RIPARIAN GUILD COMPOSITION CHANGES ALONG A REGULATED MEDITERRANEAN STREAM IN CENTRAL-WESTERN SPAIN

MARÍA DOLORES BEJARANO CARRIÓN
Department of Forestry Engineering, Technical University of Madrid
ES-28040 Madrid, Spain

MIGUEL MARCHAMALO SACRISTÁN
Department of Land Morphology Engineering, Technical University of Madrid
ES-28040 Madrid, Spain

MARTA GONZÁLEZ DEL TÁNAGO
Department of Forestry Engineering, Technical University of Madrid
ES-28040 Madrid, Spain

DIEGO GARCÍA DE JALÓN
Department of Forestry Engineering, Technical University of Madrid
ES-28040 Madrid, Spain

ÁLVARO SORDO-WARD
Department of Civil Engineering: Hydraulic and Energy, Technical University of Madrid
ES-28040 Madrid, Spain

The high heterogeneity of the Mediterranean riparian areas along with their multiple sources of degradation, make responses of vegetation to flow alteration difficult to predict. In addition, most studies on impacts of flow changes in Mediterranean corridors have specifically addressed certain species, with no easily transferable results to similar stream types in other geographic regions. Given that species tend to associate according to similarity in response to environmental conditions (i.e., hydrologic regime for riparian zones), in this study we classified the riparian species of a Spanish stream into guilds using clustering techniques and ordination analysis and examined the responses of riparian guilds to flow regulation. We compared the changes in guild abundance that occurred following the construction of a dam in 1956 which caused a significant decrease of stream discharge. For comparisons, we used pre-dam and post-dam established vegetation bands identified based on old and modern air photographs and on field measurements of woody species diameter. Responses to flow regulation varied between vegetation guilds according to the ecological requirements of their dominant species. The ability to survive water stress (i.e., Xeric guilds) and to hydrogeomorphic disturbances (i.e., Torrential guilds) resulted in a shift of certain pioneer shrub-dominated guilds (e.g., *Flueggea tinctoria* and *Salix salviifolia* dominated guilds). In contrast, new hydro-morphological conditions following damming limited the recruitment of native late-successional tree guilds which were sensitive to floods (i.e., to drag forces and to inundation and anoxia; Slow-water and Flood-sensitive guilds, respectively) and of those with greater water requirements (i.e., Hydric guilds) (e.g., *Alnus glutionosa* and *Celtis australis* dominated guilds). The guild approach provides information about the general trends in plant populations and assemblage structures and allows generalizations and comparisons among different fluvial systems.

1 INTRODUCTION

The effects of altered stream flows vary among species (Jansson *et al*. [1]; Merritt & Cooper [2]; Dynesius *et al*. [3]; Merritt *et al*. [4]). Nevertheless, species-based knowledge reveals only part of the ecological consequences of flow alterations; even more, because of the large number of plant species along rivers around the world, it is impossible to assess the impacts on all species. In addition, results from research on species are difficult to extrapolate to other geographical regions. Based on the ecological guild concept, some authors have studied the responses from groups of species (functional groups, usually referred to as guilds), assuming that species tend to associate according to similar behavior in response to environmental conditions (Simberloff & Dayan [5]; Austen *et al*. [6]). Few studies have used plant guilds to analyze riparian vegetation responses to the changing hydrology and geomorphology of rivers. The identification of riparian vegetation–flow response guilds has been recently proposed by Merritt and colleagues [4] as a tool for determining environmental flows for riparian ecosystems. The guild approach is a synecological assessment that allows generalizations and comparisons among different fluvial systems (Severinghaus [7]).

Mediterranean rivers are among the most impounded in the world (García de Jalón [8]; Grantham *et al*. [9]). Consequently, there is an increasing demand for scientific knowledge related to impacts of flow alterations to assure their sustainable management. However, in the Iberian Peninsula few studies on the specific effects of hydrologic alterations on vegetation have been conducted (but see for example: Aguiar & Ferreira [10]; González *et al*. [11, 12]). In arid region streams, riparian vegetation is particularly responsive to the hydrologic regime related to water level, flooding, and hyporheic fluxes (Ferreira & Moreira [13]; Mitsch & Gosselink [14]; Aguiar *et al*. [15]). Vegetation sensitivity to stream flow changes, coupled with increasing urban and agricultural water demands, is resulting in serious negative impacts on Mediterranean riverine ecosystems (Beguería *et al*. [16]; Pinilla [17]; Cabezas [18]).

