Regional and local patterns of riparian flora: Comparison between insular and continental Mediterranean rivers[1]

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Abstract: We studied riparian species distribution patterns along 4 rivers in 2 different Mediterranean regions of Italy, an island (Sardinia) and a continental area (Tuscany). Our aim was to determine the following aspects at 2 spatial scales: *i*) floristic patterns (species richness, life forms, and phytogeographical elements) along Mediterranean rivers; *ii*) major gradients affecting riparian flora; *iii*) the effect of biogeography on riparian vegetation with respect to longitudinal and lateral gradients. A stratified random sampling design with segments identified as strata was used to sample plant species and environmental factors. Univariate statistics were applied to detect patterns of variation in the species data at regional and local scales. Indirect ordinations of the floristic data were performed to identify and compare the main floristic gradients. Variance partitioning was performed to quantify the relative contributions of variable subsets (biogeographic location, longitudinal and lateral gradients) to the explained variance and to test whether and to what extent the influence of biogeography could be distinguished from the effects of other environmental variables. We found high floristic heterogeneity along riverbeds, with greater species richness in insular rivers, since these were located in an area recognized as a biodiversity hot spot, in line with the hypothesis of lateral, regional control of local riparian species richness. At regional scale, variation in life forms and phytogeographical element composition showed strongest correlations with climatic variables. At local scale, only the continental rivers had many differences in phytogeographical elements; these differences were linked to their greater length with respect to insular rivers, which clearly leads to many changes in environmental features. With regard to the distribution of the riverbed flora, geography emerged as the main gradient at the regional scale. After removing the "river effect," the main gradient was the structural transition of vegetation from mountain to lowland areas, which followed a complex longitudinal/lateral gradient amid increasing human disturbance. This gradient was also important at local scale, even though the lateral gradient drove the greatest variation in vegetation composition in continental rivers. Despite the high unexplained variance, variance partitioning confirmed that the longitudinal gradient strongly affected riverbed flora patterns, followed by biogeographical location. Our results support the idea that the flora of Mediterranean riparian ecosystems is not strictly "azonal" but can be defined as "semi-azonal". Species distribution showed a strong association with climate, which was the primary correlate of change in floristic composition between riparian sites at both scales. Additional local variation in plant composition was explained by riverbed morphology and degree of human disturbance.

Keywords: biogeography, gradient analysis, life forms, phytogeographical elements, plant distribution, riparian vegetation.

Résumé: Nous avons étudié les patrons de distribution des espèces riveraines le long de 4 rivières dans 2 régions méditerranéennes différentes de l'Italie, une île (Sardaigne) et une zone continentale (Toscane). Notre but était de déterminer les aspects suivants à deux échelles spatiales : *i*) les patrons floristiques (la richesse en espèces, les formes de vie et les éléments phytogéographiques) le long de rivières méditerranéennes; *ii*) les principaux gradients influençant la flore riveraine; *iii*) le rôle de la biogéographie dans la composition végétale riveraine en fontion de gradients longitudinaux et latéraux. Un plan d'échantillonnage aléatoire stratifié avec les segments de rivière comme strates a été utilisé pour échantillonner les espèces végétales et les facteurs environnementaux. Des méthodes statistiques univariées ont permis de détecter des patrons de variation dans les données d'espèces aux échelles régionales et locales. Des méthodes d'ordination indirecte des données floristiques ont été utilisées pour détecter et comparer les principaux gradients floristiques. La partition de la variance a permis d'évaluer de façon quantitative les contributions relatives de sous-ensembles de variables (emplacement biogéographique, gradients longitudinal et latéral) à l'explication de la variance et évaluer si l'influence de la biogéographie peut être distinguée des effets des autres variables environnementales, et si oui et dans quelle mesure. Nous avons trouvé une hétérogénéité floristique élevée dans les lits de rivières, les rivières insulaires possédant une plus grande richesse en espèces puisque situées dans un secteur reconnu comme étant un point chaud de la biodiversité, en conformité avec l'hypothèse d'un contrôle latéral et régional de la richesse locale en espèces riveraines. À l'échelle régionale, la variation des formes de vie et la composition des éléments phytogéographiques montraient les plus fortes corrélations avec des variables climatiques. À l'échelle locale, seules les rivières continentales présentaient plusieurs différences dans les éléments phytogéographiques, ces différences étant liées à leur plus grande longueur comparée aux rivières insulaires, ceci modifiant plusieurs de leurs caractéristiques environnementales. En ce qui à trait aux distributions floristiques dans les lits de rivières, la géographie est apparue comme le principal gradient à l'échelle régionale. Après le retrait de l'effet de la rivière elle-même, le principal gradient était la transition structurelle de la végétation entre les zones montagneuses et celles de basse altitude selon un gradient longitudinal/latéral complexe combiné à une augmentation de la perturbation humaine. Ce gradient était aussi important à l'échelle locale, même si le gradient latéral y était responsable de la majeure partie de la variation dans la composition végétale des rivières continentales. En dépit du fait qu'une grande partie de la variance n'était pas expliquée, la partition de la variance a confirmé que le gradient longitudinal a une forte corrélation des patrons floristiques des lits de rivières, l'emplacement biogéographique venant en second. Nos résultats supportent l'idée que la flore méditerranéenne des écosystèmes riverains n'est pas strictement « azonale », mais peut aussi être définie comme « semi-azonale ». La distribution des espèces était fortement liée au climat qui était la principale variable corrélée aux changements de composition floristique entre les sites riverains aux deux échelles spatiales. La morphologie du lit de la rivière et le degré de perturbation humaine expliquaient une portion supplémentaire de la variation locale de la composition végétale.

Mots-clés : analyse de gradients, biogéographie, distribution végétale, éléments phytogéographiques, formes de vie, végétation riveraine.

Nomenclature: Conti *et al.* (2005) for species and subspecies level.

