerium oleander*). These were the dominant species in the study sites.

Field procedures

The three stretches were surveyed in September 2010. The length of each stretch ranged from 80 m in the Robledillo River to 150 m in the Ruecas River (in the Estena River the stretch was 120 m long). The topography of the riverbanks colonised by riparian vegetation was defined by a set of cross-sections in each river stretch (Fig. 2). These cross-sections consisted of orthogonal transects to the river channel axis and comprised the total hydrological width occupied by riparian vegetation. Therefore, transect length varied according to this width, between 2.00 and 69.60 m (average = 14.22 m, n = 18). Surveys were performed on both river margins, although a higher sampling effort was conducted on the margins that showed better defined and more developed riparian stands. Cross-sections were spaced at least 15 m apart to reduce the vicinity effect on the collected data.

Transverse (cross-valley) patterns in riparian species distributions were examined along the cross-sections. Riparian vegetation was sampled in 1×4 m plots distributed along the cross-sections. This size minimised the variation of topographic conditions inside each plot and provided a good image of the existing vegetation. Similar plot sizes have been used in previous studies (e.g., Auble *et al.*, 2005). The plots were oriented with their longer side parallel to the channel and were spaced along the cross-sections at 1-m intervals in the first 10 m from the river channel. This distance was larger (2-10 m) after the first 10 m from the channel if the transect was long enough (15-20 m). This was due to vegetation cover is much lower within 10-15 m beyond the channel (e.g., Auble *et al.*, 2005). The number of sampling plots per cross-section varied according to the transect length and the range oscillated between 2 and 25 (average = 8.33; total n = 151 plots).

Once the plots were positioned along the transects, their geometric centre was determined. Height from the thalweg (H) was calculated for each plot, with this centre as a reference, and was used to describe the riverbank topography (Fig. 3). It was assumed that all species rooted inside a plot shared the height values of their

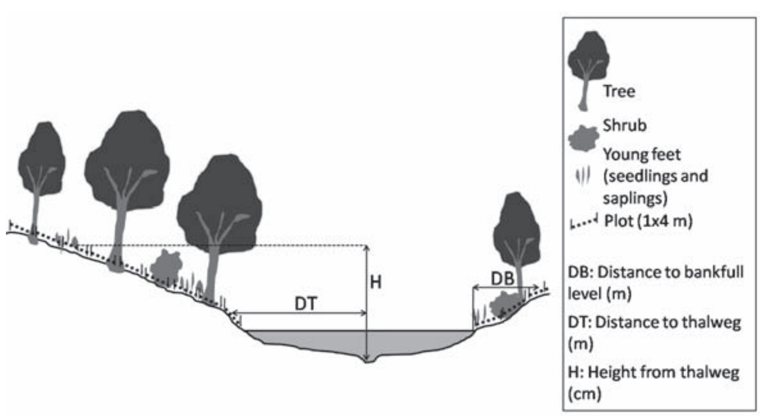

Figure 3. Schematic representation of the variables measured in the sampling plots. All measurements were made from the geometric centre of the plot (see methods for a detailed description). *Representación esquemática de las variables registradas en las cuadrículas de muestreo. Todas estas medidas se realizaron desde el centro geométrico de cada cuadrícula (ver el apartado de metodología para una descripción más detallada).*

geometric centre. In addition, other variables, such as distance to the bankfull level (DB) and distance to the thalweg (DT), were determined with the geometric centre as a reference (Table 2 and Fig. 3). However, these variables were not taken into account in the statistical analysis described below because they showed a high correlation with H.

The degree of feet development was estimated by applying one of two methods: I) measuring trunk diameter at breast height with a flexometer, in the case of alder and narrow-leafed ash; or II) estimating volume by multiplying the values of the three dimensions measured with a flexometer, in the case of oleander and salvia leaf willow. Finally, the density of young feet (plants under 30 cm height) was recorded by counting the number of seedlings and saplings rooted inside each plot (Table 2).