In this study, we investigated whether there are Mediterranean riparian guilds that show distinct responses to stream flow declines. When these phenomena were observed, our final purpose was to detect the most sensitive (i.e., which significantly decrease) and resilient (i.e., which significantly widespread) guilds to develop scientific basis to redirect flow regime management and restoration strategies in the Mediterranean region toward especially threatened plant communities. Thus, we described the woody riparian vegetation of a 62-km regulated reach of a Mediterranean stream in central-western Spain, identified riparian guilds, and evaluated each guild’s response to flow alterations in terms of changes in guild composition.

2 METHODS

2.1 Study area

The Tiétar stream is a 150-km-long tributary of the Tagus River in central-western Spain and extends over 4478 km2 (Figure 1). The Rosarito dam became operational in January 1959 and is used for irrigation (Spanish Ministry of Environment [19]). The dam has a live storage capacity of 85 x 106 m3. Water is partially diverted from the reservoir from May to October through two side channels to irrigate crops in the lower valley. Additionally, crops are also supplied directly from the main channel through direct pumping, mainly along the lower part (Tagus Basin Authority; http://chtajo.es).

The Tiétar´s stream flow is mainly sustained by surface runoff and contributions from the major tributaries. The natural total annual runoff entering the Rosarito reservoir is 766 hm^3 (1985-2000) (source: simulated natural flow using the Sacramento model: CEDEX-Spanish Ministry of Environment; http://cedex.es). The total annual runoff which comes out from the dam, for the same period, is 485 hm^3 which means a 37 % of runoff reduction. At the dam site, the greatest flow declines occur in summer when water is diverted through the two artificial side channels for irrigation; whereas reservoir filling results in a halving of the river discharge in spring. The Tiétar stream exhibits pluvial seasonal flow variability, with winter and spring peak flows, and naturally, it rarely dries up in summer. We assumed non-significant reduction of floods due to the small size of the reservoir in relation to the magnitude of floods in the area (source: Caumax software for flood simulation: CEDEX-Spanish Ministry of Environment [20]).

This study focuses on the 62-km regulated reach of the Tiétar from below the Rosarito dam to (near) the tail of the downstream Torrejón-Tiétar reservoir (Figure 1). Seven river segments downstream from the Rosarito dam were randomly chosen for analysis (Figure 1). They were assumed to be subjected to hydrologic alterations and to other minor impacts which did not significantly differ among them. The homogeneity of the geomorphic and vegetation characteristics determined the length of each river segment, which was two kilometers long on average.

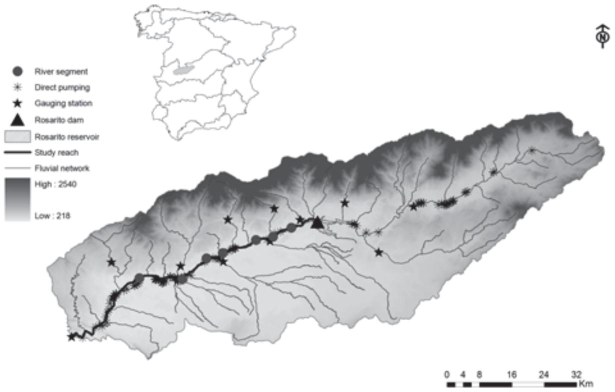

Figure 1. The Tiétar stream basin in central-western Spain.

