Influence of bedrock-alluvial transition on plant species distribution along a Mediterranean river corridor

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Abstract
The variation of riparian plant species composition along a river according to lithological features, forming more or less discrete plant assemblages, was tested using multivariate and univariate analyses. Moreover, Sørensen's index was applied to examine similarity between geological and floristic groups, and the Wilson–Shmida index to investigate species turnover. The analyses were based on field data recorded along a Mediterranean river (Rio Santa Lucia, Sardinia, Italy), where the morphology is influenced by the bedrock-alluvial transition. The results obtained from the various analytical techniques were in close agreement, and underlined that the lithological types exerted an important influence on the distribution and richness (peak in the medium and the upper river part) of riparian plants, but also in their life forms (woody species and hemicryptophytes). The distribution patterns of species along the river suggested that primary drivers in the organization of the riparian plant communities were lithological types, geomorphology and altitude. Moreover, the bedrock-alluvial transition marked the highest species turnover, linked also to a different degree of human disturbance. The results of the present study indicate that the bedrock/alluvial influence is an integral component of the patch structure, which strongly influences riparian plant distribution patterns in a Mediterranean environment.

Keywords: *β-turnover, floristic discontinuity, riparian plants, Sardinia, species richness, statistical techniques*

Nomenclature: Conti et al. (2005, 2007)

Introduction

River corridors are recognized as linear landscapes in which water flows play a key role in connecting various landscape patches (Nilsson et al. 1989; Malanson 1993; Ward 1998). Due to their extremely high habitat heterogeneity and habitat connectivity, river corridors are among the most species-rich ecosystems of temperate regions (Nilsson et al. 1989; Pollock et al. 1998; Corbacho et al. 2003).

Most understanding of vegetation environment relationships along riparian corridors has emerged predominantly from relationships established with gradients (Hughes 1988; Bowman & McDonough 1991; Glavac et al. 1992; van Coller et al. 1997). In fact, the environmental heterogeneity of riparian corridors is a function of the strong environmental gradients that extend vertically (height above the channel, Hupp & Osterkamp 1985), laterally (lateral distance away from the channel, Decocq 2002) and longitudinally (distance down river, Tabacchi et al. 1990). These are composite gradients (Austin & Smith 1989; van Coller et al. 2000), as they represent changes in a number of important environmental variables, such as flooding, water availability, soil texture and nutrients, and are, for this reason, useful descriptors of plant species distribution, providing important insights of the possible processes that determine such distribution patterns (van Coller et al. 2000).

For many riparian systems, a simple gradient approach adequately characterizes a riparian vegetation pattern and has provided insight into the main influencing processes. However, for geomorphologically complex rivers, a gradient paradigm does not

deal effectively with the complexity of the patch mosaic structure arising from dynamic fluvial processes. In fact, despite the distribution of plant species in riparian forests have repeatedly been shown to be closely associated with variation in the topography (Xu et al. 2008) and landforms (Hupp & Rinaldi 2007; Mollot et al. 2008), the influence of the complex geomorphological structure of riparian ecosystems (Gregory et al. 1991) on vegetation distribution patterns is often ignored.

The catchment geology combined with the hydrogeomorphic processes of the rivers create a high heterogeneous landscape consisting of a mosaic of different morphological units (Gregory et al. 1991). This heterogeneity is an important factor controlling vegetation development (Kalliola & Puhakka 1988; Amoros & Bornette 2002; Baattrup-Pedersen et al. 2005). Patchiness in the geomorphology is further enhanced by the presence of bedrock (van Niekerk et al. 1995), a characteristic insufficiently dealt with in riparian vegetation studies. In fact, while most attention has been focused on rivers that are predominantly alluvial controlled, few studies have looked at systems where the morphology of the river is, to a large extent, influenced by the underlying geology and bedrock lithologies (van Coller et al. 1997), features that result in variable sediment and erosion down the course of the river in response to variable channel gradients (van Niekerk et al. 1996). The presence of bedrock outcrops tends to create a complex geomorphology, and thus a complex plant species distribution (van Niekerk et al. 1995; van Coller et al. 2000). The transition from one geology to another generally also leads to topographic discontinuities that have a strong influence on ecological processes structuring biological communities (Malanson 1993; Steiger et al. 2005), generating high level of plant turnover and thus creating deep floristic discontinuities (Malanson 1993; van Coller et al. 1997). This important feature of riparian landscape is still poorly and insufficiently studied (van Coller et al. 2000), and all previous researches have not quantified the influence of the bedrock/ alluvial transition on plant species distribution. Besides, distribution patterns of river plants are scarcely investigated in Mediterranean areas (see Ferreira & Moreira 1999; Hupp & Rinaldi 2007; Salinas & Casas 2007).