Introduction

The very complex environmental patterns of vegetation in riparian zones are a result of many gradients, regarded as composite, since they represent changes in a number of major environmental variables (Gregory *et al.*, 1991; Malanson, 1993; Ward *et al.*, 2002). Longitudinal gradients are seen as the main drivers of vegetation in riparian landscapes (Tabacchi *et al.*, 1996; Ferreira & Moreira, 1999; Hughes *et al.*, 2009). Altitude is known to be the main physical factor affecting riparian vegetation along river corridors and directly influencing the erosive power of river flow in the upper and lower reaches; as are changes in habitat composition, adjacent land-use, and the resulting zonal vegetation. Several studies have demonstrated that lateral gradients can also be of great importance in structuring riparian vegetation (Aguiar, Ferreira & Moreira, 2001; Lite, Bagstad & Stromberg, 2005; Sieben, Mucina & Boucher, 2009; Yang *et al.*, 2011). Height above and lateral distance from the channel across a floodplain represent zones of different inundation frequency and flood disturbance, typically diminishing with increasing distance from (and above) the active channel. In addition, previous studies have highlighted the role of multiscale perspectives in fluvial ecology as important conceptual frameworks for recognizing how complex processes interact to produce observed ecological structure (Poole, 2002; Ward *et al.*, 2002). The use of a multiscale approach becomes even more relevant in riparian vegetation studies (Bendix & Hupp, 2000; Hughes *et al.*, 2001; Dixon, Turner & Jin, 2002; Baker & Wiley, 2009), although conclusions may be highly dependent on the assumptions, variables, and analyses used, as well as on the spatial scales considered (Bendix, 1994; van Coller, Rogers & Heritage, 2000). Most plant ecologists agree that the main determinants of riparian vegetation composition include hydrological and geomorphical processes as well as disturbance at local scale (Gregory *et al.*, 1991; Naiman, Bilby & Bisson, 2000; van Coller, Rogers & Heritage, 2000), whereas climate, bedrock geology, and site position in the watershed (*i.e.*, stream order) are determinants at landscape (*i.e.*, regional) scale (Collins, Risser & Rice, 1981; Alcaraz *et al.*, 1997; Pabst & Spies, 1998; 1999; Aguiar & Ferreira, 2005; Sarr & Hibbs, 2007). In spite of their great importance in shaping riparian vegetation patterns, factors associated with regional patterns, such as climate, often remain unmeasured (Blasi *et al.*, 2011). This is because riparian vegetation is generally considered azonal and seems to be less sensitive to climate change than zonal communities, since its major limiting factors are non-climatic in character (Kienast, Wildi & Brzeziecki, 1998; Kuzemko, 2011). However, climate influences riparian communities directly (Gentili *et al.*, 2010) through physiological effects on organisms and by limiting populations and indirectly by modifying or regulating the importance of local-scale factors and by favouring certain life forms and phytogeographical elements (Pettit, Froend & Davies, 2001; Ferreira & Aguiar, 2006; Mejías, Arroyo & Marañón, 2007). In fact, although it has a similar structure and composition in all European rivers, riparian flora shows some major distinctive features within the Mediterranean bioclimatic and biogeographic region (Polunin & Walters, 1987; Alcaraz *et al.*, 1997; Aguiar & Ferreira, 2005; Ferreira & Aguiar, 2006). Biogeographic research in western Europe (Rivas-Martinez, 2007) has also underlined differences in riparian vegetation composition between Mediterranean and Eurosiberian/Continental regions. However, in the Mediterranean basin, there is a dearth of studies assessing the relative importance of environmental factors and biogeography and their interactions at different spatial scales.

This paper explores differences in riparian plant assemblages in 2 Mediterranean regions (Sardinia and Tuscany, Italy) and the main riparian gradient contributions to plant species variation at 2 spatial scales, namely regional (rivers in different regions) and local (rivers in the same region). These regions are characterized by paleogeographical and geographical differences (*e.g.*, one is insular, the other continental) but comparable climatic and biogeographic features. Our specific objectives were 1) to determine floristic patterns (species richness, life forms, and phytogeographical elements) along Mediterranean rivers; 2) to identify the main gradients affecting riparian flora at regional scale, and to understand whether they are the same at local scale; and 3) to quantify the relative contributions of biogeography, with respect to longitudinal and lateral gradients, to flora composition.

Methods

STUDY AREA

We selected 4 rivers in 2 Mediterranean regions. One of these regions is an island (Sardinia), while the other is a continental region (Tuscany). The rivers investigated were the Santa Lucia and the Leni in Sardinia and the Albegna and the Fiora in Tuscany (Figure 1). They are major river courses in their regions and have hydrological features similar to many other Mediterranean rivers, namely lower and wider sections that dry up almost completely in summer and may flood in autumn and spring (Angiolini & Bacchetta, 2003; Landi & Angiolini, 2007; Angius & Bacchetta, 2009). The macrobioclimate of the area is Mediterranean, but along the Tuscan rivers, regional bioclimate ranges from Mediterranean pluviseasonal-oceanic to temperate oceanic-semicontinental. The floodplains of all of the rivers studied are composed mainly of volcanic rocks and sandstone in the mountain parts and alluvial sands and clays in the lower parts; the parent rocks of the sediments of each river are specified in more detail in Appendix I, following Carmignani *et al.* (2001; 2004) and Bacchetta, Pili, and Serra (2003). The 2 Sardinian rivers mostly have single-thread channel morphology with alternate bars, in some cases locally braided, while the Tuscan rivers are characterized by large riverbeds with braided and not particularly deep channels. The agro-pastoral system is the prevalent land-use in the upper and sparsely populated areas of all rivers in the study. As a result, the only sections of the mountainous upper parts of the rivers with their riparian vegetation structure still mainly determined by natural dynamics are those located in protected areas (SCI, Sites of Community Interest). Valley bottoms are characterized by highly transformed agricultural landscapes dominated
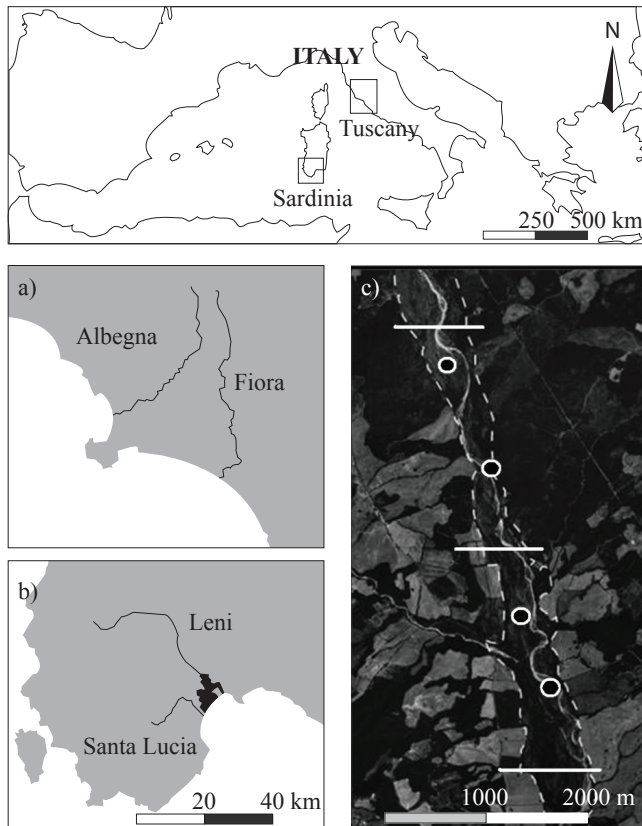
FIGURE 1. Location of study areas in the Mediterranean basin. Location of rivers in a) Tuscany and b) Sardinia. c) The aerial photo provides an example that indicates how the 2-km segments (horizontal white lines) and plots (white circles) were situated in floodplains (dotted line).

by intensive cereal crops, industrial sites, and human settlements, particularly in the lower alluvial parts of the Leni and Albegna rivers. The main features of the rivers studied are summarized in Appendix I.