2.2 Data collection

In the field, along each segment we randomly established an average of 9 – 30 m wide transects perpendicular to the river channel. We identified across each transect consecutive bands of vegetation arranged parallel to the river flow from the left to the right bank. A band consisted of a homogeneous vegetation zone with respect to the canopy, mid-stratum and ground cover of the dominant species (according to Bornette *et al*. [21]; Stromberg *et al*. [22]; Bejarano *et al*. [23]). Finally, bands of vegetation were characterized by determining biological and physical variables in the field: 1) woody vegetation species and their relative abundances; 2) diameter at breast height (DBH) using calipers for a representative number of individuals of the different cohorts of tree and shrub species; 3) mean distance to and height above the flow level during the survey season (base flow) using a Suunto level, a measuring tape and a laser distance measuring tool; 4) size class and relative abundances of riparian surface substrates by following the Wentworth scale and adding bedrock and peat (following Nilsson et al. 1994); 5) dominant fluvial landform (i.e.; active and high bars, bench, floodplain and terrace; following Hupp & Rinaldi [24]); 6) qualitative notes about dominant geomorphic processes based on evidence of incision or aggradation; and 7) absence/presence of woody debris. Measurements were carried out in July 2008.

We classified the vegetation bands surveyed in the field into pre-dam established and post-dam established. For this aim, we matched the DBH field data for each vegetation band with information from two series of orthophotographs taken prior to (spring and summer, 1956) and after (spring, 2006) the year the dam became operable (January, 1959). Along the selected river segments on both series of photographs we defined: i) ‘novel’ (post-dam) areas, those colonized after damming that corresponded to areas in transition and established stages on modern pictures but were in water, initial or colonization stages in older pictures; and ii) ’relict’ (pre-dam) areas, those already in transition and established stages in older pictures. Older pre-dam photographs were provided by the CECAF: Map and Photo Air Force Center, Spanish Ministry of Defense, whereas modern post-dam orthophotographs were downloaded from SIGPAC (Spanish Geographic Information System for Farming Lands; http://sigpac.mapa.es). ArcGis (version 9.2) was photo interpretation.

We used the HEC-RAS 4.1 (U.S. Army Corps of Engineers; http://www.hec.usace.army.mil/) step-backwater hydraulic model to calculate the bands´ inundation frequencies. We predicted the water-surface elevation at discharges corresponding to the base flow, annual winter flow, bankfull discharge (two-year return period) and four-, ten- and 25-year return period discharges for each river segment, calculated by fitting a Gumbel distribution to the data from the closest stream gauge. The channel geometry was defined for each river segment based on the cross sections per surveyed transect. Roughness coefficients for the cross sections were estimated following Arcement & Schneider [25]. This model was validated using the observed water-surface elevations at base flow (during the field season). A band was considered flooded when water exceeded half of the band’s area.

2.3 Identification of riparian guilds

We examined scientific literature for key attributes of surveyed riparian species that might condition their response to changes in flow regime or processes associated with them. The most relevant species attributes were determined by a Principal Component Analysis performed with Statgraphics Centurion (version XVI) on a set of

20 selected variables (Figure 2) describing the species life history and phenology, reproductive strategy, morphology and ecology (following Merritt *et al*. [4]. Then, we subjected our riparian composition data set (14 woody species and percentage of abundance from the surveyed vegetation bands) to a Detrended Correspondence Analysis using CANOCO (version 4.5) to evaluate species distribution trends along the Tiétar stream. Multiple regressions among DCA axes and environmental variables were used to assess how measured environmental variables influenced species spatial patterns. Categorical environmental variables were changed to dummy variables and rare species were downweighted. To quantify the relationship between the trait matrix and the community ordination we used a Canonical Correlation Analysis between the PCA space and the DCA space (Statgraphics Centurion, version XVI). Finally, we grouped surveyed vegetation bands according to their species composition using a hierarchical cluster analysis performed with PASW Statistics (version 18) on the species abundance data from each band, so that resulting vegetation groups differed from each other in riparian species associations. Each group was named according to the most important flow-related attributes of its species: drought resistance (i.e., resistance to water stress: '*Xeric*', '*Mesic*', '*Hydric*'), drag resistance (i.e., resistance to drag forces caused by floods: '*Torrential*', '*Semi-torrential*' and '*Slow-water*'), and flood resistance (i.e., resistance to inundation and anoxia: '*Flood-tolerant*' and '*Flood-sensitive*'). The between-groups linkage method and the Squared Euclidean Distance (SED) were used for analysis. The threshold in the resulting dendrogram was set manually to between three and five SED to obtain a minimal number of groups that represent the heterogeneity of the river vegetation. After comparisons with PCA and DCA results using a CCA (Canonical Correlation Analysis), vegetation groups were designated as riparian guilds, based on the criteria that each vegetation group comprising a guild contains species which share similar attributes and shares a similar environment.

