EXPLORING PATTERNS OF RIPARIAN VEGETATION ASSEMBLAGES TO REVEAL HUMAN-INDUCED LANDSCAPE CHANGE ALONG SOUTHERN SEMI-ARID MEDITERRANEAN STREAMS

ISTRAŽIVANJE OBRAZACA PRIOBALNIH VEGETACIJSKIH ZAJEDNICA RADI OTKRIVANJA PROMJENA KRAJOLIKA UZROKOVANIH LJUDSKIM DJELOVANJEM DUŽ JUŽNIH POLUSUŠNIH MEDITERANSKIH TOKOVA

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This study investigates the composition and ecological structure of riparian vegetation in southern Mediterranean semi-arid streams (north-eastern Algeria) to test how environmental filtering and anthropogenic pressures shape community assemblages. Vegetation relevé plots and a combination of landscape metrics have been used to quantify the spatial configuration and express the ecological condition of these riparian areas. Multivariate statistical process including Jaccard's distances matrix, hierarchical clustering procedures, Distance-based Linear Models (DistLM), and Generalized Linear Models (GLMs) were used to unveil the ecological status of these areas. We have identified a total of 25 woody plants (trees and shrubs) distributed in two dissimilar assemblages (SIMPROF test) promoted mainly by topographical variables, proximity to human activities, damming and aridity intensity, which explained 44.4% of total variance in woody composition according to DistLM ordination. Group 1, undisturbed landscape dominated (IndVal > 0.7, p < 0.001) by natural riparian plants such as Populus alba (stat = 0.874), Cytisus purgans (0.788), Juniperus oxycedrus (0.788), and Rubus ulmifolius (0.766), mainly align with sites located at mid to high altitudes, further from human settlements, and in undammed streams. Group 2, a human induced landscape dominated by Rhus tripartita, and associated with lower altitudes, close proximity to human development, and the presence of dams. Our best-supported GLM showed that woody species richness increased at sites with permanent stream flow (β = 0.33, p = 0.01) and higher elevation (β = 0.25, p = 0.009), but declined in riparian zones affected by damming structures. The significant effect of proximity to human habitation on species composition, but not on species richness (not retained in the best model), indicating that the complementary use of diversity metrics (species richness and composition) is crucial to properly capture the effects of human disturbance.

Keywords: riparian biota; multivariate analysis; environmental gradient; land use; disturbance

Ova studija istražuje sastav i ekološku strukturu priobalne (riparijske) vegetacije u južnim mediteranskim polusušnim vodotocima (sjeveroistočni Alžir) da bi se ispitalo kako okolišni filtri i antropogeni pritisci oblikuju sastav biljnih zajednica. Vegetacijske plohe (relevéi) i kombinacija krajobraznih metrika primijenjene su za kvantifikaciju prostorne konfiguracije i procjenu ekološkog stanja tih riparijskih područja. Multivarijatni statistički postupci, uključujući Jaccardovu matricu udaljenosti, hijerarhijsko klasteriranje, Distance-based Linear Models (DistLM) i generalizirane linearne modele (GLM), korišteni su za otkrivanje ekološkog statusa tih područja. Identificirano je 25 drvenastih biljaka (stabala i grmlja) raspoređenih u dvije međusobno različite zajednice (SIMPROF test), koje su uglavnom određene topografskim varijablama, blizinom ljudskih aktivnosti, prisutnošću brana i intenzitetom aridnosti. Ti čimbenici, prema DistLM ordinaciji, objašnjavaju 44,4 % ukupne varijance u sastavu drvenastih vrsta. Skupina 1, koju obilježava slabo poremećen krajobraz i dominacija prirodnih riparijskih biljaka (IndVal > 0,7, p < 0,001) kao što su Populus alba (stat = 0,874), Cytisus purgans (0,788), Juniperus oxycedrus (0,788) i Rubus ulmifolius (0,766), uglavnom se povezuje s lokalitetima na srednjim do većim nadmorskim visinama, udaljenijima od ljudskih naselja i u vodotocima bez brana. Skupina 2 predstavlja krajobraz pod snažnim ljudskim utjecajem, dominantna je vrsta Rhus tripartita povezana s nižim nadmorskim visinama, blizinom ljudskih aktivnosti i prisutnošću brana. Najbolji GLM model pokazao je da se bogatstvo drvenastih vrsta povećava na lokalitetima sa stalnim protokom vode (β = 0,33, p = 0,01) i većom nadmorskom visinom (β = 0,25, p = 0,009), ali se smanjuje u riparijskim zonama zahvaćenima izgradnjom brana. Značajan utjecaj blizine ljudskih naselja na sastav vrsta, ali ne i na bogatstvo vrsta (nije zadržan u najboljem modelu), pokazuje da je komplementarna uporaba pokazatelja raznolikosti (bogatstvo vrsta i sastav zajednice) ključna za ispravno bilježenje učinaka ljudskih poremećaja.

Ključne riječi: riparijska biota; multivarijatna analiza; okolišni gradijent; korištenje zemljišta; poremećaj

INTRODUCTION

There is an increasing need to provide localized information about the status and characteristics of vulnerable ecosystems, as the impact of some local factors (e.g., local land use) may counteract or amplify the effects of broader-scale drivers (e.g., climate change) (Bendix & Stella, 2013). Global datasets and broad-scale analyses often fail to capture the fine-scale environmental and ecological dynamics that are critical to understanding how ecosystems function and respond to change. Vulnerable ecosystems, such as riparian zones, which are among the richest landscapes on Earth, play a vital role in maintaining biodiversity, regulating water quality, and supporting a wide range of ecosystem services (Naiman et al., 1993; Singh et al., 2021). These ecosystems are facing growing threats from climate change, habitat destruction, and human activities (Allan, 2004), making it essential to understand their unique local conditions. Categorized as one of the fifteen globally recognized terrestrial biomes (Maraseni & Mitchell, 2016), riparian zones refer to biotic communities living on the shores of streams and lakes (Naiman et al., 2000). As ecotones, they encompass sharp gradients of environmental factors, ecological processes, and plant communities (Gregory et al., 1991). Among the various plant communities found in riparian zones, the primary focus is on woody plant communities such as trees and shrubs due to the critical roles they play in in shaping these ecosystems. The ecological functions and services provided by riparian vegetation such as the provision of physical habitat, water filtration, and erosion control are well recognized globally (Burton et al., 2005; Stella et al., 2013). However, it is impossible to list all their contributions here, particularly since this study focuses more on revealing patterns of woody riparian assemblages rather than emphasizing their benefits.