Statistical analysis

An exploratory Chi-squared test (χ^2) was applied to examine the transverse patterns in the riparian species distributions along the cross-sections. This analysis is useful for describing species' preference for (or rejection of) certain areas in environmental gradients or to determine whether they are randomly distributed along the gradients (Blanco-Garrido *et al.*, 2009). In this case, the χ^2 test was applied to detect any preferred or rejected ranges of H for each species or to determine whether they were randomly distributed along these ranges. The sampling plots were ordered ($n = 151$), and various H categories were defined (0-50 cm, 51-100 cm, 101-150 cm, 151-200 cm and 201-250 cm). The total number of plots in each category (available plots) and the number of plots occupied by the studied species in each category (used plots) were counted. The χ^2 test allowed the comparison of available and used plots. If significant differences were detected ($p < 0.05$), a partitioned χ^2 test was performed to detect the H category responsible for the differences. This test was applied separately for adults and young feet (plants under 30 cm height) to explore the distribution patterns of each group along the topographic gradient. Analyses were carried out for each species with all collected data (Robledillo + Estena + Ruecas). Before the χ^2 test was conducted, a t-test was applied to evaluate whether each species occupied different H ranges in different stream stretches (Robledillo, Estena or Ruecas). If a non-statistically significant result was obtained, it was assumed that the data from the different stretches were comparable and, therefore, that all the data could be pooled together.

A one-way ANOVA (or a t-test in certain cases) was conducted to assess the differences in the degree of feet development (trunk diameter for alder and narrow-leafed ash and volume for

Table 2. Variables measured during fieldwork, showing their codes, methods of collection and units. *Variables registradas durante el trabajo de campo, indicando el código de identificación de cada una de ellas, el procedimiento de toma de datos y las unidades de medida.*

Variables	Code	Method	Units
Distance to bankfull level	DB	Tape	m
Distance to thalweg	DT	Tape	m
Height from thalweg	H	Water level meter	cm
Number of feet of each species	—	Count of trees and shrubs of each species rooted inside the plot	—
Number of young feet	—	Count of seedlings and saplings rooted inside the plot	—
Degree of development of feet	—	Alder and narrow-leafed ash: trunk diameter measured at breast height, with flexometer Oleander and salvia leaf willow: volume, multiplying the dimension of the three axes, measured with flexometer	Diameter: cm; Volume: m^3

oleander and salvia leaf willow, see Table 2) in different H categories. Finally, a one-way ANOVA was applied to explore the variation in the densities of young feet along the topographic gradient defined by H.

Before the statistical tests were performed (t-test and ANOVAs), a normality test was conducted on all the analysed variables (H, trunk diameter, volume and the density of young feet). Transformation of variables was not necessary as they all met normality and homoscedasticity assumptions (Shapiro-Wilk test and Levene statistic).

RESULTS

Black alder

The distribution pattern of black alder was analysed in the Robledillo and Ruecas Rivers (pooled data, $n = 85$ plots; the species was not present in the Estena River) because the species occupied the same H categories in these two river stretches (t-test; $t = -1.58$, df = 25, $p = 0.126$). Black alder preferentially occupied the lower areas of the topographic gradient (0-150 cm