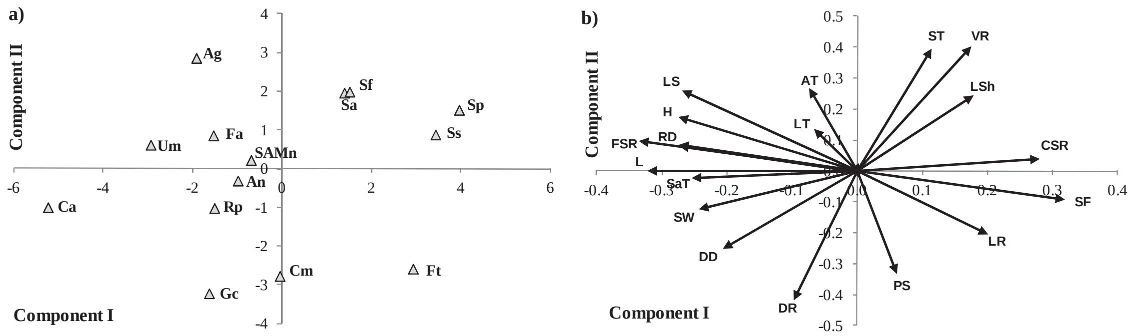

Figure 2. PCA diagrams. (a) Dispersion of the woody species in the Tiétar stream. (b) Weight for the species characteristics considered. Woody species are abbreviated as follows: Ft: *Flueggea tinctoria* (L.); Ss: *Salix salviifolia* (Brot.); Sa: *Salix atrocinerea* (Brot.); Sp: *Salix purpurea* (L.); Sf: *Salix fragilis* (L.); SAMn: *Sambucus nigra* (L.); Rp: *Robinia pseudoacacia* (L.); Gc: *Genista cinerea* (L.); Fa: *Fraxinus angustifolia* (Vahl); Cm: *Crataegus monogyna* (Jacq.); Ca: *Celtis australis* (L.); An: *Acer negundo* (L.); Ag: *Alnus glutinosa* (L.); Um: *Ulmus minor* (Mill.). Species characteristics are abbreviated as follows (in alphabetical order): AT: anoxia tolerance; CSR: coarse substratum resistance; DD: dispersal duration; DR: drought resistance; FSR: first sexual reproduction timing; H: height; L: longevity; LS: leaf size; LSh: leaf shape; LT: leaf thickness; LR: light requirements; PS: presence of spines; RD: rooting depth; SaT: salt tolerance; SF: stem flexibility; ST: Submergence tolerance; SW: seed weight; VR: vegetative reproduction.

2.4 Changes of riparian guild composition after flow regulation

DCA was also used to investigate plant community composition patterns prior to and after dam construction by locating the pre-dam and post-dam surveyed vegetation bands within the ordination axis. Additionally, we compared pre–dam and post–dam guild abundances to detect changes following the construction of the dam and, if so, whether this took place specifically for certain guilds. Shifts in the dominance of woody vegetation guilds were assessed by analyzing their pre- and post-dam frequencies.

3 RESULTS

The most common tree species within the 314 vegetation bands analyzed were *Alnus glutinosa* (L.) Gaertn. (black alder), *Fraxinus angustifolia* Vahl. (narrow-leaf ash) and *Celtis australis* (L.) (Mediterranean hackberry).

Other native tree species were *Ulmus minor* Mill. (elm) and *Crataegus monogyna* Jacq. (hawthorn). Rare exotic species were *Acer negundo* (L.) (box elder) and *Robinia pseudoacia* (L.) (false acacia). The native shrubland was dominated by *Salix salviifolia* Brot. (sage-leaf willow) and the Ibero-African shrubby spurge *Flueggea tinctoria* (L.) G.L. Webster (Spanish name tamujo). Other shrubs were *Sambucus nigra* (L.) (elder) and *Genista cinerea* (L.). Willow species such as *S. atrocinerea* (Brot.), *S. purpurea* (L.) and *S. fragilis* (L.) were rare.