SAMPLING DESIGN AND FLORISTIC DATA

As a goal of this study was to analyze riparian plant species, the sampling design considered only floodplains. To identify floodplains, the widths of which ranged from 5 to 450 m, we analyzed geological and land cover layers with GIS software (ArcMap 9.3, ESRI, Redlands, California, USA), first selecting areas with alluvial lithology, then removing cultivated land near the river. The resulting floodplain areas were divided into river segments (*sensu* Poole, 2002) that were drawn at 2-km intervals along the river, from source to mouth, excluding any areas occupied by dams or lagoons. Using a stratified random sampling design with segments identified as strata, the plots were allocated along all river corridors to include variations in species assemblages and environmental features (see, for example, Figure 1c). Two plots of 10 × 10 m were co-located randomly in all segments except 1, for a total of 189 plots (see Appendix I). The dimensions of the plots proved adequate to detect the vegetational mosaic of the floodplains, because they matched relevant variation in the structure of the data. Plots of this size (100-m^2) have also been used to explain relationships between species richness and environmental features in forests (Schuster &

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Diekmann, 2005) and grasslands (Gross *et al.*, 2000). From April to July 2007–2009 we recorded the presence/absence of all vascular plant species in each plot, as suggested by Tamàs, Podani, and Csontos (2001). On the assumption that the interannual variability in climate essentially remained small during this 3-y period, we then pooled the floristic data. The presence/absence approach has proven to be particularly suitable for floristic studies that focus on species lists for landscape units or sample plots.

SPECIES ATTRIBUTES

Each of the species was allocated to 1 of 7 Raunkiaer life forms based on the position of the plant's growth point (perennating bud) in relation to the soil and water surface (Raunkiaer, 1934; Govaerts, Frodin & Radcliffe-Smith, 2000): phanerophytes (trees with buds more than 3 m above ground); nanophanerophytes (tall shrubs with buds 0.5 to 3 m above ground); chamaephytes (dwarf shrubs with buds less than 50 cm above ground); hemicryptophytes (perennial herbs with buds at ground surface); geophytes (perennial herbs with a bulb or other perennating organ below ground surface); hydrophytes (fully aquatic herbs with submerged buds or buds buried in soil beneath the water); and therophytes (annual herbs that complete their entire life-cycle during the favourable season and weather the unfavourable season as a seed). Species were also classified into floristic groups based on similarities in their worldwide geographical distributions (Stott, 1981). The geographical distribution of each species was assessed from reviews, monographs, and distributional data on flora, particularly *Flora d'Italia* (Pignatti, 1982) and, for endemics, Bacchetta and Pontecorvo (2005). For this study, preliminary phytogeographic data were combined and classified into 8 floristic assemblages termed "phytogeographical elements" (groups of plant taxa that share similar centres and limits of total geographical distribution; Qian, 1999): circum-Mediterranean (taxa with geographical distribution largely restricted to Mediterranean coasts); Euro-Mediterranean (species with centre of distribution along Mediterranean coasts and extending into northern and eastern regions); Eurasiatic (species distributed only in Europe and Asia); boreal (species widely distributed in all temperate—including boreal and arctic—regions of Europe, Asia, and North America); Atlantic (species mainly restricted to Atlantic coasts of Europe); wide-distribution (species widely distributed across all or nearly all continents without special distribution centres); endemic (endemic or subendemic species); and alien (plants introduced intentionally or otherwise by humans). The terminology and delimitation of the phytogeographical elements are from standard reference works, particularly Takhtajan (1986).

PLOT ATTRIBUTES MEASURED

The environmental variables used in this study were altitude (m asl), mean annual temperature (°C), mean annual rainfall (mm), distance from running water (m), and height above running water (m). The altitude of each plot was obtained by Digital Elevation Model (DEM 75 × 75 m). Climatic data from the meteorological stations closest to the sampling sites were obtained through regional databases (the Tuscan Regional Agrometereological Service and the

Hydrometeorological Department of the Sardinian Regional Environmental Protection Agency). Horizontal distances from and height above (vertical distance) running water were measured in the field during spring/early summer plant sampling, at times of low river conditions.

BIOGEOGRAPHIC CHARACTERIZATION

All study areas belong to the Mediterranean region. The biogeographic classification of the Mediterranean region proposed by Rivas-Martínez *et al.* (2002) recognizes an Italo-Tyrrhenian province composed of 3 subprovinces: Sardinian, Corsican, and Tuscan-Calabrian. However, many similarities, not only floristic, suggest considering Sardinia (site of the insular rivers) and Corsica a single province, which, together with the Tyrrhenian province (site of the continental rivers), belong to an Italo-Tyrrhenian super-province (see Appendix I), as formerly proposed by Ladero Alvarez *et al.* (1987).

STATISTICAL ANALYSIS

At regional and local scale we applied *i*) Sørensen's index (Sørensen, 1948) to evaluate similarities in floristic composition and *ii*) *t*-tests to assess the significance of life form and phytogeographical elements percentages. Pearson's correlation coefficient (matrix not shown) was used to explore correlations between and within percentages of life forms and phytogeographical elements of rivers in a given region. A cumulative species–area curve for insular and continental rivers was calculated for the plot by adding each quadrat randomly to compare species richness between regions sampled with different numbers of plots.

Floristic data were then analyzed by a series of unconstrained ordination analyses (Detrended Correspondence Analysis, DCA) to find the axes with maximum variation in floristic composition of the study sites and thus describe the general pattern of species distribution along the gradients (Lepš & Šmilauer, 2003). Rare species were downweighted and the scaling was set to focus on inter-species distances and Hill's scaling (ter Braak & Šmilauer, 2002). The data from all sites were first ordered to calculate the length of the main gradient (SD) and describe the general patterns in species distribution along the gradients (Lepš & Šmilauer, 2003). Partial DCA (pDCA), a version of DCA in which ordination is performed after statistically partialling out variation in the original data set associated with 1 or more sets of covariables (ter Braak & Šmilauer, 2002) was then carried out. In our case the rivers were designated as covariables to determine whether measured variables were consistently related to floristic composition across all rivers, irrespective of any other difference between rivers. Thirdly, to determine whether floristic gradients between continental and insular rivers were similar, separate DCAs including only Tuscan or Sardinian data were undertaken. The Pearson's correlation test was performed to examine relationships between sample scores of regional and local ordinations and environmental variables on DCA axes 1 and 2, respectively.

To quantify the relative contributions of 3 groups of variables (biogeography [at province level], longitudinal gradients [temperature, rainfall, and altitude], and lateral gradients [distance from and height above the channel]) to explained variance and to test whether and to what extent their contributions to the composition of riverbed plant assemblages can be separated, we performed variance partitioning using canonical ordination techniques (Borcard, Legendre & Drapeau, 1992; Økland & Eilertsen, 1994). Because a unimodal method was appropriate (length of the first DCA axis > 4 SD; see Lepš & Šmilauer, 2003), 3 partial Constrained Correspondence Analyses (CCAs) were run to quantify the unique contribution of each of the 3 groups of variables. Each partial CCA used 1 of the 3 groups of variables as constraining variable and the other 2 groups as covariables. Other partial CCAs were performed to quantify the fractions of variance explained by the joint effects of 2 groups of variables, according to the procedure described by Anderson and Gribble (1998).