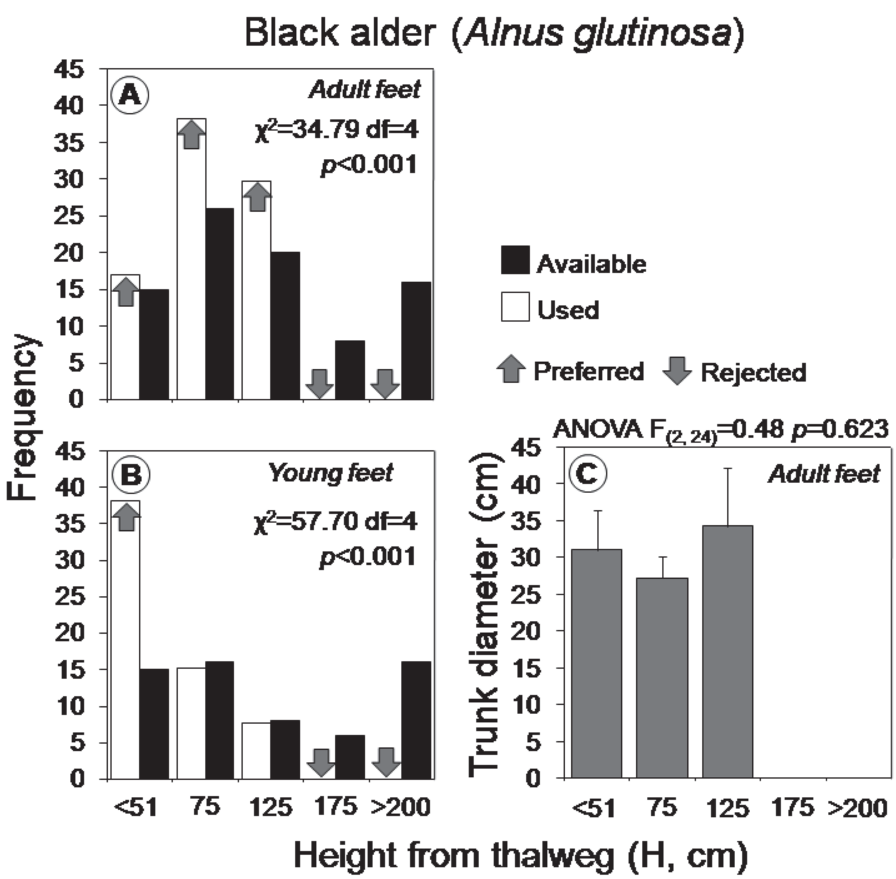

Figure 4. Preferences of adult feet (A) and young feet (B) of black alder along the topographic gradient represented by H (height from the thalweg). Black bars represent the available plots in each H category. White bars represent the frequency of use by alder. Preferred or rejected ranges are indicated with vertical arrows (partitioned-χ^2, $p < 0.05$). Numbers on the X-axis represent the mid-point of each category. (C) Variation in the average diameters of the trunks (± standard error) in the different H categories. *Preferencias de los pies adultos (A) y de regeneración (B) de alisos a lo largo del gradiente topográfico definido por la variable H (altura respecto a la línea de vaguada). Las barras negras representan las cuadrículas disponibles en cada rango de H. Las barras blancas representan las cuadrículas con presencia de alisos (frecuencia de uso) en cada uno de estos rangos. Los rangos de H preferidos o rechazados se representan con flechas verticales (χ^2-subdividido,* p *< 0.05). Los números del eje X representan el punto medio de cada rango. (C) Variación del diámetro medio de los troncos (± error estándar) en los diferentes rangos de H.*

height from the thalweg) and displayed a rejection for higher areas (Fig. 4A). Young feet were analysed with data from the Robledillo River (only this stretch contained young feet, $n = 61$). Black alder young feet also occurred in the range of 0 to 150 cm, rejecting higher positions (Fig. 4B). A noticeably high recruitment rate occurred at heights < 51 cm. The other ranges (H between 51-150 cm) were occupied according to their availability. Black alder feet showed similar trunk diameters along the topographic gradient ($F_{(2,24)} = 0.48$, $p = 0.623$; Fig. 4C).

Salvia leaf willow

The distribution pattern of salvia leaf willow along the topographic gradient was similar to that of black alder. The pattern was analysed in the Estena River ($n = 66$), as it was the only site in which the species was present in a significant number of plots. Salvia leaf willow showed a higher preference for lower areas of the topographic gradient, specifically for the range between 51 and 150 cm, and a strong rejection for higher areas (Fig. 5A). The species had a larger volume in the range between 101 and 150 cm (Fig. 5B), although this was not significant ($t = -0.89$, df = 5, $p = 0.413$), most likely due to the very low number of feet ($n = 7$). The distribution pattern of young feet could not be analysed due to the small data set available ($n = 5$ plots).

Narrow-leafed ash

The analysis of narrow-leafed ash was conducted in the Estena River ($n = 66$ plots) because the number of observations in the Robledillo River was too low ($n = 4$). Narrow-leafed ash showed a preference for the H category between 151 and 200 cm. Its preference for the category from 51 to 100 cm was lower than expected. The remaining categories were occupied according to their availability (Fig. 6A). This species, therefore, occupied the entire topographic gradient, with a higher density in the intermediate areas where the mean narrow-leafed ash trunk diameter was larger (Fig. 6C), although this was not significant (ANOVA $F_{(3,38)} = 0.25$, $p = 0.858$).