Here, we present the results of a study carried out along a Mediterranean river whose upper stretch is bedrock controlled, and whose lower part is alluvial controlled. The question of main interest is the extent to which plant species composition, forming more or less discrete plant coenoses, varies along the river according to lithological types (bedrock/alluvial). To test and measure the influence of the bedrock-alluvial transition on species distribution,

life forms and richness, we used multiple, both univariate and multivariate, statistical techniques. This approach provided added assurance that the results obtained by any one method were real (see Mollot et al. 2008). We also used the method of Borcard et al. (1992) to explore how lithological type and elevation are related to the compositional variation in a Mediterranean riparian area. To investigate the presence and location of meaningful discontinuities in riparian plant distribution and richness along the river corridor, we analyzed the degree of floristic continuity/discontinuity with the Wilson–Shmida index, a β-turnover measure for species presence/absence data along environmental gradients (Wilson & Shmida 1984).

Study area

The Santa Lucia River is located in the south-western part of Sardinia, between $39°09'10''$ and $39°06'56''$N, $9°01'17''$ and $8°46'51''$E (Figure 1). It represents the main river of the Sulcis region and the catchment basin is almost 110 km^2. The stretch investigated extends for almost 20 km along the riverside floodplain, and flows in a prevalent NE direction in the upper part and SE in the lower. The altitudinal range is of almost 500 m, and the river does not have any tributary.

The climate belongs to the Mediterranean type and is substantially homogeneous in the study area, with total annual rainfall ranging from 546 to 1172 mm (mean monthly maximum 193.5 mm in December and minimum 3.3 mm in July), and mean temperature ranging from $13.1°$C to $18.5°$C (mean monthly maximum $28.1°$C in August and minimum $6.7°$C in January).

According to the climatic data available and in agreement with the bioclimatic classification by Rivas-Martínez (2002), it may be stated that the bioclimate of the studied area is Mediterranean Pluviseasonal Oceanic (MPO). Thermotypes vary from the upper thermomediterranean to the lower mesomediterranean belt with ombrotypes ranging from upper dry to lower humid (Bacchetta 2006). During summer, the river dries up almost totally, while in autumn and spring it is affected by flood events.

The Santa Lucia river flows in the upper part over outcrops of resistant rock (bedrock), in the form of Palaeozoic granites and metamorphytes, while in the lowlands there is a Quaternary sediment accumulation (alluvial) with cobblestones, sands and clays deposited by streams (see Bacchetta et al. 2003, 2005; Bacchetta 2006). This bedrock-alluvial transition is also underlined by the change in geomorphology and the elevation gradient of the riverbed. In the mountainous part, the river flows into a narrow valley
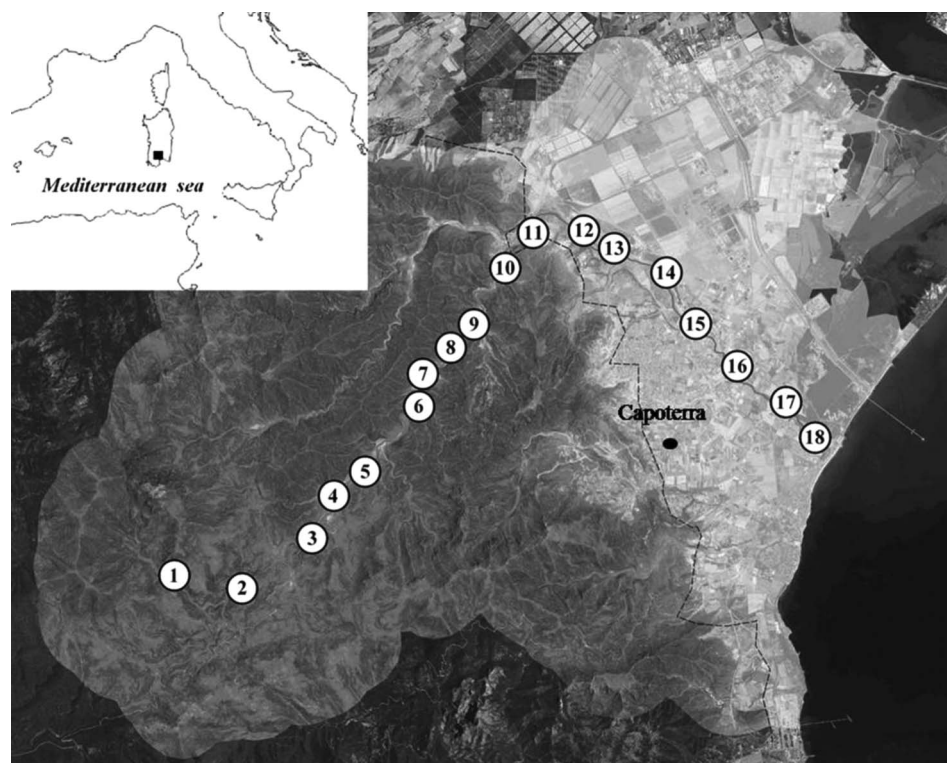
Figure 1. Santa Lucia River basin (scale 1:120000) with plots signed as circles (and their respective number) and the geographical localization of the study area. Dotted line marks the borderline between bedrock (on the left) and alluvial (on the right).