For all DCAs and CCAs, the statistical significance of the first and second and all canonical axes, respectively, was tested using Monte Carlo tests with 499 unrestricted permutations. To ensure normality, species and plot attribute data were log-transformed prior to statistical analysis. STATISTICA 6.0 (StatSoft Inc., 1995) was used for univariate analysis, and Canoco 4.5 (ter Braak & Šmilauer, 2002) was used for ordination analysis.

Results

FLORISTIC PATTERNS AT DIFFERENT SCALES

The flora encountered was composed of 493 taxa for the continental and 428 for the insular rivers, making a study area grand total of 745 taxa. Among these, 252 (33.8% of the total flora) were exclusive to Sardinia, 317 (42.6%) were exclusive to Tuscany, and 176 (23.6%) were common to both regions. Species richness ranged from 9 to 68 species per plot, with a mean of 28 species, for continental rivers and from 8 to 54 species, with a mean of 31 species, for insular rivers. The plots of species–area relationships for continental and insular rivers were quite similar for the 2 regions (Figure 2).
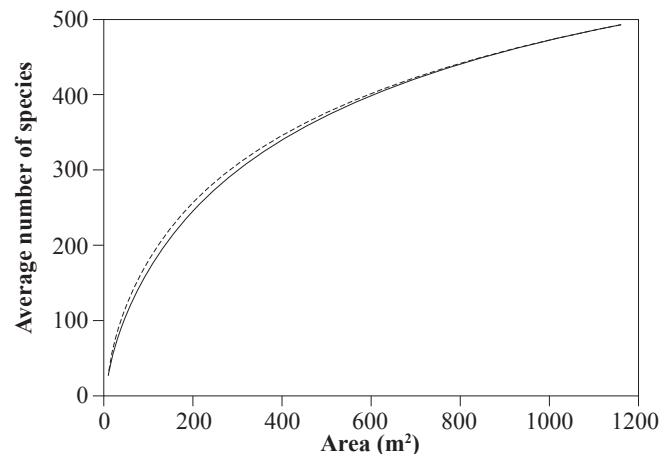
FIGURE 2. Species–area curves showing the average number of species observed (y axis) in each sampling area (x axis). Dashed line = Sardinian species, Black line = Tuscan species.

The most frequent species in all rivers were synanthropic and typical of less developed substrates; these species included *Avena fatua* (percentage of occurrence: 89%), *Rubus* gr. *ulmifolius* (88.8%), and several other herbaceous species (*Anagallis arvensis*, *Foeniculum vulgare*, *Dittrichia viscosa*, and *Lolium rigidum*). The similarity in species between the 2 regions was low (Sorensen index 0.37), suggesting high floristic heterogeneity. The Sorensen index was higher within the regions (continental rivers 0.62; insular rivers 0.78).

A *t*-test revealed that life forms and phytogeographical element percentages were significantly different at the regional level, except for chamaephytes, hemicryptophytes, and wide-distribution species (Table I). The 2 main life forms in both regions were hemicryptophytes and therophytes, with higher percentages of the first for continental

and of the latter for insular rivers. A significantly higher number of woody species was found in continental rivers as against geophytes in insular rivers. Among phytogeographical elements, wide-distribution plants were the most frequent in all rivers. Insular riverbeds differed widely in percentages of circum-Mediterranean, Atlantic, endemic, and alien species, while continental rivers differed in percentages of Euro-Mediterranean, Eurasiatic, and boreal species.

Regarding local differences, a *t*-test (Table II) revealed a relatively homogeneous life-form distribution, except for significant differences in the percentages of phanerophytes and nanophanerophytes between rivers within a region and in hemicryptophytes for insular rivers. Considering phytogeographical elements, marked differences were found between continental rivers for Eurasiatic and circum-Mediterranean species, while the insular rivers were found to be quite similar. We observed that annual herbs were positively correlated with Mediterranean species in both regions (circum-Mediterranean in Sardinia, euro-Mediterranean in Tuscany), as were chamaephytes with endemic species (Pearson's correlations: $r > 0.40$, $P < 0.01$). Correlations among life forms also showed similar trends, with herbaceous plants (hemicryptophytes and therophytes) negatively correlated with woody species (phanerophytes and nanophanerophytes). In insular rivers, wide-distribution species showed a positive correlation with aliens and a negative correlation with endemic, euro-Mediterranean, and circum-Mediterranean plants.

FLORISTIC AND ECOLOGICAL GRADIENTS

Only relevant and significant Pearson's correlations ($r > 0.40$, $P < 0.01$) between species and plot attributes and axes were considered. In all ordinations the length of the main gradient highlighted high floristic heterogeneity (Table IIIa) and the first 2 axes were significant at $P = 0.002$. On the basis of dissimilarities in species composition, the plots along continental and insular rivers were well separated within the space of the DCA on the first

TABLE I. Mean percentage (± SD) of life forms and phytogeographical elements in continental and insular riverbeds. *P*-values stand for significant differences (*t*-test) at regional scale (df = 187; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; ns = not significant).

	Rivers		
Attributes	Insular	Continental	P
Life forms			
Phanerophytes	11.3 ± 11.1	22.3 ± 16.2	***
Therophytes	36.4 ±15.5	26.9 ± 15.8	***
Chamaephytes	3.0 ± 3.8	3.8 ± 5.2	ns
Geophytes	14.8 ± 8.5	8.1 ± 6.2	***
Hemicryptophytes	30.2 ± 11.5	33.1 ± 12.7	ns
Hydrophytes	0.2 ± 0.9	0.0 ± 0.3	*
Nanophanerophytes	4.1 ± 4.8	5.7 ± 4.5	***
Phytogeographical elements			
Alien	3.7 ± 3.7	1.6 ± 2.5	***
Atlantic	4.4 ± 3.8	2.3 ± 2.6	***
Boreal	2.2 ± 3.6	6.5 ± 5.3	***
Circum-Mediterranean	29.6 ± 11.6	11.8 ± 6.9	***
Wide-distribution	30.0 ± 11.0	27.8 ± 9.6	ns
Endemic	3.9 ± 4.4	1.2 ± 2.0	***
Eurasiatic	6.5 ± 4.6	23.9 ± 10.2	***
Euro-Mediterranean	19.7 ± 7.6	24.9 ± 9.7	**

TABLE II. Mean percentage (± SD) of biological and chorological forms in the 4 rivers. *P*-values stand for significant differences (*t*-test) at local scale (df = 71 for insular rivers, 114 for continental rivers; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; ns = not significant). - = No species was found.