Changes in riparian plant assemblages are driven by a combination of natural and anthropogenic disturbances. Fluvial geomorphology and hydrology (González et al., 2010; Mollot et al., 2008) along with climate features (Ferreira et al., 2005) are the primary natural determinants of the shape and structure of riparian woodland. Besides, anthropogenic disturbances including land-use changes (Allan, 2004), agricultural expansion, urban development (Burton et al., 2009; Ferreira et al., 2005), and water regulation (e.g., damming or channelization) (Aguiar et al., 2018) exert significant pressures on riparian ecosystems. While shifts in the structure of woody plant communities, under multiple environmental changes have been extensively studied in the northern part of the Mediterranean ecoregion (eg: Aguiar et al., 2018; Angiolini et al., 2017; Corbacho et al., 2003; Ferreira et al., 2005; Leo et al., 2019; Zaimes, 2020), the situation in the southern Mediterranean remains largely unexplored. The southern side of this ecoregion, which includes parts of North Africa, faces unique environmental pressures such as increased aridity, higher temperatures, and growing human activity, all of which could significantly alter the structure and composition of riparian ecosystems. Thus, Mediterranean riparian habitats exhibit a more pronounced ‘island character’ compared to those in more humid regions, due to the steep microclimatic contrast between the riparian environment and the surrounding uplands showing clear floristic dissimilarities (Moore et al., 2005; Sabo et al., 2005). Human activities, water shortage and drought can be more important explaining woodland patterns than riparian habitat availability in the context of semi-arid Mediterranean basin (Bruno et al., 2014; Zaimes, 2020). The common riparian landforms observed often consist of naturally narrow galleries composed mainly of resilient species adapted to flash floods, low precipitation and seasonal droughts (Aguiar & Ferreira, 2005; Lite et al., 2005; Salinas & Casas, 2007). However, this resilient pattern is compromised by the increasing human alterations that make these environmental regimes in these areas more unpredictable (Bruno et al., 2014). Given these pressures, the status of Mediterranean riparian vegetation, especially in these extreme zones, requires continuous monitoring and updates. Regular assessment of its ecological health is crucial to detect changes in species composition, habitat quality, and the ability of these ecosystems to continue providing essential services. Effective management strategies must be based on real-time data to mitigate the impacts of human activities and ensure the resilience of riparian woodlands in the face of ongoing environmental challenges. At the best of our knowledge the most relevant investigation of the woody riparian in the southern part of the Mediterranean basin such as Algeria the largest country of north Africa dates back to 1999 and was conducted by Bensettiti and Lacoste (1999). Thus, there is an urgent need for focused research in this area to fill these gaps, assess the current state of riparian vegetation, and provide insights into the drivers of ecological change. This will support better-informed conservation initiatives that consider the unique characteristics of the southern Mediterranean riparian ecosystems.

The aim of the current study is to analyse how natural riparian woodlands (with the exception of cultivated species) respond to environmental gradients (e.g., altitude, slope, aridity), and to reveal human-induced landscape change in the Southern Mediterranean Basin. This study addresses the following two questions: (1) Which factors shape the richness of species, abundance and composition of riparian vegetation? and (2) What are the key plant species of indicator environmental changes?

MATERIALS AND METHODS

Study area

Standing as the first barrier against the vast Sahara, the Aures Mountain chain, covering a total area of 12,428 km², is the largest forested physical boundary between northern and

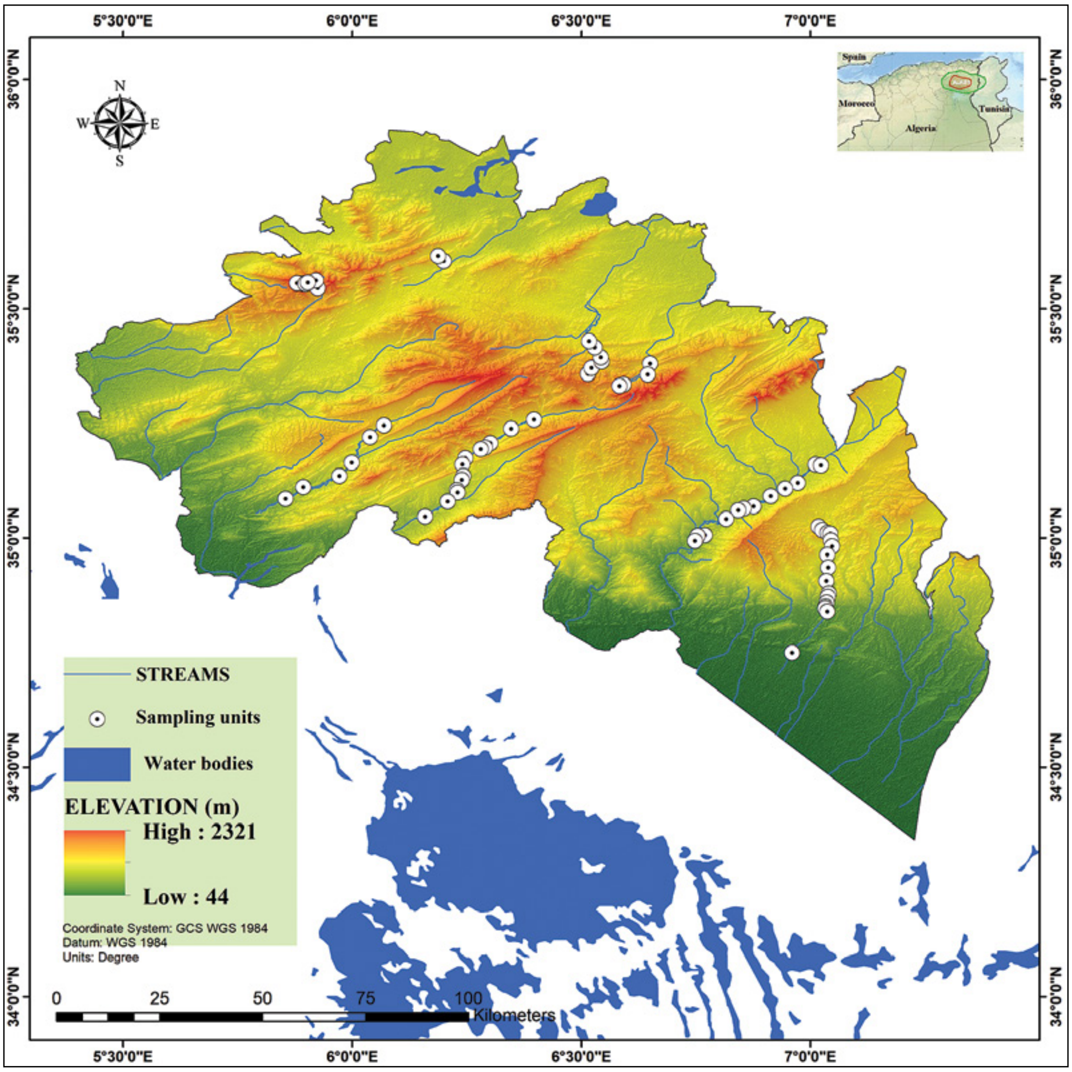


Figure 1 *Location of the Aures massif in northeastern Algeria showing the 61 survey units and the altitudinal gradient*

Source: DEM data were obtained from the Copernicus Data Space Ecosystem via Google Earth Engine. The map was produced using ArcGIS