with a V profile, while at the transition from bedrock to alluvial lithology, it widens over an alluvial conoid (Figure 1). In the mountain part, located in a protected area (SCI – Site of Community Importance), the landscape is characterized by low-intensity agro-pastoral systems and by woodlands dominated by holm-oak (*Quercus ilex*) with cork-oak (*Quercus suber*); in the lower part, there are industries, villages and extensive grazing areas. Phytosociological surveys by Angius and Bacchetta (2009) reported the class *Quercetea ilicis* for woodlands surrounding the river and the classes *Nerio-Tamaricetea* and *Salici purpureae-Populetea nigrae* for the riparian woods (for syntaxa nomenclature see Bacchetta et al. 2009). At the end of its course, the river flows into a wetland included in a protected area (SCI).

Methods

Field methods and selected variables

Since one of the goals of this study was the analysis of riparian plant species of the Santa Lucia River, sampling was carried out considering only the floodplain. For the analyses of plant composition along the river, we used a stratified random sampling design. To avoid the possibility of having grouped plots and with the aim to represent variations in species assemblages and environmental features (Angiolini et al. 2011), the river was divided, from the source to the mouth, into nine sections each 2 km in length and perpendicular to the direction of flow; for each section two plots of 10 m × 10 m were placed randomly. This dimension was found to be adequate to detect the vegetational mosaic of the floodplain, because it makes it possible to explain the relationships between species richness and environmental features both in forests (Schuster & Diekmann 2005) and in grasslands (Gross et al. 2000). For each plot, we recorded all vascular plant species present from May to July 2008.

The distribution of plots in different lithological types, and the description of the lithological types and geomorphology obtained with a geographical information system (GIS, using 1:25000 digital maps) are shown in Table I and Figure 1. The elevation of each plot was derived from DTM (10 × 10 m) and normalized by a log transformation for the statistical analyses.

Life forms were checked in the field and expressed by the abbreviations reported in Pignatti (1982) based on Raunkiaer's (1934) classification, that is: phanerophytes (P), nanophanerophytes (NP), hemichryptophytes (H), therophytes (T), geophytes (G) and chamaephytes (Ch).

Table I. Plot distribution and main topographic features of the study area.

Plots	Lithological types	Geomorphology	Elevation
1–10	Bedrock (outcrops of granites and metamorphytes)	Steep sides, from incised in the bedrock gulley to moderately incised	From 402 to 90 m asl.
11–18	Alluvials (pebbles, sands and clays)	Level lands. Accumulation of sediment	From 90 to 0.5 m asl.

Statistical analyses

Cluster analysis, carried out for the species by plots matrix, was used to investigate if sample groups classified based only on floristic similarity correspond to their lithological types. Two-Way INdicator SPecies ANalysis (TWINSPAN, Hill 1979) is based on division of sequential reciprocal averaging ordinations and separated sample locations into groups according to the presence or absence of species. The cluster analysis evaluates first the similarity between the different sites in order to subsequently group together those with a larger number of shared elements. The technique, which arranges the groups in dendrograms, is a multivariate analysis strategy widely acknowledged as a particularly valuable tool for assessing the floristic similarities between territories (Medina-Cazorla et al. 2010). Since we are interested to know if there was a correspondence between lithological types and floristic composition, we applied the Sørensen index (Sørensen 1948) between groups of plots identified by cluster analysis on the basis of their floristic homogeneity (using first and second cut level of cluster) and groups delineated by taking into account the lithological types.

Classification was followed by a multi-response permutation procedure (MRPP, Mielke 1984) to test the differences in plant assemblages across the lithological types. The T-statistic was applied to measure between-group separability. A large negative T value (≤ -9.0) indicates high separability (i.e. the more negative, the greater the species differences among the groups). The A statistic estimated the within-group homogeneity and was chance-corrected. The A statistic has a maximum value = 1.0 with higher values indicating a high degree of homogeneity. Moreover, A is usually < 0.1 when there are a high number of species.