	Insular rivers			Continental rivers		
Attributes	Santa Lucia	Leni	P	Fiora	Albegna	P
Life forms						
Chamaephytes	3.9 ± 4.7	2.4 ± 3.2	ns	3.1 ± 4.4	5.0 ± 5.9	ns
Geophytes	12.3 ± 5.7	16.1 ± 9.5	ns	7.3 ± 5.4	9.3 ± 7.1	ns
Hemicryptophytes	24.5 ± 10.3	33.2 ± 11.1	**	32.3 ± 10.7	34.4 ± 15.2	ns
Hydrophytes	0.3 ±0.9	0.2 ± 0.8	ns	0.0 ± 0.4	-	ns
Nanophanerophytes	6.4 ± 4.9	3.0 ± 4.4	**	6.5 ± 4.6	4.5 ± 4.1	**
Phanerophytes	17.6 ± 12.2	8.0 ± 9.1	**	24.5 ± 15.1	19.2 ± 17.4	**
Therophytes	35.0 ± 15.6	37.2 ± 15.9	ns	26.4 ± 16.3	27.8 ± 15.1	ns
Phytogeographical elements						
Alien	2.8 ± 3.7	4.1 ± 3.7	ns	1.9 ± 2.7	1.2 ± 2.3	ns
Atlantic	4.1 ± 2.7	4.6 ± 4.2	ns	2.6 ± 2.5	1.8 ± 2.8	*
Boreal	1.9 ± 2.4	2.3 ± 4.1	ns	7.5 ± 5.4	5.1 ± 4.7	*
Circum-Mediterranean	33.4 ± 13.5	27.7 ± 10.1	ns	9.6 ± 6.2	14.9 ± 6.9	***
Endemic	4.3 ± 4.1	3.7 ± 4.5	ns	1.1 ± 1.8	1.3 ± 2.3	ns
Eurasiatic	6.1 ± 2.9	6.8 ± 5.3	ns	26.2 ± 8.8	20.8 ± 11.3	***
Euro-Mediterranean	21.4 ± 6.7	18.8 ± 7.9	ns	23.3 ± 10.1	27.3 ± 8.7	*
Wide-distribution	26.0 ± 9.2	32.1 ± 11.5	*	27.9 ± 9.9	27.6 ± 9.3	ns

ordination axis (Figure 3a). This represented a climatic and geographic gradient, as it emerged from strong correlations with climatic variables (negative correlation with rainfall and positive correlation with temperature) and phytogeographical elements (negative correlation with Eurasiatic and boreal, positive correlation with circum-Mediterranean) (Table IIIc). The second axis separated insular rivers (the Leni and Santa Lucia; Figure 3a) and represented a longitudinal gradient (negative correlation with altitude) and an overall gradient of human disturbance, as suggested by the phytogeographical elements (positive correlation with alien and wide-distribution species) (Table IIIc). Based on partial DCA analyses (Figure 3b), continental rivers were distributed along the first axis, while insular rivers were dispersed along the second axis. In contrast with the previous ordination, the main axis of the partial DCA showed a highly negative correlation with woody species and a highly positive correlation with herbaceous species (hemicryptophytes and therophytes), while the second axis had the highest positive correlations with wide-distribution and alien species and negative correlations with altitude and rainfall. Separate ordinations were performed with continental (Figure 3c) and insular (Figure 3d) plots to detect the main local gradients within rivers of a given region and their correlations with environmental variables (Table IIId). The longest gradient of the DCA performed on insular rivers was shorter than that of continental rivers. For insular rivers the main axis showed a strong negative correlation with altitude and rainfall, while for continental rivers the first axis showed a strong negative correlation with rainfall and the second showed strong correlations with 2 variables, altitude (strong negative correlation) and temperature (strong positive correlation). When species attributes were considered, the first axis was correlated negatively with woody species and positively with hemicryptophytes in both regions and positively with wide-distribution species for insular rivers and with Euro-Mediterranean species for continental rivers. Atlantic species were negatively correlated with the first axis for continental rivers.

VARIANCE PARTITIONING

The total variance in species composition explained by the 3 predictors (lateral gradient, longitudinal gradient, and biogeography) was low (12%) (Figure 4). The longitudinal gradient was the main variable to influence the floras of the 4 rivers, with the highest unique value in the data (4.82%, accounting for more than 40% of the total variance). Biogeography (at the province level, see Appendix I) had a unique value corresponding to 2.44%, while the lateral gradient, had a unique value of 2.17% (explaining about 20% and 18% of the total variance, respectively). Figure 4 also shows that a high percentage of variation, corresponding to 2.13% (*i.e.*, more than 17% of the total variance explained), was shared by the factors longitudinal gradient and biogeographic location, while the amount of variance shared by the lateral gradient and these 2 factors was marginal (0.07% and 0.06%). The amount of variance shared among all 3 variables was very low (0.31%).

TABLE III. Summary of axes 1 and 2 (a) of an ordination with all plots (DCA), of a partial ordination (pDCA) with all plots, of a DCA with only insular plots (DCA Sardinia) and of a DCA with only continental plots (DCA Tuscany). Pearson's correlations (*r*) are shown among life forms (b), phytogeographical elements (c), environmental variables (d), and ordination axes. Significant differences (*P* < 0.01) are indicated by numbers in bold. Variance is the cumulative percentage of variance and gradient (SD) is the length of gradients expressed as standard deviation.