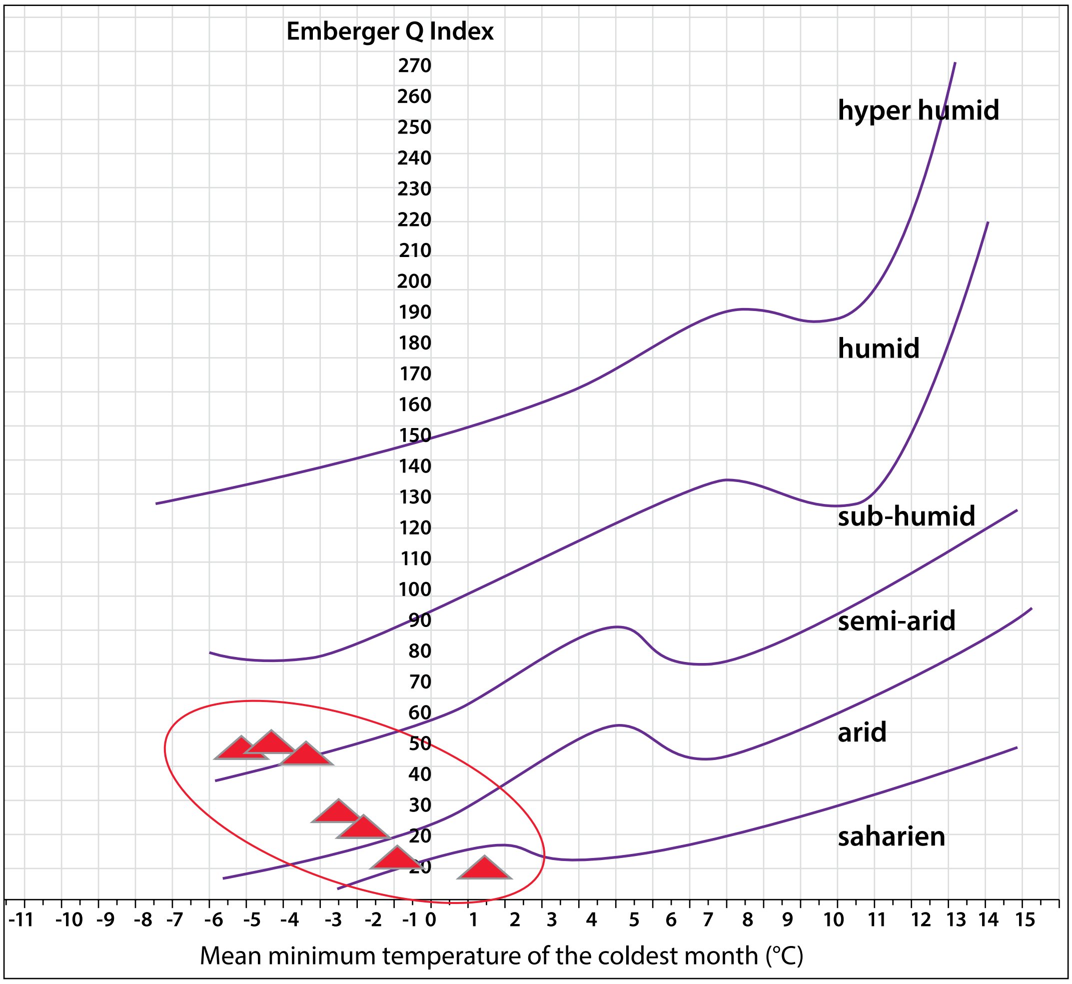


Figure 2 *Climate classification of the seven studied watercourses based on the Emberger Q Index and the mean minimum temperature of the coldest month (Red triangles indicate the locations of the seven watercourses)*

Source: Temperature and precipitation data for the period 1981–2022 were obtained from the NASA POWER Data Access Viewer (approximately 0.5° spatial resolution) and used to calculate the Emberger Q index. Bioclimatic classes follow Emberger's classification

southern Algeria (Fig.1). Lying between 34°90` and 35°60` north latitude, and 5°10` and 7°10` east longitude, the massif of Aurès is located in the Eastern part of the Saharan Atlas (Bezzih et al., 2021). The most notable forest formations are to be found there. The cedar and pine forests form veritable forests combined with several species, particularly the holm oak (*Quercus ilex subsp. ballota* (Desf.) Samp) (Vela & Schäfer, 2013), the only Algerian thuriferous stands (*Juniperus thurifera subsp. Aurasiaca* and a stand of small-leaved Zen oak (*Quercus faginea subsp. faginea*) (Bezzih et al., 2021; Vela & Schäfer, 2013).

Over the period 1981–2022, monthly average temperatures and precipitations showed significant variations, contributing to a wide range of bioclimatic belts, ranging from the subhumid to the semiarid on the Saharan level. According to the most common climatic classification for the Mediterranean region using the Emberger's quotient (Emberger, 1930; Vessella & Schirone, 2022) the studied streams belong to four bioclimatic belts: Saharan, arid, semiarid and subhumid (Fig. 2).

Sampling design

Riparian vegetation was surveyed from the source to the mouth of seven watercourses located in a mountainous region, the Aurès mountain chains of north-eastern Algeria (Fig. 1). The data were collected from 61 sampling riparian units (a 10-hectare circular plot) distributed along a total length of 244.7 km across seven rivers (Table 1).

Table 1 *Summary of the sampled rivers*

Name of the river	Number of sampled plots	Sampling kilometres (km)
Taberdga	16	46.8
Laarab	12	54.7
L'Abiad	13	45.3
Abdi	6	47.4
Chemora	7	30.6
Chelia	4	11.4
Refaa	4	8.5

Source: Google (2024)

Each plot of approximately 180 m radius was supposed to include the river bed, the floodplain and the adjacent upland (Fig 3). We believe that our surveys within this plot limits (ecotones: from a functional standpoint) allow us to cover all plants communities supposed to influence stream habitat and ecosystem processes and, conversely influenced by stream hydrology, microclimate and increased human activities (Decocq, 2002; Goebel et al., 2003). The three geomorphic sub-units (riverbed, floodplain, and upland) were delignated using field-based indicators, including topographic breaks, channel morphology, sediment texture, and flooding evidence (e.g., scour marks and depositional features). For the purposes of this study, we considered the riverbed as the permanently flooded channel, the floodplain as the adjacent area subject to temporary flooding, and the upland as the portion of the riparian zone outside the flood influence. We use vegetation relevé conducted according to Braun-Blanquet Approach 1964 (Ivanova, 2024). Using a stratified random sampling design, we placed six random plots (each 30×30 m) two on the banks, positioned adjacent to the active channel margin (approximately < 20 m from the bank) and four in the buffer zones,

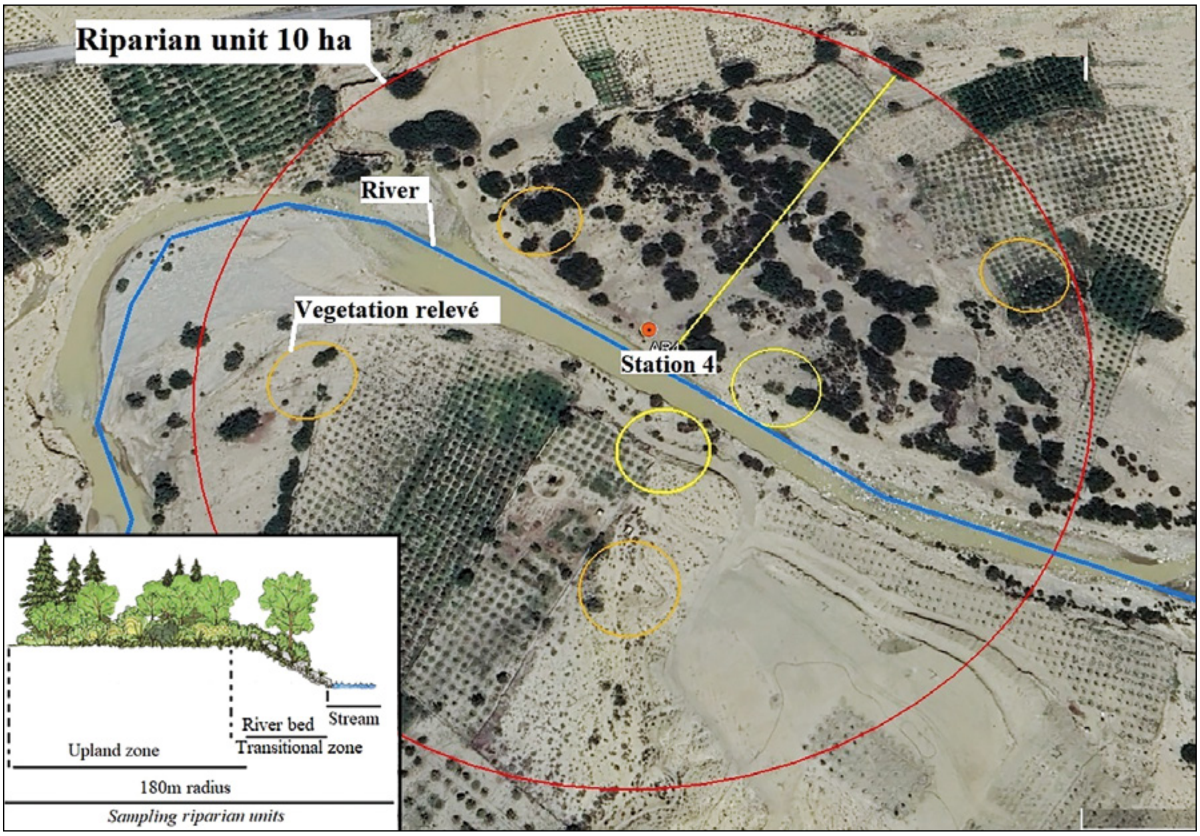


Figure 3 *Scheme illustrating the boundaries of riparian units, with six vegetation relevés conducted within each unit*
Source: Google (2024)