The characteristic species of each lithological type were then explored by an INdicator SPecies ANalysis using the IndVal method (Dufrène & Legendre 1997) as implemented in PC-ORD (McCune & Mefford 1999), which is a useful method to identify indicator species and/or species assemblages that characterize groups of samples. The null hypothesis was no difference in species response across lithological types. The result produced indicator values (IV) (Dufrène & Legendre 1997), ranging from zero (no indication) to 100 (perfect indication), that stand for the relative frequency within each lithological type. A Monte Carlo test with 499 permutations was used to evaluate the statistical significance of the maximum indicator value recorded for a given species (Dufrène & Legendre 1997; McCune & Mefford 1999; McCune & Grace 2002).

Differences on percentage of life forms and richness values were investigated with a *t*-test. Richness values were log transformed to normalize the data distribution.

To check if the dominant floristic gradient agrees with cluster analysis results and/or lithological classification, and to evaluate the length of the gradient, indirect gradient analysis was carried out using Detrended Correspondence Analysis (DCA; ter Braak 1995). This ordination technique was also used to visually represent if plots from the different lithological types show a different pattern of species richness. We subsequently introduced environmental features (lithology and altitude) as passive variables, which allowed direct comparison of the ordination axes with these variables.

To describe consistent relationships between the lithological types (L) and the floristic composition, after removing the compositional variability explained by the altitude, we used a partial ordination (Lepš & Šmilauer 2003). Partial canonical correspondence analyses (CCAs) (gradient length of 4.58 SD) with the four-step procedure described by Borcard et al. (1992) were performed. Within each CCA, Monte Carlo tests with 999 unrestricted permutations were performed to determine the significance of the trace statistics and of the first eigenvalue (ter Braak & Šmilauer 2002).

To determine how much the lithology of the area influences the floristic composition of the river corridor, we used a measure of β-diversity recommended when sample data can be arranged along a single environmental gradient, known as beta turnover (βt), which gives a direct, intuitive measure of the degree of species turnover between adjacent pairs of plots along a longitudinal gradient according to the formula proposed by Wilson and Shmida (1984):

$$\beta_T = \frac{g(H) + l(H)}{2\alpha}$$

where H is the habitat gradient; $g(H)$ and $l(H)$ are the number of species gained and lost, respectively,

moving along the habitat gradient H; α is the average number of species found in plot along H.

The more dissimilar two groups are, the higher is the index, reaching a maximum of 1 at total dissimilarity. This index is one of the most frequently used indices, and results are comparable to those of other β-diversity indices (Koleff et al. 2003; Magurran 2004). Analyses carried out on presence/absence data guaranteed that the changes in species composition were genuine species turnover, and not merely a change in species/cover abundance (Demars & Harper 2005).

Clustering was carried out using PC-ORD (McCune & Mefford 1999), ordination using CANOCO 4.5 (ter Braak & Šmilauer 2002), and other statistical analyses using the STATISTICA 6.0 software package (StatSoft Inc. 1995).

Results

A total of 201 taxa were identified along the Santa Lucia River. More than one-third of the species were found in only one plot, and about half in less than three plots. Only one species (*Nerium oleander* ssp. *oleander*) was present in more than 70% of the plots, while 10 species were present in more than 50% of the plots (see Table II). The species exclusive of a single lithological type were 90 (44.8%) for bedrock and 53 (26.4%) for alluvial. The mean value of species richness for the study area is 35.06 ± 5.52 SD.

Univariate analyses for species richness and life forms

Average richness of species is significantly higher in bedrock (40.3 ± 10.25 SD) than in alluvial (28.5 ± 8.47 SD) ($t = 2.48$, df $= 16$, $P < 0.05$). The

Table II. List of the most frequent species in the riparian vegetation of Rio Santa Lucia, and number of plots in which the species was found for each lithological type (bedrock, alluvial). The relative percentage (%) of the presence on the total number of plots is also shown.

	Number of plots			
Most frequent species	Bedrock	Alluvial	Total	%
Nerium oleander ssp. *oleander*	9	5	14	77.8
Rubus gr. *ulmifolius*	9	3	12	66.7
Geranium purpureum	9	2	11	61.1
Sonchus oleraceus	3	8	11	61.1
Piptatherum miliaceum	4	6	10	55.6
Rubia peregrina ssp. *peregrina*	6	4	10	55.6
Salix purpurea ssp. *purpurea*	6	4	10	55.6
Allium subhirsutum	8	1	9	50
Asparagus acutifolius	4	5	9	50
Dittrichia viscosa	1	8	9	50
Phillyrea latifolia	9	0	9	50

average percentage of life forms for bedrock and alluvial species resulted significantly different for phanerophytes and nanophanerophytes, with a higher frequency in bedrock (24.28 ± 10.2 SD and 10.5 ± 2.6 SD) than in alluvial (18.72 ± 12.99 SD and 2.71 ± 3.75 SD) ($t = 1.41$, df $= 16$, $P < 0.01$ and $t = 3.43$, df $= 16$, $P < 0.05$), and for hemicryptophytes, which have a higher percentage in alluvial (29.48 ± 4.04 SD) than in bedrock (14.87 ± 5.35 SD) ($t = -4.32$, df $= 16$, $P < 0.01$). The other life forms showed no differences between the lithological types.