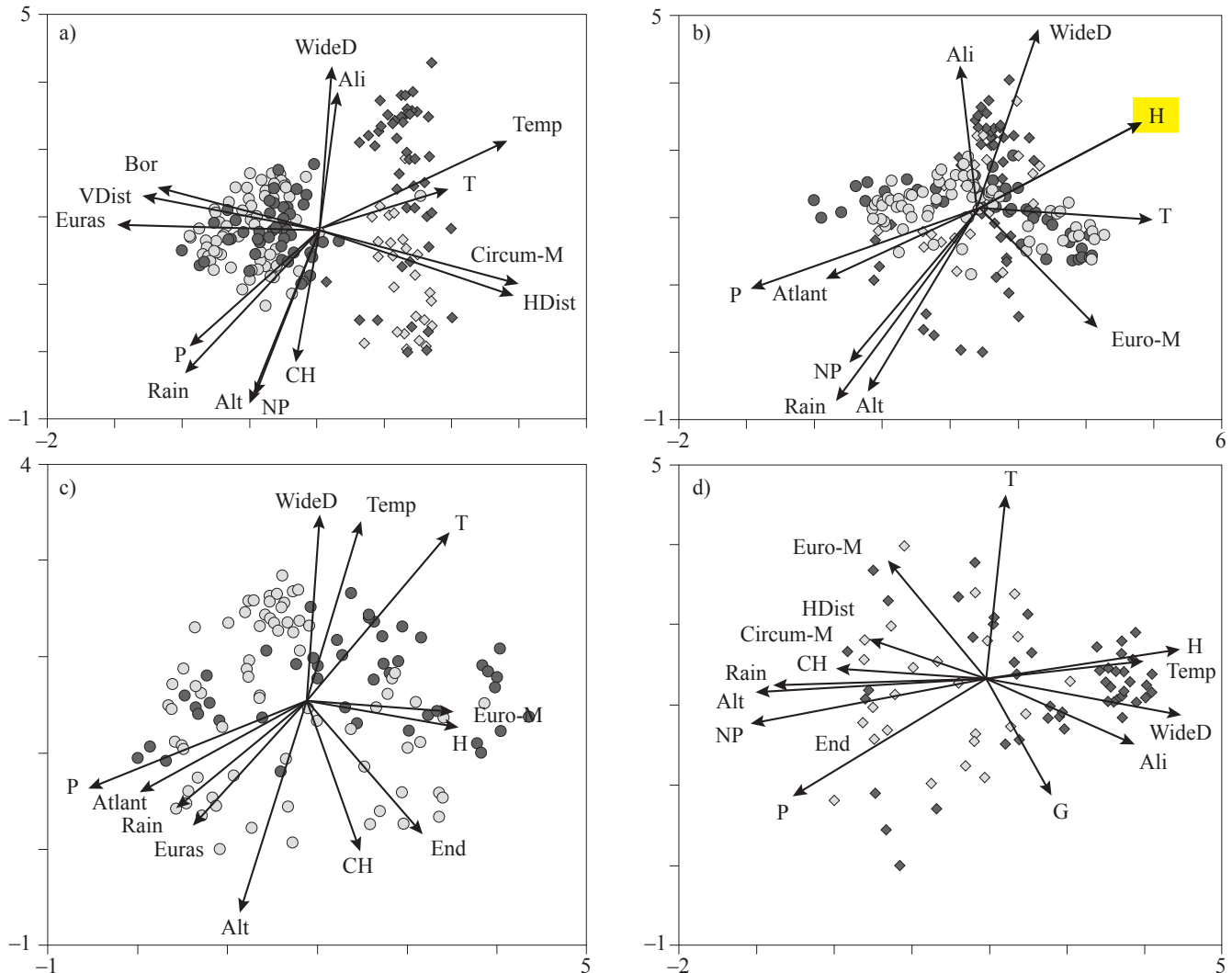|	DCA		pDCA		DCA Sardinia		DCA Tuscany	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
a) Summary of ordination								
Eigenvalues	0.584	0.415	0.435	0.336	0.608	0.319	0.525	0.292
Gradient (SD)	4.008	4.282	4.259	4.042	4.099	3.981	4.354	2.849
Variance (%)	5.300	9.100	4.300	7.600	8.600	13.100	6.500	10.100
b) Life forms								
Chamaephytes	−0.050	**−0.450**	0.03	−0.390	**−0.490**	0.03	0.14	**−0.450**
Geophytes	0.28	0.25	−0.290	**0.38**	**0.40**	**−0.460**	−0.270	−0.070
Hemicryptophytes	0.01	0.22	**0.54**	0.05	**0.640**	0.21	**0.58**	−0.110
Hydrophytes	0.09	0.14	0.02	0.14	0.08	0.11	−0.120	−0.120
Nanophanerophytes	−0.290	**−0.550**	**−0.430**	−0.430	**−0.820**	−0.240	−0.360	−0.350
Phanerophytes	**−0.550**	−0.360	**−0.750**	−0.160	**−0.730**	**−0.510**	**−0.830**	−0.290
Therophytes	**0.53**	0.28	0.50	0.04	0.10	**0.620**	**0.490**	**0.620**
c) Phytogeographical elements								
Alien	0.15	**0.41**	−0.090	**0.46**	**0.42**	−0.270	−0.190	0.18
Atlantic	0.14	−0.150	**−0.420**	−0.110	−0.340	−0.020	**−0.610**	−0.300
Boreal	**−0.490**	0.18	−0.070	00.24	0.25	−0.120	−0.210	0.01
Circum-Mediterranean	**0.740**	−0.090	0.06	−0.110	**−0.490**	0.04	0.30	0.08
Wide-distribution	0.13	**0.620**	0.15	**0.58**	**0.650**	−0.040	0.05	**0.620**
Endemic	0.36	−0.320	0.08	−0.260	**−0.450**	−0.310	0.36	**−0.420**
Eurasiatic	**−0.790**	−0.080	−0.160	−0.110	00.19	0.03	**−0.470**	**−0.480**
Euro-Mediterranean	−0.020	−0.310	**0.41**	**−0.470**	−0.290	**0.42**	**0.53**	−0.100
d) Environmental variables								
Temperature (°C)	**0.750**	0.39	0.13	0.36	**0.51**	0.07	0.17	**0.670**
Rain (mm/y^{-1})	**−0.500**	**−0.410**	**−0.400**	**−0.430**	**−0.770**	−0.080	**−0.450**	**−0.380**
Altitude (m asl)	−0.300	**−0.610**	−0.370	**−0.530**	**−0.820**	−0.160	−0.280	**−0.710**
Horizontal distance (m)	**0.740**	−0.120	0.06	−0.110	**−0.490**	0.04	0.30	0.08
Vertical distance (m)	**−0.510**	0.17	−0.070	0.24	0.25	−0.120	−0.210	0.01

FIGURE 3. Biplots of sample scores with environmental and species attributes superimposed for DCA ordinations of a) all plots across all rivers; b) all plots across all rivers, with "rivers" as covariables (partial DCA); c) plots of continental rivers; d) plots of insular rivers. Only variables showing significant correlation with axes (*P* < 0.01) are represented. See Table III for correlations between variables and axes. Plots of different fluvial types are represented as circles for continental rivers (Fiora in light grey and Albegna in dark grey), and diamonds for insular rivers (Santa Lucia in light grey and Leni in dark grey). Legend of species and plot attribute abbreviations (letters in bold): CH = chamaephytes; G = geophytes; H = hemicryptophytes; NP = nanophanerophytes; P = phanerophytes; T = therophytes; Ali = alien; Atlant = Atlantic; Bor = boreal; Circum-M = circum-Mediterranean, End = endemic; Euras = Eurasiatic; Euro-M = Euro-Mediterranean; WideD = wide-distribution; Alt = altitude; Rain = rainfall; HDist = horizontal distance from running water; VDist = vertical distance above running water; Temp = temperature.

Discussion

FLORISTIC PATTERNS

SPECIES RICHNESS

Our results underline the importance of riparian landscapes for biodiversity conservation, particularly in Mediterranean areas (Corbacho, Sánchez & Costillo, 2003), in line with many other studies (Naiman & Décamps, 1997; Pollock, Naiman & Hanley, 1998; Naiman, Décamps & McClain, 2005). We found high species richness per plot compared to floristic inventories of 100-m² plots performed in other Tuscan habitats (mountain woods, open clay grasslands; see Chiarucci *et al.*, 2008) and compared to species richness recorded in mountain areas of Sardinia (Bacchetta, 2006). In insular rivers we found a greater mean number

of species, in line with the hypothesis of lateral, regional control of local riparian species richness (Mouw & Alaback, 2003; Renöfält, Nilsson & Jansson, 2005). The insular rivers are situated in an area recognized as a biodiversity hot spot, with more than 61% of insular species growing in an area less than one tenth that of the region. This is presumably due to high local geological diversity and the wide range of habitats present (Bacchetta, 2006) and suggests that plant species richness in the area determines plant species richness on the riverbanks.