placed outside the near-channel zone (typically 50–150 m from the channel), in each of the 61 riparian units previously delineated, resulting in 366 plots (Fig 3). Our floristic survey was undertaken between the winter-spring high-flood level and the summer low-water level, at approximately 5 km intervals along the studied fluvial corridors, (during May and early June 2023). The riparian units were spaced at ~5 km intervals along the longitudinal course of the river to ensure spatial independence and coverage of regional environmental gradients. All woody species recorded in the field were collected and prepared as herbarium specimens for identification. Species were identified using regional floras (Meddour et al., 2021; Quézel & Santa, 1963) and subsequently confirmed by a taxonomic expert from the National School of Forests, Batna (Algeria). These herbarium specimens were used only for verification and were therefore not deposited as official vouchers. Cultivated species, defined as planted or actively managed individuals associated with agricultural activities, were excluded from the analysis. In particular, all fruit-tree species were excluded, and this was done at the species level.

In order to understand the spatial patterns of riparian vegetation, it is important to consider the influence of environmental factors and topographic features as well as land use and human activities. For this reason, a set of 11 variables expected to influence riparian vegetation variation were selected. To extract the value of each variable, the methodology used is based on satellite data analysis (The processing of all variables was performed in ArcGIS), as well as measurements and observations in the field (Table 2).

Statistical analysis

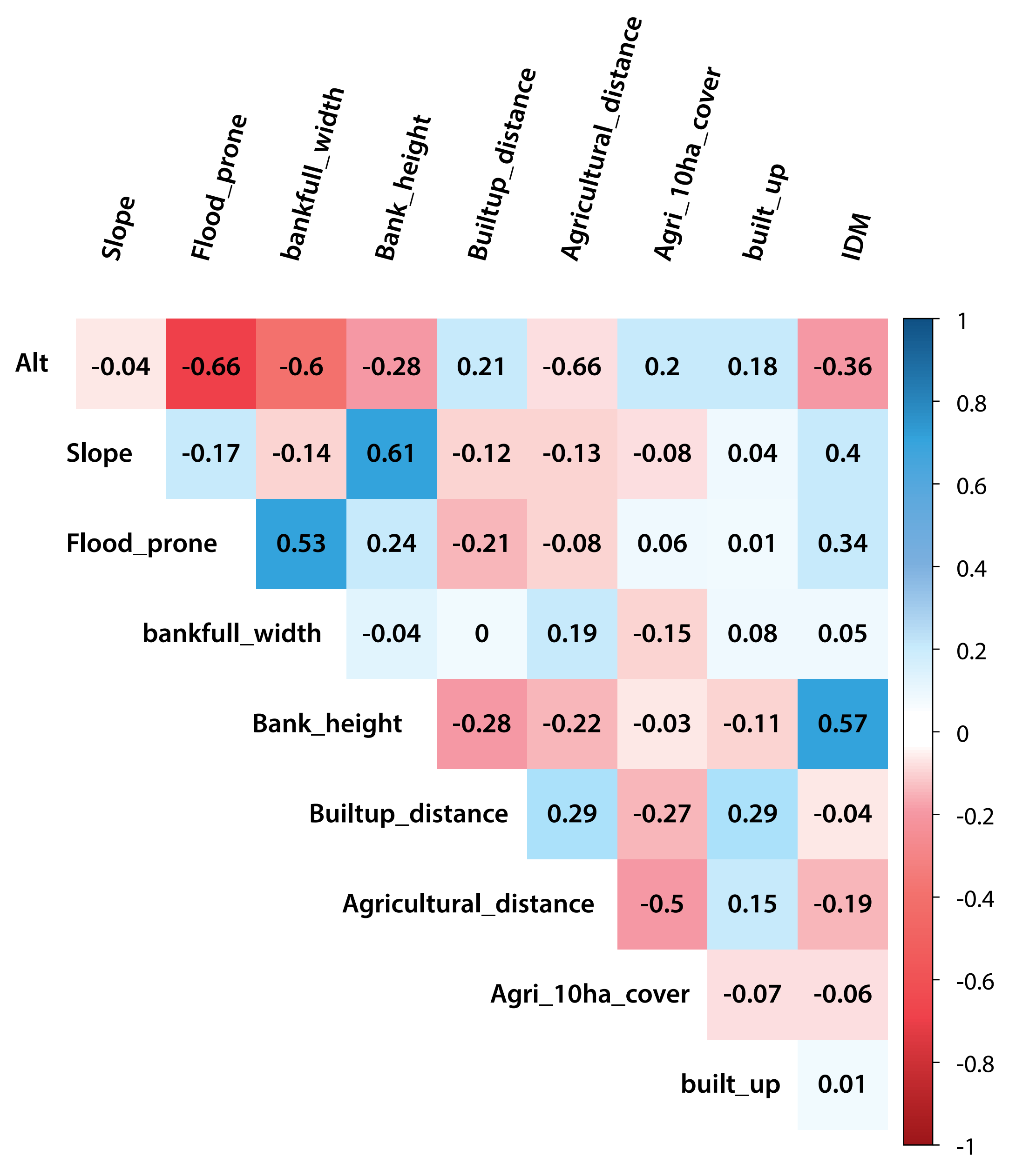
Environmental variables were transformed when necessary to improve normality and reduce skew. Variables were log-transformed ‘$x' = \log(x+1)$,’ while proportional data were logit-transformed ‘$x' = \log(x+\epsilon \,/\, 1-x+\epsilon)$’ where ϵ =

Table 2 *Variables used in the multivariate analysis aiming to explain spatial variation in riparian vegetation of the Aurès mountain chains of north-eastern Algeria*

Variables	**Description and units**	**Source**
	Dependent variable	
Riparian woody (tree and shrub) species	Number of species per 10-hectare plot	Observation in the field
	Independent variable	
Altitude	Elevation (m)	**Satellite data:** Copernicus Data Space Ecosystem: https://dataspace.copernicus.eu/ Google Earth Engine: https://earthengine.google.com/ ESA WorldCover: https://esa-worldcover.org/en Resolution 10-20 m, accessed in May and June 2023
Slope	Slope (°)	
Flood prone	Area that is likely to be inundated with water (m)	
Bankfull width	Channel width (m) area that is inundated or saturated by water at frequency duration	
Bank height	Vertical distance (m) from the water of a river to the top of its bank	
Flow	Intermittent vs permanent water flow	
Built-up distance	The distance between the centre of the sampling plot and the nearest urban area (m) (cities and small or rural villages)	
Agricultural distance	The distance between the centre of the sampling plot and the nearest agricultural area (m)	
Agricultural cover per 10-hectare plot	Surface of agricultural area per 10-hectare plot (ha)	
Damming	Presence or absence of dams, damming coded as 0/1	
IDM	De Martonne aridity index = Total yearly precipitation / mean temperature + 10 (computed for a custom climatological period (January 2001 - December 2023)	NASA POWER Data Access Viewer: (~0.5°): https://power.larc.nasa.gov/ (accessed in September 2023)

0.001 was added to accommodate zeros. Due to the varying measurement scales of environmental variables, all variables in the environmental variable matrices were standardized to z-scores, expressed as standard deviations from the mean (Legendre & Gallagher, 2001). Spearman's correlations were then used to identify highly correlated variables. Accordingly, considering the variables showing Spearman correlation coefficients greater than 0.7, those with a greater number of significant correlations were discarded for subsequent analysis to avoid redundant information. The 'corrplot' package in R v3.3.5 was used and annual precipitation and temperature were the highly correlated variable (Spearman coefficient = -0.85). Given the ecological importance of the removal of these two variables, and since one is not a desirable option, we chose to include a composite index that combines both. The most relevant index for the Mediterranean region is the De Martonne aridity index (Pellicone et al., 2019). The final result of Spearman's correlations analysis with the retained variables is presented in the figure 4.