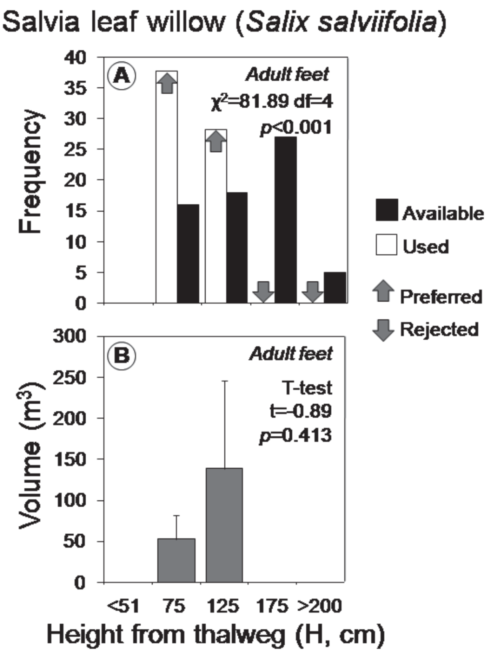

Figure 5. (A) Preferences of adult feet of salvia leaf willow along the topographic gradient represented by H (height from the thalweg). Black bars represent the available plots in each H category. White bars represent the frequency of use by willow. The preferred or rejected ranges are indicated with vertical arrows (partitioned-χ^2, $p < 0.05$). Numbers on the X-axis represent the mid-point of each category. Data from the 0-50 cm range were not available in the Estena River. (B) Variation in the average volumes (±standard error) in the different H categories (see methods for a detailed description of volume calculation). *(A) Preferencias de los pies adultos de sauces a lo largo del gradiente topográfico definido por la variable H (altura respecto a la línea de vaguada). Las barras negras representan las cuadrículas disponibles en cada rango de H. Las barras blancas representan las cuadrículas con presencia de sauces (frecuencia de uso) en cada uno de estos rangos. Los rangos de H preferidos o rechazados se representan con flechas verticales (χ^2-subdividido,* p < 0.05*). Los números del eje X representan el punto medio de cada rango. No hubo datos de la especie en el rango 0-50 cm en el tramo del río Estena. (B) Variación del volumen medio de los sauces (±error estándar) en los diferentes rangos de H (ver el apartado de metodología para una descripción detallada del cálculo del volumen).*

Narrow-leafed ash young feet occupied the entire topographic gradient, showing a slight preference for lower areas (Fig. 6B). The recruitment pattern of narrow-leafed ash was described in further detail by assessing the variation in the numbers of seedlings and saplings per sampling plots along the H ranges and the ranges where seed germination was more successful. This exploratory analysis could not be conducted for the other species due to a high dispersion of data (black alder) or a low number of cases (salvia leaf willow). The analysis showed that the density of narrow-leafed ash seedlings and saplings in the intermediate areas of the gradient was three times larger than in the higher or lower areas (Fig. 6D).

Oleander

The analyses for oleander were conducted on the Robledillo River dataset (n = 61 plots). Oleander occupied the entire topographic gradient. However, the species showed a preference for the range from 201 to 250 cm and rejection for areas below 50 cm. The other ranges were occupied according to their availability (Fig. 7A).

Young feet showed a preference for the range from 0 to 150 cm (Fig. 7B). The lack of seedlings and saplings in the ranges occupied by the less-developed adult feet (201-250 cm) was remarkable (Fig. 7B). The exploratory analysis of the densities of young plants along the riverbank topographic gradient could not be performed with this species (Fig. 7), due to the high dispersion of data. The volume of adult feet showed a decreasing trend from the lower to upper areas of the topographic gradient (Fig. 7C).

DISCUSSION

Our results reveal a strong relationship between riverbank topography and riparian species distribution. The different riparian species analysed here had different topographic distributions along the riverbanks, which allows for the definition of