LIFE FORMS

Hemicryptophytes were well represented along all rivers, suggesting tolerance to flooding and continuous modifications due to fluvial dynamics (Lite, Bagstad & Stromberg, 2005). In contrast, many woody species cannot survive on

Lateral gradient
2.64

Longitudinal gradient
7.35

a
2.17

d
0.06

b
4.82

g
0.31
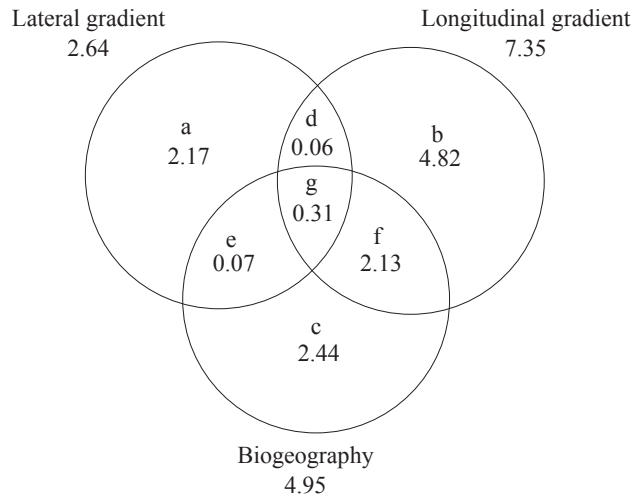
e
0.07

f
2.13

c
2.44

Biogeography
4.95

FIGURE 4. Variation partitioning of species composition data represented as a Venn diagram, indicating 3 groups of variables (biogeography, and longitudinal and lateral gradients) with their percentages of explained variance. Various sets of partially Constrained Correspondence Analyses (CCAs) were compared. All CCA analyses had *P*-values < 0.01 in a Monte Carlo test. The diagram shows the partitioning of explained variance into 7 components: a) partial effects of the lateral gradient, b) partial effects of the longitudinal gradient, c) partial effects of biogeography, d) partial joint effects of the lateral and longitudinal gradients, e) partial joint effects of the lateral gradient and biogeography, f) partial joint effects of the longitudinal gradient and biogeography, and g) partial joint effects of the lateral gradient, longitudinal gradient, and biogeography. Numbers outside the circles stand for the total variance explained by each variable (including all joint effects).

frequently inundated portions of the corridor or on unstable sediment created by recurrent flooding (Ward *et al.*, 2002). The negative correlation between herbaceous species and woody plants reflected these differences. The greater occurrence of therophytes and geophytes along insular rivers may be related to climatic harshness and intermittent flows (Ferreira & Moreira, 1999; Ferreira *et al.*, 2004). These 2 forms are also favoured by the traditional field management systems of Sardinia, where dead grass is burned off (Fenu & Bacchetta, 2008), a practice demonstrated to promote herbaceous bulbous species and annuals and to limit woody species (Ishida *et al.*, 2008). The other regional distribution pattern of clear significance concerned phanerophytes, which were found with higher percentages in continental riverbeds. The higher percentages of these species reflected low human disturbance in this region (Aguiar & Ferreira, 2005), and the presence of wider riverbeds with more stable conditions (Angius & Bacchetta, 2009).

PHYTOGEOGRAPHICAL ELEMENTS

The riparian flora of all rivers was dominated by wide-distribution species, generally linked to semiarid riverbeds (Aguiar & Ferreira, 2005) and, in the Mediterranean region, to human disturbance (Pignatti, Pignatti & Ladd, 2002; Bacchetta, 2006). Euro-Mediterranean and Eurasiatic elements were also well represented along continental rivers, as were Mediterranean species along insular rivers. This different distribution pattern at regional scale matched changing climatic conditions across the study area;

conditions are becoming increasingly xeric in insular sites (Blasi, 1996), producing species dominance patterns altered by elimination of species typical of more mesic areas (Alcaraz *et al.*, 1997; Collins, Risser & Rice, 1981). Endemic species are usually scarce or absent in riparian areas, as reported for many rivers in the Mediterranean basin (see Aguiar *et al.*, 2007; Giménez *et al.*, 2004); however, endemics represented a high percentage (more than 4% on average) of the species found along the insular rivers in our study (see also Angius & Bacchetta, 2009; Bacchetta & Pontecorvo, 2005), due to the long isolation of the island during the Tertiary Period, which has contributed to the differentiation of neo-endemics specific to each area (Médail & Quézel, 1997). Their positive correlation with chamaephytes indicates that endemic species in the Mediterranean basin are mainly stress-tolerant species, well adapted to harsh habitats like river alluvial terraces and incoherent soils. As well, more alien plants were found along insular rivers, presumably related to the high susceptibility of Mediterranean insular ecosystems to biological invasions (DAISIE, 2009). The negative correlation of aliens with endemic and Mediterranean species, and the positive correlation with wide-distribution species, shows that aliens were largely restricted to anthropogenic habitats, where levels of native plants are often low, as noted by Affre *et al.* (2009) for Mediterranean islands.

REGIONAL AND LOCAL DIFFERENCES

At regional scale, our results indicated high floristic heterogeneity between the continental and insular rivers, as shown by the low Sorensen index, the few shared species, the different most frequent species, and the different distribution trends among almost all life forms and phytogeographical elements. This was probably due in part to variations in environmental features, which have different importance in different regions (Neilson *et al.*, 1992), but also in part to historical and biogeographical factors, such as *i*) different geological origins and paleogeographic histories affecting the pools of available species in each area (Whittaker, Willis & Field, 2001), the latter being determined by evolutionary and historical processes and being of proven importance for understanding community composition (Nilsson *et al.*, 1989; 1994; Danvind & Nilsson, 1997; Partel & Zobel, 1998); and *ii*) the insularity of Sardinia. However, the riparian flora revealed some similarities between the 2 regions as regards the most frequent species, linked prevalently to habitats subject to human impact. The most similar riparian areas were therefore highly disturbed ones, since alterations to the internal structure of Mediterranean riparian corridors determined proliferation of opportunistic or nitrophilous terrestrial species (Ferreira & Aguiar, 2006) shared by all the rivers studied. At local level, differences between rivers in a given region were probably due to factors that vary differently within a region (Neilson *et al.*, 1992). Continental rivers were found to have higher floristic heterogeneity than insular rivers and many differences in life forms and phytogeographical elements, probably due to their different geological settings and greater length.