Two way INdicator SPecies ANalysis (TWINSPAN)

The hierarchical classification (Figure 2) suggested the existence of two major floristic groups of sites, with 59.1% between-group dissimilarity (first cut level, types A and B), almost completely dependent on the bedrock-alluvial division (see Table I). The indicator species for the bedrock plots were *Allium subhirsutum* and *Phillyrea latifolia*. The two main floristic assemblages were subdivided into four classes at the second cut-level, with 44.4% (A1 and A2 with *Carduus pycnocephalus* and *Olea sylvestris* as indicator species) and 48.5% (B1 and B2) between-group dissimilarity. This result could be partly associated with specific geological substrates (A1 = granites; A2 = metamorphytes), and partly with the fact that B2 grouped plots located on soils with higher salinity than B1 plots (with *Eucalyptus camaldulensis* as indicator species), due to their proximity to the sea.

Sørensen index

The Sørensen similarity index for groups of plots derived by cluster analysis and groups of plots delineated using lithological types is shown in Table III. The correspondence between bedrock-alluvial and A-B cluster groups of the first-cut level was even higher. Bedrock matched very well with both A1 and A2. The correspondence of alluvial versus B1 and B2 was anyway high. For all the other combinations, the values of the similarity index were substantially lower, and generally less than 0.5.

Multiple response permutation procedure

This analysis clearly indicated a relationship between the lithological types (bedrock and alluvial) and plant species composition (Table IV). The division among groups was statistically highly significant ($P < 0.001$), both in terms of within-group homogeneity and among-group separability. The T-statistic, which measures heterogeneity between
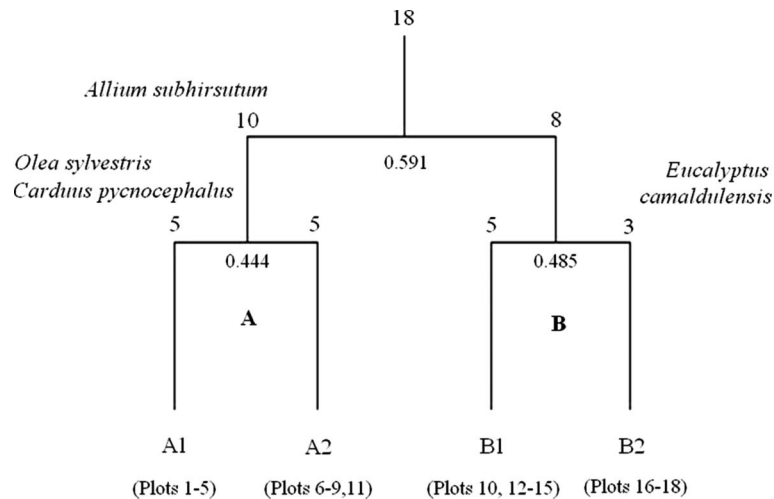
Figure 2. Dendrogram derived from TWINSPAN showing plots number, eigenvalues and indicator species (where they exist) for each division.

Table III. Sørensen index between cluster groups and bedrock/alluvial.

	Bedrock	Alluvial
A	**0.960**	0.491
B	0.372	**0.839**
A1	**0.872**	0.318
A2	**0.750**	0.570
B1	0.341	**0.616**
B2	0.222	**0.694**

Note: Values of similarity higher than 0.6 are reported in bold.

Table IV. MRPP test statistics measuring separability and agreement between bedrock and alluvial plots.

Statistic	Measures	Result	P-value
T	Separability between groups	−9.19	$P < 0.001$
A	Agreement within groups	0.14	$P < 0.001$

lithological types, was −9.19, indicating that a dissimilarity in plant communities among the lithological types exists. This analysis also produced a significant, though not high, A value ($A = 0.14$), which suggested a similarity of plant assemblages within each group.