The compositional gradient in woody species per plot matrix was explored by multivar-



	Slope	Flood_prone	bankfull_width	Bank_height	Builtup_distance	Agricultural_distance	Agri_10ha_cover	built_up	IDM
Alt	-0.04	-0.66	-0.6	-0.28	0.21	-0.66	0.2	0.18	-0.36
Slope		-0.17	-0.14	0.61	-0.12	-0.13	-0.08	0.04	0.4
Flood_prone			0.53	0.24	-0.21	-0.08	0.06	0.01	0.34
bankfull_width				-0.04	0	0.19	-0.15	0.08	0.05
Bank_height					-0.28	-0.22	-0.03	-0.11	0.57
Builtup_distance						0.29	-0.27	0.29	-0.04
Agricultural_distance							-0.5	0.15	-0.19
Agri_10ha_cover								-0.07	-0.06
built_up									0.01

Figure 4 *Correlation matrix of the retained variables (IDM: De Martonne aridity index)*

iate analyses. Community composition was converted to presence–absence and used to compute a Jaccard dissimilarity matrix ('vegan' package in R). To reduce noise caused by extremely infrequent taxa, species occurring in fewer than four riparian units were excluded prior to analysis (Borcard et al., 2011; Bruno et al., 2014). Jaccard's index (Paul, 1901) is one of the most widely used similarity indices in ecology for detecting species assemblages association. Based on the Jaccard's distances matrix, hierarchical clustering procedures using the average-linkage (UPGMA) method was then conducted for woody species to investigate patterns of interspecific spatial associations (Pang et al., 2023). The SIMPROF (Similarity Profile, 'clustsig' package in R) test was used to identify significant clusters from the obtained groups (Clarke et al., 2008) with $\alpha = 0.05$ and 999 permutations. The selected groups were than tested for beta diversity dispersions using ANOVA (i.e., heterogeneity in species composition within groups) using 'betadisper' from the 'vegan' package in R. The significance was assessed with 999 permutations. Such analysis helps to identify groups with higher variability, highlighting thereby patterns of species assemblage heterogeneity induced by a variety of environmental drivers (Bevilacqua et al., 2012). Finally, indVal index (Species Indicator Values) was used to compute indicator values of species within the selected groups of sites using 'indival' function from the R package 'labdsv' (Roberts, 2015). Distance-based Linear Models (DistLM) was used to depict differences in woody riparian composition (dependent variable matrix) in relation to a set of explanatory variables (independent variable matrix) (Borcard et al., 2011; Legendre & Gallagher, 2001). In order to select only the most important factors for the parsimonious model, 'adonis2' function from the R package 'vegan' was used for performing distance-based multivariate analysis of variance (PERMANOVA: unrestricted permutation test with 999 runs): *adonis2(Jaccard_matrix., data=data, permutations=999).* It is designed to test how much variation in a multivariate response matrix (woody species composition) can be explained by one or more explanatory factors (environmental variables) (Borcard et al., 2011). Results were visualized using dbRDA ordination plots with the significant environmental variables influenced clustered assemblages (Oksanen et al., 2016). Differences in riparian vegetation composition (number of plant species) of the clustered assemblages were investigated using a Kruskal–Wallis ANOVA by mean rank tests. Then, in order to evaluate the relationships between plant species richness and environmental predictors (only those selected before), we fitted generalized linear models (GLMs) assuming a Poisson error distribution (number of species: count data). Model selection followed an information-theoretic approach based on AICc (Guthery et al., 2003). A candidate set of 64 a priori models was generated using the dredge function in the MuMIn package. Competing models were ranked by AICc, and only those within ΔAICc < 2 were considered to have substantial support. All models were checked for normally distributed residuals, homogeneity of variance, outliers and over-dispersion (overdispersions ~ 1). Multicollinearity (Variance Inflation Factor) was checked and VIF values estimated using the *performance* package in R for assessment of regression models performance.

RESULTS

Species composition

A total of 25 woody plants were identified to species level, including 8 tree and 17 shrub species (Table 3). By evaluating the dominant taxa (the most frequented species), we found that trees were mostly composed of *Pinus halepensis*, *Cupressus sempervirens, and Populus alba* and shrubs were mainly composed of *Nerium oleander, Tamarix* sp., and *Rhus tripartita* (Table 3) (Supporting Table 1).

Patterns of woody riparian assemblages

The clustering procedures, combined with SIMPROF analysis, identified several significantly distinct woody riparian groups. However,

Table 3 *Woody plants identified at the Aures region, north-eastern Algerian highlands*

Shrub species	Share (%)	Tree species	Share (%)
Nerium oleander	27.68	*Pinus halepensis*	19.92
Tamarix sp.	22.04	*Cupressus sempervirens*	14.78
Rhus tripartita	12.99	*Populus alba*	12.09
Juniperus oxycedrus	8.96	*Quercus ilex*	5.65
Cytisus purgans	7.79	*Eucalyptus globulus*	3.22
Retama raetam	7.79	*Ulmus* sp.	3.22
Fraxinus xanthoxyloides	7.73	*Quercus faginea*	2.15
Rubus ulmifolius	6.98		
Ziziphus lotus	5.91		
Juniperus phoenicea	5.79		
Capparis spinosa	4.97		
Crataegus laciniata	4.03		
Pistacia atlantica	3.86		
Ziziphus jujuba	3.49		
Rosa canina	3.22		
Berberis hispanica	2.15		
Rosa montana	1.07		

Source: Field survey, species frequency was calculated as the number of plots in which a species was observed at the study site (six plots) divided by the total number of plots surveyed (366 plots)

only two groups were selected due to their high level of dissimilarity, exceeding 0.8 (Figure 5). Group 1 comprised most stations characterized by relatively similar woody species composition, whereas Group 2 formed a distinct cluster, indicating marked compositional differences between the two groups. Beta diversity analysis demonstrated a significant difference in disper-