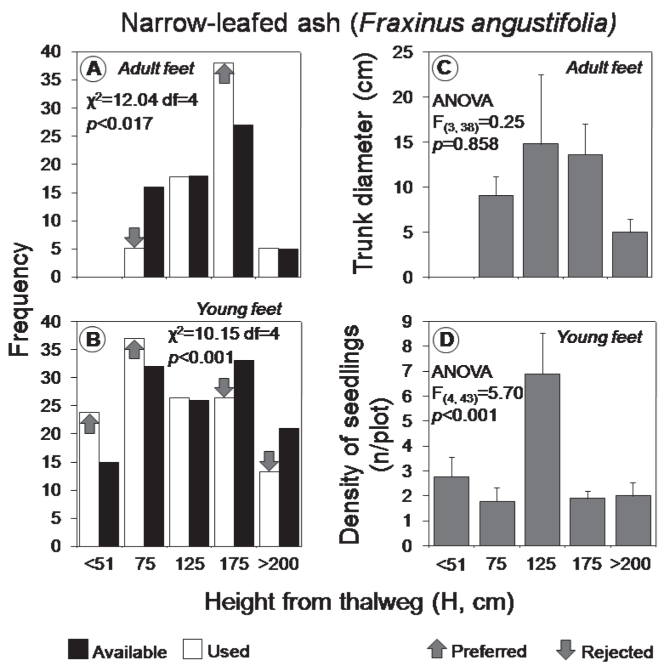

Figure 6. Preferences of adult feet (A) and young feet (B) of narrow-leafed ash along the topographic gradient represented by H (height from the thalweg). Black bars represent the available plots in each H category. White bars represent the frequency of use by narrow-leafed ash. The preferred or rejected ranges are indicated with vertical arrows (partitioned-χ^2, $p < 0.05$). Numbers on the X-axis represent the mid-point of each category. Data from the 0-50 cm range were not available in the Estena River. (C) Variation in the average diameters of the trunks, and (D) variation in the average numbers of young feet per plot (±standard error) in the different H categories. *Preferencias de los pies adultos (A) y de regeneración (B) de fresnos a lo largo del gradiente topográfico definido por la variable H (altura respecto a la línea de vaguada). Las barras negras representan las cuadrículas disponibles en cada rango de H. Las barras blancas representan las cuadrículas con presencia de fresnos (frecuencia de uso) en cada uno de estos rangos. Los rangos de H preferidos o rechazados se representan con flechas verticales (χ^2-subdividido,* p < 0.05*). Los números del eje X representan el punto medio de cada rango. No hubo datos de la especie en el rango 0-50 cm en el tramo del río Estena. (C) variación del diámetro medio de los troncos y del (D) número medio de pies de regeneración por cuadrícula (±error estándar) en los diferentes rangos de H.*

a theoretical pattern of preferential topographic areas for each species (Fig. 8). For black alder, this pattern includes a preferential zone in the range of 0-150 cm from the thalweg, with adults being more common between 51 and 150 cm and young feet being more common in the lower range (0-50 cm). The physiological adaptations of black alder (Claessens, 2003; Claessens *et al.*, 2010) could explain the relative dominance of black alders in these areas. Adult salvia leaf willow shares its preferred area with alder in the 51-150 cm range. This result is consistent with the description of salvia leaf willow as an endemic species of the Iberian Peninsula capable of bearing a relatively wide set of environmental conditions but always linked to the lower ranges of the topographic gradient in dryland rivers (Garilleti *et al.*, 2012). The topographic preferences of salvia leaf willow in the studied stretches can thus be distinguished from those of other *Salix* species in diverse dryland areas (Horton *et al.*, 2001) and especially in non-Mediterranean environments, where they are commonly distributed irrespective of riverbank topography (Ohtsuka *et al.*, 2006).

Some authors have revealed different riverbank preferences for narrow-leafed ash in riparian areas (Décamps *et al.*, 1988; Temunović *et al.*, 2012). In our study, narrow-leafed ash was more common in the upper strip (151-200 cm) than in the strip preferred by alders and willows, whereas young feet covered the entire riparian range. This result appears to contradict the oc-