The PCA of the plant species attributes showed a separation between pioneer shrub species on the positive side of the first axis (percentage variance = 38.5 %) and tree species on the negative side (Figure 2). This was primarily determined by the species morphology and life cycle and phenology strategies (Figure 2). A significant separation also appeared along the second axis between tree species (cumulative percentage variance of axes I and II = 60.2 %; Figure 2). Axis II mainly contained the species ecological attributes; it represented a water balance gradient with the water stress resistant tree species on the negative side (Figure 2). There were six statistically significant components (i.e., when eigenvalues < 1), which accounted for 88.2 % of the total data variance.

First two axes of DCA explained the 36 % of the total variation of species data and they accounted for the 60 % of species-environment relation (eigenvalue axis I = 0.72; axis II = 0.55). Species-environment correlations were high (Pearson´s correlation coefficient r axis I = 0.76 and r axis II = 0.5). The most important variables that contributed significantly to inter-band floristic heterogeneity were tree and shrub establishment timing and height and landform, geomorphic processes and canopy coverage along the first axis, and the size of substratum particles along the second axis (Figure 3). Applying a Canonical Correlation Analysis, a high correlation resulted between the two principal canonical axes from the two spaces (i.e., PCA and DCA spaces; first principal canonical axis r = 0.91; P < 0.0001 and second principal canonical axis r = 0.75; P < 0.01), which supports the association between the trait matrix and the community ordination.

Clustering techniques grouped the bands into nine groups according to their species composition and abundances. DCA showed that the above-defined vegetation groups differed significantly, being distinctly arranged depending on site characteristics (Figure 3) and according to the ecological requirements of the group associates (Figure 2). This result supported their designations as riparian guilds. Bands characterized by the '*Xeric/Torrential*' guild (i.e., bands dominated by *Flueggea tinctoria*), the '*Mesic/Torrential*' guild (i.e., bands co-dominated by *F. tinctoria* and *Salix salviifolia*) and the '*Xeric/Semi-torrential*' guild (i.e., bands co-dominated by *F. tinctoria* and *Fraxinus angustifolia*) colonized the coarsest substrates and were very often found at river–disturbed sites (Figure 3). Bands characterized by the '*Hydric/Torrential*' guild (i.e., bands dominated by *Salix* species) shared the highly disturbed habitat with those described before, with the exception that they preferred finer substrates and had greater water requirements (Figure 3). Bands characterized by the '*Hydric/Semi-torrential*' guild (i.e., bands co-dominated by *Salix salviifolia* and *F. angustifolia*) and the '*Generalist*' guild (i.e., bands dominated by *F. angustifolia*) showed flexibility for habitat conditions (Figure 3). At the other extreme, bands characterized by the '*Xeric/Slow-water/Flood-sensitive*' guild (i.e., bands dominated by *Celtis australis*) and the '*Xeric/Slow-water/Flood-tolerant*' guild (i.e., bands dominated by *Ulmus minor*) were generally found on the highest and less frequently flooded landforms, although the latter slightly better tolerated inundation (Figure 3). Finally, bands characterized by the '*Hydric/Slow-water/Flood-tolerant*' guild were located on rarely flood-disturbed landforms but presenting good water access (Figure 3).