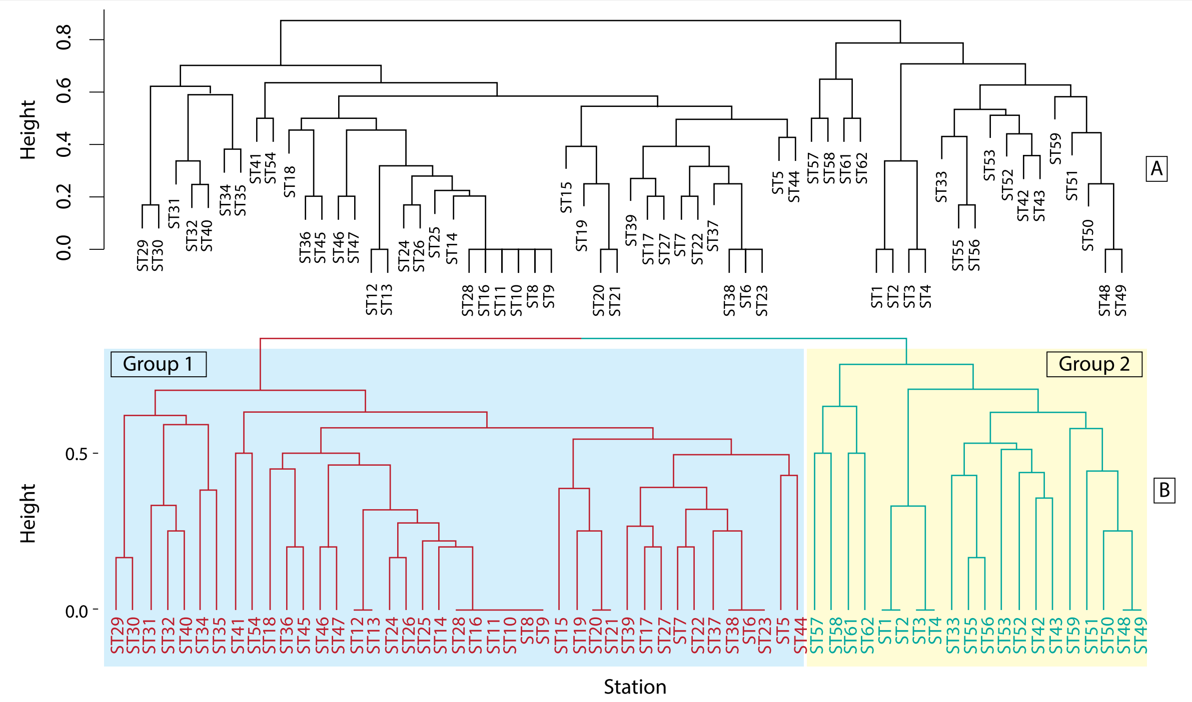


Figure 5 *Hierarchical clustering (Jaccard distance; average linkage, UPGMA) showing: (A) the full dendrogram for all surveyed stations and (B) clusters identified by SIMPROF analysis (α = 0.05), which indicated two significantly distinct groups of riparian units: Group 1 (blue) and Group 2 (yellow). Solid coloured branches denote statistically supported groups; labels correspond to station codes*

Source: Jaccard distance calculated from presence–absence data (Supporting Table 1)

Table 4 *Best DistLM results for woody species composition (999 permutations)*

Variable	Individual explained variance (%)	F-value	P-value
Altitude	25.03	24	0.001
Slope	3.35	3.23	0.005
Dist_HA	6.31	6.06	0.001
Damming	5.02	4.82	0.002
Flow	2.23	2.11	0.045
Altitude*IDM	2.4	2.33	0.021
Residual	54.9		

Source: Environmental variables were extracted using Google Earth Engine and ArcGIS. Statistical analyses were conducted in R

sion between the two groups (ANOVA using ‘betadisper’: F = 33.52, p < 0.001) (Figure 6). Group 1 displayed higher dispersion, suggesting greater variability in species composition compared to Group 2. Multilevel pattern analysis using the IndVal method identified 14 species significantly associated with the groups derived from the clustering analysis (alpha = 0.05). Of the 24 species analysed, 13 were significantly associated with Group 1, and 1 species was associated with Group 2 (Supporting Table 2). In Group 1, highly significant indicator species (IndVal > 0.7, p < 0.001) included *Populus alba* (stat = 0.874), *Cytisus purgans* (0.788), *Juniperus oxycedrus* (0.788), and *Rubus ulmifolius* (0.766), among others. Additional significant indicators included *Pinus halepensis*, *Rosa canina*, *Ulmus* sp., and *Fraxinus xanthoxyloides*. Less strongly associated, but still significant, were species such as *Quercus ilex*, *Crataegus laciniata*, *Capparis spinosa*, *Berberis hispanica*, and *Quercus faginea* (p < 0.05). In Group 2, *Rhus tripartita* was the sole significant indicator species (stat = 0.685, p = 0.001).

The significant variables selected during the DistLM analysis including altitude, slope, proximity to human-built areas (cities and small villages), damming, hydrological regime (flow), and an interaction term between altitude and aridity intensity (Table 4).

Among these, altitude explained the largest proportion of variance (25.03%), followed by proximity to human-built areas (6.31%) and a dam construction (5.02%), making them the most influential contributors. Linking these variables to the floristic patterns identified earlier, we found that the high compositional variability and species richness in Group 1 align with sites located at mid to high altitudes, further from human settlements, and in undammed streams (undisturbed group in figure 6). In contrast, the more homogeneous species

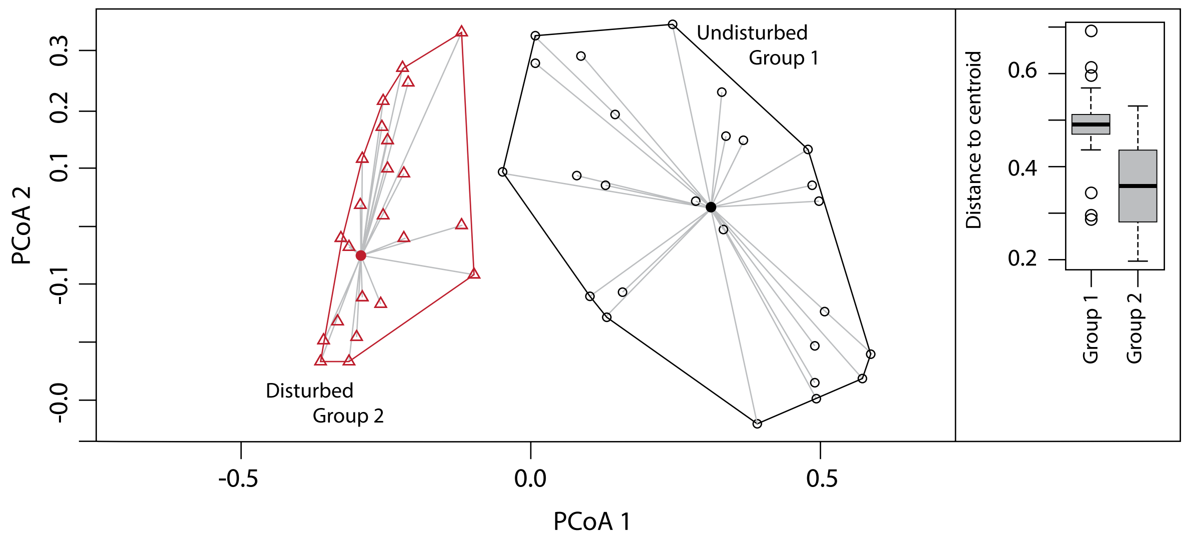


Figure 6 *Beta diversity comparison showing the extent of dispersion of the sites within each group*