INdicator SPecies ANalysis

Twenty-three species (11.4%) exhibited a significant correlation with lithological types based on the Indicator Value (IV, Table V). Woody species showed a distinct distribution relative to the geological types; those associated to bedrocks were *Q. ilex*, *Juniperus oxycedrus* ssp. *oxycedrus* and *P. latifolia*, while those associated to the alluvial were the halophyte *Tamarix gallica* and the exotic

Table V. The number of presences indicating how often the species was found in bedrock/alluvial plots, and the affinity of the species (Indicator Value, IV) for each of the two lithologies. Only the significant species ($P < 0.05$) are reported.

	Number of presences			
	Bedrock plots	Alluvial plots	IV	P
Species linked to bedrock				
Allium subhirsutum	8	1	69.2	0.02
Anthemis arvensis	5	0	50	0.04
Arisarum vulgare	6	0	60	0.01
Carex distachya	6	0	60	0.007
Cyclamen repandum	7	0	70	0.002
Geranium purpureum	9	2	70.4	0.01
Hypericum hircinum ssp. *hircinum*	5	0	50	0.03
Juniperus oxycedrus ssp. *oxycedrus*	7	0	70	0.004
Lagurus ovatus	5	0	50	0.04
Phillyrea latifolia	9	0	90	0.001
Quercus ilex	6	0	60	0.01
Rubus gr. *ulmifolius*	9	3	63.5	0.03
Selaginella denticulata	5	0	50	0.04
Smilax aspera	7	1	59.4	0.02
Torilis arvensis	7	0	70	0.001
Species linked to alluvial				
Cyperus badius	0	5	62.5	0.007
Daucus carota	0	7	87.5	0.001
Dittrichia viscosa	1	8	90.9	0.001
Eucalyptus camaldulensis	1	5	27.9	0.045
Foeniculum vulgare	0	5	24.7	0.009
Phragmites australis	0	5	62.5	0.005
Sonchus oleraceous	3	8	76.9	0.009
Tamarix gallica	0	7	87.5	0.001

E. camaldulensis, only rarely found in bedrocks. The herbaceous species also showed a distinct distribution pattern corresponding to lithological types. Many pioneer and/or nitrophylous hemicryptophytes

were associated with the alluvial areas, like *Dittrichia viscosa*, *Daucus carota*, *Foeniculum vulgare* and *Sonchus oleraceus*, together with halophytes more likely to be found in slow-flowing waters (*Phragmites australis* and *Cyperus badius*).

Detrended Correspondence Analysis

The plots distribution along the first DCA axis, that explained 13.8% of the total variance of species data and 60.8% of species-environmental relation, agreed with TWINSPAN results (Figure 3). The length of the gradient was 4.58 S.D., underlying a high plant species heterogeneity in the riparian corridor. In the first axis, the bedrock-alluvial transition seemed to explain the floristic differences along a decreasing altitudinal gradient. Two groups of plots were clearly separated and included: on the left side of axis 1, sites of the upper course with outcrops of bedrock (TWINSPAN A); on the right side, sites of the lower course with alluvial soils (TWINSPAN B). Species with the highest fit ranges shown in Figure 3 were almost the same as those detected by INSPAN. The DCA analysis demonstrated that richness distribution is not homogeneous along the longitudinal gradient of the Santa Lucia River, and that the bedrock zone harbors more plant species than the alluvial zone. A general pattern of increasing species richness with increasing elevation was also evident.

Partial Canonical Correspondence Analysis

Partial CCAs were carried out, and the trace and sum of all canonical eigenvalues were calculated for each. The contribution of altitude (A) and bedrock/alluvial lithological types (L) to variance of the

species matrix can be partitioned as shown in Figure 4. In total, 20.4% of the variation can be explained. A and L explain 8.6% and 7.3% of the species data, respectively, and their interaction explains 4.5%. Permutation tests on the trace value showed that the available explanatory variables explain a significant part ($P < 0.002$) of the variation.

Wilson–Shmida index

The overall result that emerged from applying the Wilson–Shmida formula was the high heterogeneity of plant species composition between all pairs of plots (values between 0.416 and 0.826). The index also highlighted the fact that the turnover in floristic composition was not constant along the riparian corridor, but that it was generally higher in the alluvial part (see Table VI). The highest value was found for 9 vs. 10, followed by 10 vs. 11, underlying in this way that more than 70–80% of the plant species (82.6% and 73.9%, respectively) changed at the transition between bedrock and alluvial (Table VI). For the bedrock-controlled part, the highest value was found between plots 1 and 2 (63.4%). Another significant discontinuity (turnover >60% of the species) appeared in the alluvial zone, between plots 15 and 16, 16 and 17, and 17 and 18.