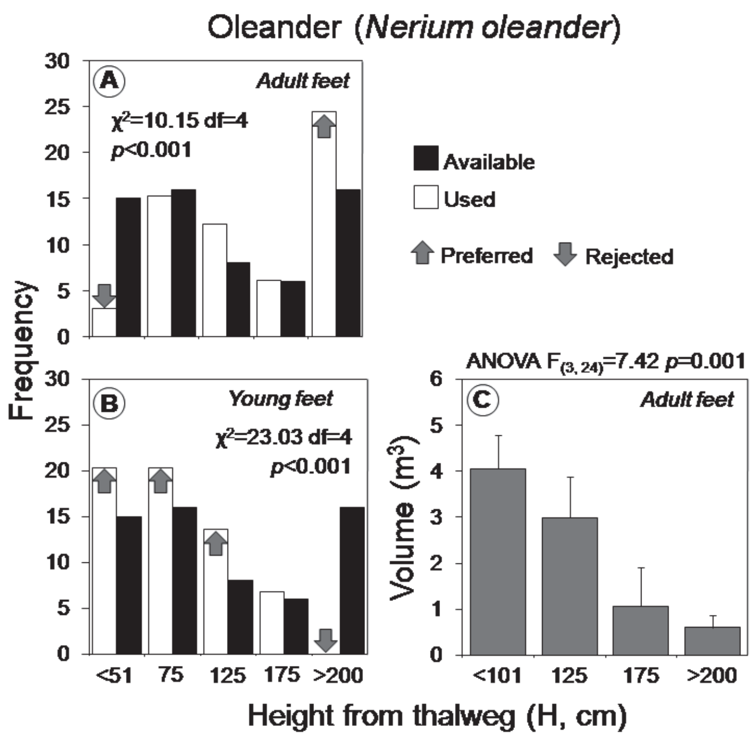

Figure 7. Preferences of adult feet (A) and young feet (B) of oleander along the topographic gradient represented by H (height from the thalweg). Black bars represent the available plots in each H category. White bars represent the frequency of use by oleander. The preferred or rejected ranges are indicated with vertical arrows (partitioned-χ^2, $p < 0.05$). Numbers on the X-axis represent the mid-point of each category. (C) Variation in the average volumes (± standard error) in the different H categories (see methods for a detailed description of volume calculation). *Preferencias de los pies adultos (A) y de regeneración (B) de adelfas a lo largo del gradiente topográfico definido por la variable H (altura respecto a la línea de vaguada). Las barras negras representan las cuadrículas disponibles en cada rango de H. Las barras blancas representan las cuadrículas con presencia de adelfas (frecuencia de uso) en cada uno de estos rangos. Los rangos de H preferidos o rechazados se representan con flechas verticales (χ^2-subdividido,* $p < 0.05$*). Los números del eje X representan el punto medio de cada rango. (C) Variación del volumen medio de las adelfas (± error estándar) en los diferentes rangos de H (ver el apartado de metodología para una descripción detallada del cálculo del volumen).*

cupation pattern displayed by adult feet. However, this trend could be explained by the species' anemochorous strategy, which allows seeds to germinate far from the mother feet, despite the strong shading effect of the maternal plants (Debussche & Lepart, 1992; Fraxigen, 2005). In addition, the presence of young feet throughout the riparian range could be influenced by competition and inhibition, as shown by Debussche & Lepart (1992). Oleander is different, as adult oleander prefers higher areas (201-250 cm). Similar to narrow-leafed ash, oleander young feet were also widely distributed throughout the riverbank topographic gradient but showed a preference for lower areas. The decreasing trend in the volume of adult feet from lower to higher areas could indicate that, despite the low number of plants thriving in the lower areas, the few feet that are present there can reach a higher degree of development due to the higher water availability. According to Herrera (1991), the seeds and young seedlings (less than 1 year old) of oleander depend on very specific hydroecological conditions for optimal germination and development. This preference for sites with a steady supply of soil moisture makes the species an atypical example of a sclerophyllous Mediterranean scrub species.

Compared with the young feet, the adult feet of the four species showed distinguishable traits in their topographic distribution along riverbanks, reflecting their different physiological adaptations and life strategies. In our study, young feet did not show such distinguishable topographic preferences, most likely due to biotic and abiotic factors limiting their survival. Nevertheless, they were more frequently associated with areas close to water than were their related adults and appeared to be more common in proximity to larger adult feet.