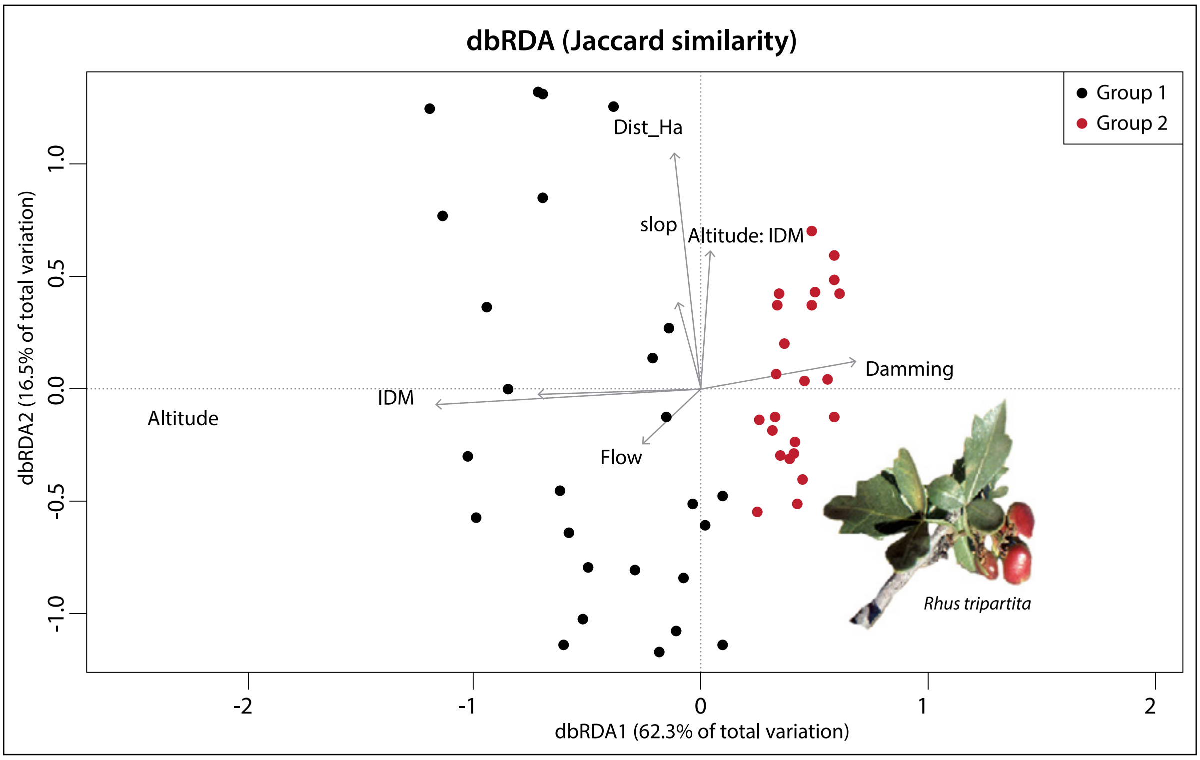


Figure 7 *dbRDA ordination plot relating composition cluster grouping and significant environmental variables from DistLM analysis*

Source: Environmental variables were extracted using Google Earth Engine and ArcGIS. Jaccard similarity calculated from presence–absence data (Supporting Table 1). Statistical analyses were conducted in R

composition of Group 2 (disturbed group in figure 6), dominated by *Rhus tripartita*, is associated with lower altitudes, close proximity to human development, and the presence of dams (Figure 7).

Species richness

The Kruskal–Wallis test revealed significant differences in species richness between woody riparian assemblages, with Group 1 exhibiting higher richness than Group 2 (χ^2 = 34.51, df = 1, p < 0.0017). The best-supported model identified during model selection (the model with the lowest AICc and model weight = 0.38) showed that most variables influencing species composition (as identified in the DistLM analysis) also explained variation in species richness, except proximity to human built-up areas, which was not retained (Table 5).

The best model-estimates showed that woody species richness increased significantly with altitude (β = 0.25, p = 0.009) and at sites with permanent flow (β = 0.33, p = 0.01), but declined with increasing slope (β = -0.18, p = 0.009) and in the riparian zone affected by damming constructions Table (6).

Table 5 *Summary of the best-supported candidate generalized linear models (GLMs) explaining variation in woody species richness across riparian units, ranked by AICc*

Model	df	logLik	AICc	delta	Weighting coefficients
12456	7	-125.09	266.29	0	0.38
1246	6	-126.65	266.85	0.56	0.29
12346	7	-125.85	267.81	1.52	0.18
123456	8	-124.67	268.11	1.82	0.15

1 = Altitude, 2 = Damming, 3 = Distance to habitation, 4 = Flow, 5 = IDM, 6 = Slope

Source: Environmental variables were extracted using Google Earth Engine and ArcGIS. Number of plant species recorded at each site (field survey, Supporting Table 1)

Table 6 *Model-averaged parameter estimates for environmental predictors of woody species richness, derived from the top-ranked GLMs (ΔAICc < 2)*

Term	Estimate	Std.Error	z value	Pr (>|z|)	VIF
Intercept	1.67	0.09	17.89	<0.001	
Altitude	0.25	0.07	3.22	0.001	1.99
Flow (permanent)	0.33	0.12	2.57	0.01	1.59
Slope	-0.19	0.06	-3.08	0.002	1.65
IDM	-0.12	0.07	-1.79	0.07	1.98
Damming (Before)	-0.37	0.15	-2.38	0.01	1.89

Source: Environmental variables were extracted using Google Earth Engine and ArcGIS. Number of plant species recorded at each site (field survey, Supporting Table 1)

DISCUSSION

Species composition

There were 25 woody species excluding cultivated species in all sampled plots recorded in the Aures region, north-eastern Algeria. In general, riparian strips in this study were both narrow and extremely poor in woody species compared to fluvial corridors in the northern part of the Mediterranean basin, namely 39 woody species in the Portuguese part of the Tagus River basin (Aguiar & Ferreira, 2005), 66 species in the north and central mainland of Portugal (Aguiar et al., 2018), 74 species in the Segura River basin, Spain (Bruno et al., 2014), and 67 woody species in the Panaro River, Northern Italy (Gumiero et al., 2015). At regional (North Africa) scales, phytosociological syntheses of riparian vegetation are very scarce, the most relevant attempts date back to 1999 by Bensettiti and Lacoste (1999). The global territory of this study englobes the occidental part of the Mediterranean Sea, where the data on woody riparian vegetation from Algeria were quite limited. Generally, we shared similar observations with this study, where the riparian woodland vegetation along the highland streams was mainly represented by assemblages of *Salici-Populetum alba* infiltered by abundant sub-association of *Nerio-Tamaricetea*. These assemblages are typical for the Maghreb riparian communities, a vegetation taxon to which halophyte and xerophytes species belong (Bensettiti & Lacoste, 1999; Salinas & Casas, 2007). Additionally, due to their location at the edge of the Algerian Sahara, the Aurès riverbeds support the occurrence of Saharo-Mediterranean vegetation species such as *Rhus tripartite* (Benaissa et al., 2019). These woody patches, though limited in height and coverage are notable for their ability to develop in soils deprived of organic matter (Taibaoui et al., 2020) and act as the last forested barrier before the Sahara, playing a critical role in buffering the surrounding ecosystems from further desert encroachment.