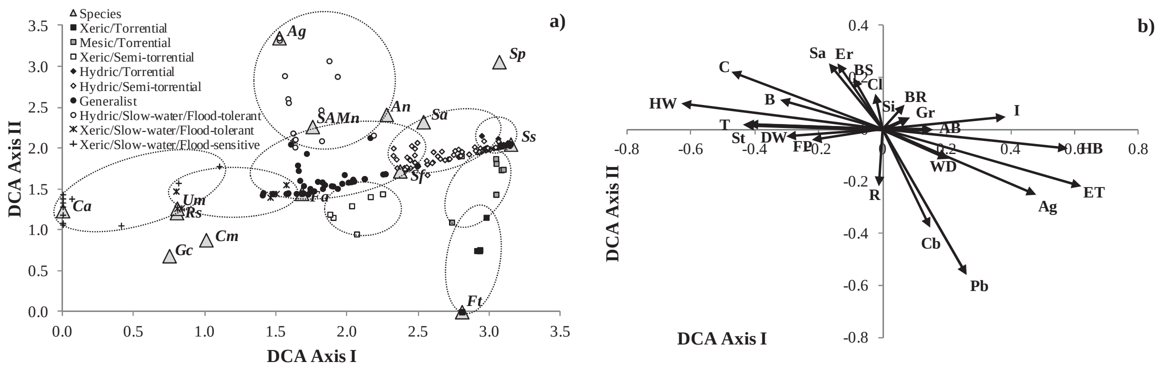

Figure 3. DCA diagrams. (a) Species–samples biplot of the DCA of the whole data set (i.e., species composition in the surveyed vegetation bands along the Tiétar River). Triangles represent woody species, whereas the remaining symbols represent the sampled bands. Each dash large circle indicates a riparian guild which is

assigned to the sampled bands it includes, according to the cluster analysis. (b) Retrospective projection of the environmental variables which characterized the sampled bands. Environmental variables are abbreviated as follows (in alphabetical order): AB: active bank; Ag: aggradation; B: bench; BR: bed-rock; BS: bank slope; C: canopy cover; Cb: cobble; Cl: clay; DW: distance to the water edge; Er: erosion; ET: establishment timing; FP: floodplain; Gr: gravel; HB: high bank; HW: height above the water level; I: inundation frequency; Pb: pebble; R: degree of regulation; Sa: sand; Si: silt; St: stability; T: terrace; WD: woody debris. See legend to Figure 2 for species abbreviations.

The '*Xeric and Mesic/Torrential* and *Semi-torrential*' guilds appeared only among the established post-dam bands. Pre-dam established bands characterized by the '*Hydric/Torrential* and *Semi-torrential*' guilds were scarce (Figure 4). In contrast, the relative proportion of bands characterized by the '*Hydric* and *Xeric/Slow-water/Flood-tolerant* and *Flood-sensitive*' guilds which established during the pre-dam period was significantly higher than that of the post-dam established bands (Figure 4). Among the surveyed bands characterized by the '*Generalist*' guild, half of them were colonized after damming (Figure 4). Finally, among the surveyed bands characterized by the the '*Xeric/Slow-water/Flood-tolerant*' guild, two quarters were colonized after damming (Figure 4).

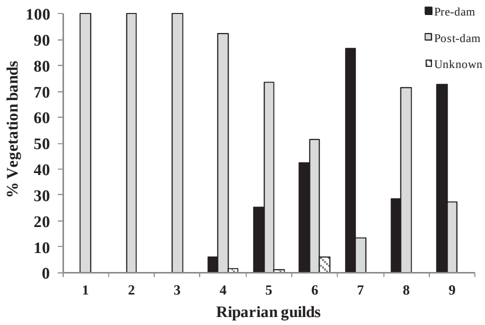

Figure 4. Relative proportion of the riparian guilds defined for the Tiétar stream that established during the pre-dam and post-dam periods along the study reach. X-axis contains the riparian guilds: 1: '*Xeric/Torrential*'; 2: '*Mesic/Torrential*'; 3: '*Xeric/Semi-torrential*'; 4: '*Hydric/Torrential*'; 5: '*Hydric/Semi-torrential*'; 6: '*Generalist*'; 7: '*Hydric/Slow-water/Flood-tolerant*'; 8: '*Xeric/Slow-water/Flood-tolerant*'; 9: '*Xeric/Slow-water/Flood-sensitive*'.