Discussion

Effect of bedrock-alluvial transition on plant species distribution, richness and life forms

The heterogeneous plant species distribution in this Mediterranean river corridor emerged from the results of various analyses: (i) high dissimilarity
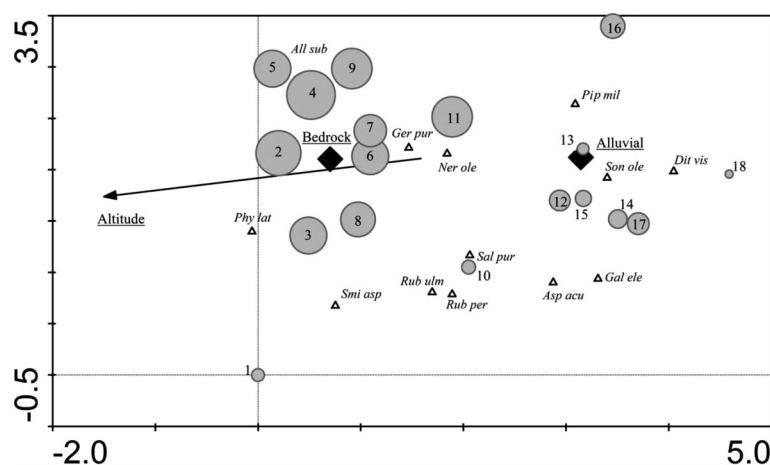

Figure 3. DCA diagram with plots (circles), species (triangles), altitude (arrow) and lithological types centroids (diamonds); the number showed is the plot number. The bigger circles stand for plots with higher species richness. Only species with fit-range >50 are shown. Abbreviation stands for: *Allium subhirsutum*, *Phillyrea latifolia*, *Geranium purpureum*, *Nerium oleander* ssp. *oleander*, *Piptatherum miliaceum*, *Dittrichia viscosa*, *Sonchus oleraceus*, *Galactites elegans*, *Salix purpurea* ssp. *purpurea*, *Rubus* gr. *ulmifolius*, *Asparagus acutifolius*, *Rubia peregrina*, *Smilax aspera*.
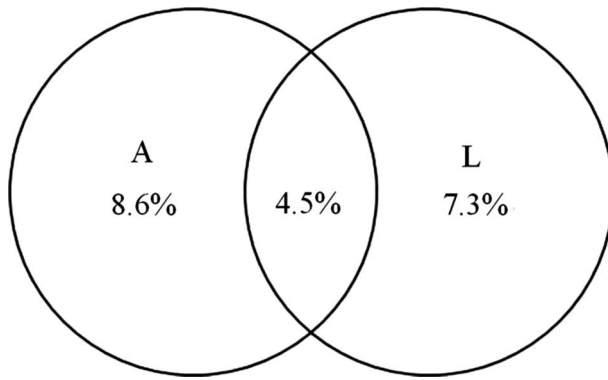
Figure 4. Variance partitioning (expressed as percentage of variance explained) of the effects of altitude (A) and lithological types (L).

Table VI. Wilson–Shmida Index calculated between adjacent plots along the longitudinal gradient, with the lithology of the pair of plots (B = Bedrock; BA = from Bedrock to Alluvial; A = Alluvial).

Plots	Wilson–Shmida index	Lithological types
1 vs. 2	0.634	B
2 vs. 3	0.437	B
3 vs. 4	0.583	B
4 vs. 5	0.541	B
5 vs. 6	0.581	B
6 vs. 7	0.420	B
7 vs. 8	0.525	B
8 vs. 9	0.632	B
9 vs. 10	0.826	B
10 vs. 11	0.739	BA
11 vs. 12	0.653	A
12 vs. 13	0.560	A
13 vs. 14	0.416	A
14 vs. 15	0.500	A
15 vs. 16	0.614	A
16 vs. 17	0.625	A
17 vs. 18	0.645	A

shown by the cluster analysis (first and second cut level); (ii) high number of species found in less than three plots; (ii) length of the gradient in the DCA ordination, and (iii) high value of species turnover along the longitudinal gradient. These strong differences in specific composition within the riparian vegetation can be explained, in part, by patchiness, or habitat heterogeneity of the floodplain (Begon et al. 1990; Everson & Boucher 1998; Ferreira & Stohlgren 1999; Amoros 2001; Goebel et al. 2003). Nevertheless, the effect of bedrock and alluvial lithology on floristic assemblages is also evidenced by the results obtained using multiple analytical techniques. The first TWINSPAN division, the negative T value obtained in the MRPP analysis, and the strong similarities (Sørensen index) between the lithological and cluster groups indicated a distinct difference in floristic distribution patterns associated to the two lithological types.