Assemblage patterns

In our study of the north-eastern Algerian highland streams, the clustering procedures, combined with SIMPROF analysis, identified two distinct groups: one more homogeneous and the other more heterogeneous in terms of beta diversity. Although the influence of altitude was clearly evident in shaping these groups, explaining 25% of the variance in community composition (Distance-based Linear Model), this pattern suggests a natural successional gradient in riparian vegetation. However, this natural succession appears to be disrupted by high levels of human disturbance. The DistLM further revealed a notable effect of anthropogenic pressures, such as damming and proximity to human habitations, as key drivers of the observed community transition. Landscape alteration caused by human activities such as urbanization, agriculture, and infrastructure development is a globally recognized problem that reduces habitat diversity and threatens local (Pennington et al., 2010; Ruas et al., 2022; Stieger & Mckenzie, 2024). Our findings reflect this trend, showing reduced beta diversity in areas impacted by damming and proximity to human settlements leading to a high vegetative configuration homogeneity. Man-made riparian complexes are often characterized by high structural and vegetative homogeneity, both horizontally and vertically (Corbacho et al., 2003). In more humid areas of the northern Mediterranean basin, these environments are typically dominated by highly invasive and opportunistic species such as *Typha*, as well as introduced genera such as *Eucalyptus* and *Populus* (Beerling, 1991; Nilsson et al., 1989). In contrast, in more arid regions, such as the one in our study, these environmental conditions favour the proliferation of xerophytic species, particularly *Rhus tripartita*. On this basis, one particularly alarming issue in the study area is the human disturbance of riparian corridors, primarily due to agricultural activities especially apple cultivation. The region has become one of the main apple-producing areas in Algeria, yielding approximately 1.6 million quintals during the agricultural season (Abdessemed et al., 2022; Frah et al., 2009; Khaoula et al., 2025). These orchards are generally established in close proximity to water resources, with the studied streams serving as the main source. It has a double impact: first, the replacement of native vegetation, especially where orchards are planted directly in riverbeds due to reduced water flow (presence of cultivated species are noted in almost all the study sites) and second, the intensive extraction of water through river irrigation, which alters the hydrological regime of the streams. In addition to riparian vegetation landscape changes driven by agricultural activities, damming emerged as a second significant factor influencing the structure of woody riparian vegetation in our study. The DistLM revealed a strong association between dam presence and the homogenization of vegetation structure. It is well established that alterations to the water flow regime caused by damming can disrupt ecosystem equilibrium, affecting both biotic components (such as vegetation and other living organisms) and abiotic components (including sediment transport and nutrient cycling) (Braatne et al., 2008). River damming is a widespread human activity that has been practiced for millennia and represents one of the most significant anthropogenic impacts on freshwater ecosystems (Aguiar et al., 2018). The findings of this study provide further evidence of the detrimental effects of damming on the integrity of freshwater ecosystems, particularly through the homogenization of riparian habitats. As noted by Bejarano et al. (2018), riparian plant guilds tend to become simpler and likely less diverse following flow regulation. According to the Kruskal–Wallis test, the disturbed group exhibited more limited and less varied vegetation compared to the riverbeds in the undisturbed group, which were characterized by mixed vegetation and a more complex riparian structure. The high compositional variability and species richness in this group align with sites located at mid to high altitudes, further from human settlements, and in zones with cooler temperatures and higher precipitation (higher IDM) (DistLM analysis). The undisturbed riverbeds are characterized by mixed vegetation formations, including both tall trees and shrubs, which contribute to a more complex riparian structure. Significant tree species identified (IndVal, $p<0.001$) include *Populus alba*, as well as some specimens of *Quercus ilex* and *Quercus faginea*. *Populus alba* tends to occur spontaneously in riparian zones along entrenched streams, particularly in the high plateaus of northern Algeria (Labiod el al., 2007). These areas typically feature rivers with steep slopes and elevated banks, creating microenvironments well-suited to this species. In contrast, *Quercus ilex* and *Quercus faginea* are often accompanied by a limited number of evergreen shrubs that are not typically characteristic of riparian zones, such as *Juniperus*, *Rosa canina*, *Rosa montana*, *Berberis hispanica*, and *Capparis spinosa*. These species are generally more representative of north-eastern Algerian forests (Djema & Messaoudene, 2009) and are primarily observed in the upper zones of the remaining riparian units, embedded within pre-forest and forest landscapes.

Species richness patterns

The parsimonious GLM indicated that, similar to species assemblage composition, species richness (expressed as the number of woody species) was influenced by the same environmental variables selected during the DistLM analysis. However, proximity to human settlements (measured as distance to built-up areas such as cities and villages) did not have a significant effect and was therefore not retained in the final model. These findings align with previous studies that emphasize the role of ecological drivers as key filtering factors shaping riparian taxonomic richness (Fu et al., 2022). More specifically, riparian woody species richness in the Aurès dry region was influenced primarily by water availability and topography (altitude and slope). Water availability is widely recognized as one of the most important determinants of plant species richness, particularly in regions with pronounced precipitation seasonality (Espinosa et al., 2011; López-Angulo et al., 2020; White & Hood, 2004) such as our study area. Similar patterns were also reported in semi-arid regions of the northern Mediterranean. For example, along the Tagliamento River, north-eastern Italy (Karrenberg et al., 2003) and in the Tagus River basin, Portugal (Aguiar & Ferreira, 2005), broad-scale geographical variables, such as altitude and water availability (i.e., flow regime), were identified as the primary drivers of riparian plant richness, followed by reach-scale variables such as riverbank structure. While common patterns in mountainous regions suggest that plant species richness either decreases with altitude or follows a hump-shaped curve, peaking at mid-elevations (Bertuzzo et al., 2016; Namgail et al., 2012; Rahbek, 2005; Vittoz et al., 2010; Wang et al., 2024), these trends were not evident in our data and species richness increased along the altitudinal gradient. There is limited information from the Algerian highland montane systems (Djema & Messaoudene, 2009), which in fact are ideal for studying biodiversity patterns along altitudinal gradients as these montane chains are a transitional zone and stand as a natural barrier to the north African Sahara. Although several mechanisms were proposed to explain altitudinal declines in species richness (Lee et al., 2021), the positive relationship observed in our study may be attributed to the fact that higher-altitude sites of the studied region fall within the habitat range of Algerian cedar, oak and Aleppo pine forests (50% of the cedar forest of Algeria in the Aurès region) (Bentouati & Bariteau, 2006; Lakhdari et al., 2024). In these areas, riparian zones shift from a typical semi-arid Mediterranean configuration, characterized by narrow, species-poor strips along watercourses, to more developed riparian forests that support relatively higher plant richness.

The combination of multivariate analysis (targeting species assemblage composition) and univariate analysis of a diversity metric (species richness) offered complementary aspects to understand riparian plant distribution. It showed that some environmental variables influence both species composition and richness, whereas others affect only composition. For instance, both damming and human proximity significantly shaped community composition; however, only damming had a marked effect on species richness. Human proximity influenced assemblage composition but did not significantly affect richness. While damming is widely recognized as one of the most severe anthropogenic disturbances affecting river ecosystems (Ceschin et al., 2015), strongly altering both riparian plant composition (as discussed above) and species richness, the finding that human proximity influences species composition but not richness deserves further consideration. Urbanization gradients may simultaneously promote the loss of sensitive species (through habitat degradation, pollution, or hydrological alteration) and impose the establishment of new species that are better adapted to the disturbed conditions created by human settlements (Schwoertzig et al., 2016). This turnover in community identity can alter species composition without necessarily reducing overall richness, as species lost from the system may be numerically replaced by newly arriving or tolerant taxa. Another plausible explanation is that the effects of human disturbance may not manifest as a reduction in the number of plant species, but rather through decreases in woody cover, the loss of understory vegetation, or a narrowing of the riparian corridor (Corbacho et al., 2003). Indicating that species richness alone is insufficient as a proxy for diversity, and should be complemented with multiple structural and ecological indicators to properly capture the effects of human disturbance.

CONCLUSIONS

Due to the absence of a recent national forest inventory and the lack of updated riparian categorization in Algeria as well as in all North African countries, our understanding of the current state of riparian habitats in the region remains limited. Our findings shed light on two critical aspects of riparian vegetation in unexplored and characteristic mountainous regions of North Africa. First, we have unveiled species assemblage associations and identified the environmental drivers that shape their spatial distribution. Second, we have identified trends in species richness, highlighting how woody biodiversity patterns shift across different environmental conditions. Our multivariate analysis identified three primary drivers influencing both the structure of riparian landscapes and woody species richness in this semi-arid area, and more importantly water availability followed by river damming and finally altitude. Additionally, the data confirm that human activities significantly affect the richness of the species and the composition of riparian woody communities. While river damming influences both species composition and richness, it also contributes to the homogenization of riparian landscape configurations, potentially reducing ecological diversity and resilience. The finding that human proximity influences species composition but not richness deserves further consideration. Indicating that species richness alone is insufficient as a proxy for diversity, and should be complemented with multiple structural and ecological indicators to properly capture the effects of human disturbance.

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S.T.: literature review, resources, review and editing, supervision.

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