Many studies have shown that changes in environmental factors, from the local to the regional scale, influence the dynamics of riparian vegetation (Dixon *et al.,* 2002; Harper *et al.,* 2011; Aguiar *et al.*, 2011; Fernandes *et al.*, 2011; Engelhardt *et al.,* 2012). These factors include river regulation, land use, and climate characteristics. In our study, we found that local factors, such as those related to riverbank topography, are also important for understanding the riparian patterns in Mediterranean rivers and should be included in any management strategy. In addition, other factors, such as the feedbacks between biotic processes and physical drivers, should be carefully integrated into management (Stella *et*

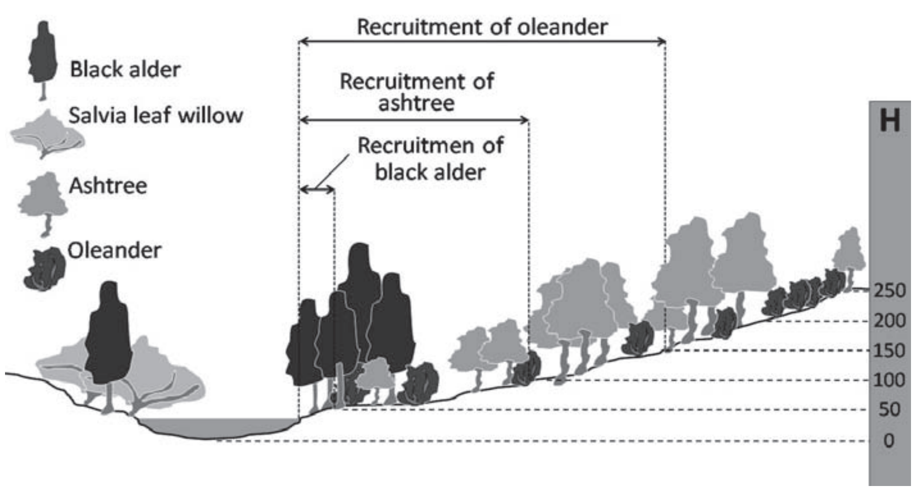

Figure 8. Theoretical distribution patterns of the analysed species along the topographic gradient represented by H (height from the thalweg, cm) according to the results of this study. The preferred areas for young feet (shown as recruitment zones) are also shown in the diagram. *Patrón teórico de distribución de las especies analizadas a lo largo del gradiente topográfico definido por la variable H (altura respecto a la línea de vaguada, cm) según los resultados obtenidos en el presente estudio. Se muestran también las zonas preferentes de regeneración de cada especie.*

al., 2013a, 2013b) because they appear to be key to the long-term conservation of riparian areas.

The management and restoration of riparian habitats have traditionally faced significant challenges in Mediterranean areas. These challenges include the fact that the common approach for restoration is based on the creation of more stable sites (Kondolf *et al.*, 2013) and that there is a lack of restoration initiatives based primarily on the requirements of riparian species (Bonada & Resh, 2013). On many occasions, the restoration of riparian areas has resulted in failed native species reforestation. That lack of success is quite likely due to the fact that the reforestation designs did not take into account how riparian dynamics and the structure of riparian vegetation species respond to key factors such as riverbank topography (Sweeney & Czapka, 2004). As shown by King & Keeland (1999), reforestation efforts greatly depend on these characteristics to successfully create the specific habitat features required by wildlife. The requirements and preferences of riparian species should, therefore, be integrated into the management and restoration of riparian habitats in the Mediterranean and worldwide. Effective integration should take into consideration, as shown by the findings of this study, the relative topographic distribution of native species, the interactions of adult and young feet, and the stressors potentially impacting the present and future dynamics of the riverbank areas.

CONCLUSIONS

Based on the results of this study, and to improve its applicability, the following conclusions and recommendations are provided:

1. The relative distribution of riparian species in minimally altered riparian habitats is highly dependent on riverbank topography. The four species analysed in this study have shown specific preferences along the riverbank topographic gradient.

2. This study has shown the preference of black alders and salvia leaf willows for the lower areas of the riverbank and the preference of narrow-leafed ash and oleander for the higher areas. Differences did not only arise between species but also between adult and young feet, indicating complex and varied life strategies. These results are novel for Mediterranean rivers and reveal the effect of riverbank topography on the structure and composition of riparian forests.

3. To improve our understanding of the functioning of riparian stands, studies of the influence of riverbank topography on the distribution of other riparian species are recommended. The incorporation of a wider array of biotic and abiotic variables into the analysis of riparian Mediterranean forests is also important for reaching a better understanding of riparian structure and functioning.

4. The results from this study could help develop better restoration and management strategies, in which reforestation designs pay attention to the natural and spatial patterns of riparian vegetation in relation to topography.

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