4 DISCUSION

In this study we evidence that riparian guilds along the Tiétar`s corridor respond to four main environmental gradients: flood inundation, moisture, canopy and substrate grain size. We also show that certain species characteristics control their tolerance to drag and drowning, water and light requirements and substrate preferences. Consequently, the environmental gradients existing within the Tiétar´s riparian corridor result in a dynamic mosaic of vegetation patches (Hupp & Osterkamp [26], where species with similar characteristics are clustered together and locations are determined by habitat conditions (Friedman *et al*. [27]; Hupp & Rinaldi [24]). Water withdrawals for agriculture have decreased stream discharge in the Tiétar stream during the last 50 years, reducing water availability for plants significantly. Shifts toward the dominance and decline of particular riparian guilds along the Tiétar stream during the post-dam period indicate that some guilds (i.e., pioneer shrub guilds) can take advantage of the conditions created by flow regulation, while others cannot (i.e., native late-successional guilds).

The proliferation of the '*Torrential*' and '*Semi-torrential*' guilds in the Tiétar stream after damming (dominated by *Flueggea tinctoria* and *Salix* species) is evident along the newly exposed areas which undergo frequent fluvial disturbance events. Conditions on such landforms limit the proliferation of species to those with flexible stems, rapid reproduction, and resistance to burial and re-sprouting ability. The segments closest to the dam contain the coarsest substrates due to trapping of fine sediment in the reservoir and scouring processes downstream of the dam. These coarse substrates contribute to summer water stress and difficulty of rooting, creating conditions only adequate for the '*Xeric/Torrential*' guilds (Gasith & Resh [28]; Aguiar *et al*. [15]). The combined effects of ground water contributions and the higher water-holding capacity of finer substrates result in less water depletion during the dry season in the lowland segments, allowing the spread of obligate phreatophytes along these segments (i.e., '*Hydric/Torrential*' guilds; Naumburg *et al*. [29]).

The ability of *F. angustifolia* to succeed in fluvial-disturbed areas behaving as a pioneer in the Tiétar stream is mirrored in this species association with *Salix* species individuals (i.e., the '*Hydric/Semi-torrential*' guild). Furthermore, mature individuals of *F. angustifolia* were also found on more distant and higher landforms with other non-obligate phreatophyte species where their long roots and trunk facilitate access to water and light. These indicate a shift in the composition and structure of late-successional riparian forests from being initially dominated by the '*Slow-water*' guilds mainly represented by *Alnus glutinosa* and *Celtis australis* species in more humid or drier areas, respectively (Garilleti *et al*. [30]), to becoming dominated by the '*Generalist*' guild dominated by *F. angustifolia* species.

The significant low number of post-dam bands characterized by the '*Hydric/Slow-water/Flood-tolerant*' guild indicates a failure at some point during critical steps in the life cycle of its species under the new hydrogeomorphic conditions. In the Tiétar stream, the survival of *A. glutinosa* seedlings on newly emerged river banks, where water availability is guaranteed, might be hampered by frequent fluvial disturbance events on these surfaces. Similar argumentation may also explain the decrease of the post-dam '*Xeric/Slow-water/Flood-sensitive*' guild, whose species cannot survive prolonged submergence when flooding. Our results are not conclusive on the effect of regulation on *Ulmus minor* forests. Surveyed bands characterized by the '*Xeric/Slow-water/Flood-tolerant*' guild were very few and mortality of this species could be a consequence of the Dutch elm disease (Díez & Gil [31]). Exotic species, such as *R. pseudoacacia* and *A. negundo*, were found more frequently on newly emerged areas. However, they are still very rare, indicating that they are not competitive with other native species after damming.

We demonstrate statistically significant changes in several riparian attributes after flow alterations, as expected according to the riparian vegetation–flow response guild theory (Merritt *et al*. [4]). The '*Hydric*', '*Slow-water*' and '*Flood-sensitive*' guilds in the Tiétar stream have become the guilds most threatened by regulation as a result of the significant decrease in recruitment of the species due to the decrease in discharge and maintenance of floods after damming. On the contrary, the most '*Generalist*' riparian traits together with the '*Xeric*' and '*Torrential*' traits have expanded significantly during the post-dam period. We support here the use of "indicator-guilds" rather than "indicator-species" (Verner [32]), suggesting that the effect of similar stream-flow alterations to those described for the Tiétar stream might similarly affect analogous guilds in other regions.

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