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REGIONAL AND LOCAL GRADIENTS

In our study, the main gradient affecting riparian flora at regional scale was geographical, in line with the findings of Sieben, Mucina, and Boucher (2009). This result was probably due in part to the high species turnover between insular and continental areas, as discussed above, and can be considered a specific outcome of these regions. However, the longitudinal gradient was also confirmed as a major gradient for riparian vegetation. Climatic factors vary along geographical and longitudinal gradients, directly or indirectly influencing vegetation composition and structure. Our findings support the idea that climate constrains Mediterranean riparian ecosystems, as suggested by the few other regional-scale analyses of riparian vegetation (Collins, Risser & Rice, 1981; Alcaraz *et al.*, 1997; Sarr & Hibbs, 2007). In our case, climatic conditions typical of the Mediterranean area had important indirect ecological effects on vegetation: *i*) favouring colonization of riverbanks by species with low soil moisture requirements (Ferreira & Moreira, 1999) derived from adjacent land use; such species formed the prevalent portion of the riverbed flora (Ferreira & Aguiar, 2006); *ii*) causing hydrological intermittency of the rivers, in which aquatic and hygrophilous species, less affected by climatic variables, were scarce in comparison to other fluvial systems (Naiman, Décamps & Pollock, 1993). Climatic differences between and along the rivers therefore substantially influenced Mediterranean riverbed flora, in spite of the well-known azonality of such vegetation. After removing the "river effect", the main gradient at regional level was found to be linked to vegetation structure, which corresponded to the main gradients also at local scale. The controls on riparian vegetation structure may be a complex combination of factors, the relative influences of which are hard to separate (Bendix, 1994). In our rivers the different distributional trends of herbaceous and woody species followed the transition from mountain to lowland areas along the longitudinal gradient, which was linked to climate, altitude, and increasing human disturbance, but also to changes in riverbed morphological features from small to large horizontal distances from the main channel of the river along the lateral gradient (see Angiolini *et al.*, 2011). Thus, longitudinal and lateral gradients occurred together, confirming that they are partially nested environmental gradients (Sieben, Mucina & Boucher, 2009). The increasing gradient of riverbed width from upland to lowland causes a decrease in the depth and speed of water flow, increasing the sedimentation necessary for establishment and maintenance of lateral riparian zonation. In the continental rivers, however, the lateral gradient seemed to be more important and was linked to the particular morphological characteristics of Tuscan riverbeds (see Appendix I and Landi & Angiolini, 2007) and to the more natural conditions of the medium/lower reaches of the rivers. This finding confirms the suggestion of certain authors (*i.e.*, Bendix, 1994; Yang *et al.*, 2011) that lateral gradient variations become relatively important when sampling in riparian habitats is expanded along the transverse direction.

BIOGEOGRAPHY *VERSUS* LONGITUDINAL AND LATERAL GRADIENTS

Partial ordination results were consistent with the longitudinal gradient being the major predictor of riparian plant species distribution. However, biogeographical differences were also found to be strongly correlated with riverbed flora. Quantifying the role of historic and paleogeographic factors on their own confirmed our prior assumption that biogeographical differences account not only for variations in zonal vegetation, but also for variations within vegetation known to be azonal, such as that of riparian corridors. This is true both at macroscale (*e.g.*, Mediterranean *versus* Eurasiatic) (Whittaker, Willis & Field, 2001; O'Brien, 2006) and at regional scale (see Sieben, Mucina & Boucher, 2009; Kuzemko, 2011), as found in our study area, since the 4 rivers are all located in the Mediterranean biogeographic region but belong to different biogeographic units. On the other hand, the high percentage of variance shared between biogeographic location and the longitudinal gradient underlined strong linkages between these 2 variables, associated with climate change. The lateral gradient was less evident and was almost completely independent of the other 2 variables. It should also be underlined that the percentage of variance explained by the different factors was relatively low, since many other gradients (not addressed in our study), such as differences in land use, may potentially account for a substantial proportion of unexplained biotic variation (Salinas & Casas, 2007).

Conclusion

Our findings support a multiscale perspective for controls on riparian flora along rivers at the Temperate/Mediterranean transition in Italy, as climate drives major floristic changes between rivers of different Mediterranean regions, while riverbed morphological and human disturbance gradients govern the local distribution of riparian flora in rivers of a given region. This perspective complements existing knowledge of multiscaled drivers in riparian vegetation, as well as detailed studies of the effects of riparian gradients and geomorphology on riparian vegetation mosaics along Mediterranean rivers (Ferreira & Moreira, 1999; Aguiar & Ferreira, 2005; Salinas & Casas, 2007; Angiolini *et al.*, 2011; Nucci *et al.*, 2012). The differences in composition and physiognomy between continental and insular river vegetation underline that, although all the study sites described in this paper are in the Mediterranean region, drought-adapted flora are more important in the drier environments of a truly Mediterranean climate. This argues against the premise of "azonal" riparian vegetation and suggests that in Mediterranean rivers, where the truly aquatic and hygrophilous species are few, while those well-suited to marked edaphic dryness are frequent, the term "azonal" riparian flora should be modified to "semi-azonal". More generally, our results support the idea that a better understanding of the multiscale factors affecting regional riparian floras, and of the biogeography of riparian vegetation in particular, may complement and strengthen the conceptual foundations of riparian ecology.

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Appendix I

APPENDIX I, TABLE I. Main features of the 4 rivers: a) physical characteristics, b) climate, c) geology and d) biogeographic characterization. The number of plots for each river is indicated in parentheses.

Rivers	Insular		Continental	
	Santa Lucia ($n = 25$)	Leni ($n = 48$)	Albegna ($n = 48$)	Fiora ($n = 68$)
a) Physical characteristics				
Basin area (km²)	110	130	750	820
Length (km)	25	33	70	80
Floodplain width (m)	Max 61.1	Max 88.2	Max 231.8	Max 435.8
	Min 19.8	Min 24.5	Min 40.2	Min 12.5
	Mean 38.2	Mean 41.8	Mean 103.8	Mean 129.4
b) Climate				
Bioclimate	Mediterranean Pluviseasonal-oceanic		Mediterranean pluviseasonal-oceanic, Temperate oceanic, Semicontinental	
Ombrotype	Dry, Subhumid		Subhumid, Humid	
Thermotype	Thermomediterranean	Mesomediterranean	Mesomediterranean, Mesotemperate	Mesomediterranean, Mesotemperate, Supratemperate
c) Geology				
Upper	Granites, metamorphytes	Granites, metamorphytes	Shales, marls, clays	Shales, sandstones, conglomerates, limestones
Lower	Pebbles, sands, clays	Cobblestones, sands, clays	Pebbles, sands, clays	Pebbles, sands, clays
d) Biogeographic characterization				
Region	Mediterranean		Mediterranean	
Subregion	W. Mediterranean		W. Mediterranean	
Superprovince	Italian, Tyrrhenian		Italian, Tyrrhenian	
Province	Sardinian, Corsican		Tyrrhenian	