Results from INSPAN agree with the previous, since 23 species were found to be significantly correlated with lithological types. Among the woody species, sclerophyllous trees and shrubs and all nemoral herbaceous species linked to Mediterranean hardwooded zones, like *Arisarum vulgare*, *Carex distachya*, *Cyclamen repandum*, and *Selaginella denticulata*, are related to the bedrock, while the exotic *E. camaldulensis* occurred on the alluvial zone, since in the last century woods of this species were planted in coastal areas in order to fight malaria, a typical disease of Mediterranean marshy zones, and were also employed in paper industries. In lowland alluvial areas, the presence of *T. gallica* was favored by high salinity, due to natural and/or man-induced factors, that negatively affect tree health, triggering dieback of many riparian woody species (Salinas & Casas 2007). There were also clear distinctions in the distribution of understorey plants between lithological types, since the nitrophilous, pioneer (see Wacquant 1990), and hygrophylous species were more frequent in the alluvial area. All these data show that all types of riverbanks were colonized by species with scarce soil moisture needs, due to climatic harshness and intermittent flows typical of the southern basins of Mediterranean rivers (Ferreira & Aguiar 2006). These species tend to become the prevalent part of riverbed flora as indicated in Santa Lucia river by *N. oleander* ssp. *oleander* and *Rubus* gr. *ulmifolius* that dominate shrubby extrazonal vegetation along Mediterranean temporary watercourses (Jasprica et al. 2007; Bacchetta et al. 2009).

The life forms analysis agrees with previous results, showing that woody species (phanerophytes and nanophanerophytes) were clearly related to woodland landscape of both the upper reaches of the stream and less accessible zones of the basins. Besides, the bedrock part corresponds to narrow streams with steep slopes (and consequent lack of alluvial benches) in which the riparian zone tends to take on the characteristics of the adjacent forests (see Gregory et al. 1991; Richardson et al. 2005; Landi & Angiolini 2006). The herbaceous perennial species (hemicryptophytes), which were more strongly related to gradients of light availability and soil moisture than trees and shrubs (Decocq 2002), are related to alluvial lithology. This opposite distributional pattern may also be related to the contrasting life history traits between life forms, with herbaceous species, in particular the most ruderal and xeric annuals, likely to recover from disturbance more quickly than woody species, due to their shorter lifespan and higher colonization rates (Tabacchi et al. 1998; Bagstad et al. 2005; Lite et al. 2005; Salinas & Casas 2007).

The DCA ordination strongly suggests that altitude plays a role in determining the distribution of riparian plants between lithological types. In fact, along the Rio Santa Lucia corridor, the contrast between bedrock and alluvial separates two types of altitudinal gradients (strong in the upper part of the river, low in the lower part) with a gradual replacement of the process of erosion with sedimentation (see also Buer et al. 1989; Bacchetta et al. 2003, 2005; Landi & Angiolini 2006). Indeed, the lithological and altitudinal variables employed here were able to explain almost 16% of the total variation, and each has offered a similar contribution to the explained variation on the species. These two environmental factors are also responsible for the main structure of the surrounding landscape. One expected environmental gradient would be that in lower alluvial-controlled stretches of streams with the most favorable areas (low slope, depth of soil, roads, etc.), especially near the coast, the human activities (agriculture and urbanization) would generally increase (see also Corbacho et al. 2003; Bombino et al. 2007). This is supported also by the high percentage of shared variance between lithology and altitude. The unexplained variation was quite high (79.6%), a result that is not uncommon in ecological studies, because species abundance or occurrence data are often very noisy (ter Braak 1986; ter Braak & Šmilauer 2002; Guisan et al. 1999). Moreover, other studies using partial CCA have obtained similar levels of unexplained variation (see e.g. Borcard et al. 1992; Borcard & Legendre 1994; Titeux et al. 2004). The high amount of unexplained variance in the data set may be logically interpreted as evidence of important but unmeasured deterministic factors (i.e. transversal gradient, flooding, surrounding landscape, etc.). However, it can also be attributed to the existence of large fractions of random compositional variance in the data or, as recently demonstrated (Økland 1999), may arise from purely statistical reasons and does not need interpretation.

Species richness was significantly higher in the medium-upper bedrock course compared to the floodplain alluvial lithological type. This observation can be explained by three factors. First, clear-cutting of the fertile alluvial soils for agriculture, presently mostly covered by crops, has had a great impact on riparian vegetation causing a strong decrease in species richness (Angius & Bacchetta 2009). Secondly, in small stretches of bedrock-controlled streams with steeper slopes, infrequent but intense disturbances (such as landslides and debris flows, for instance in the case of flood events) create a high degree of landscape heterogeneity, which maintains high values of species richness (Richardson et al. 2005). Third, in the narrower bedrock-controlled riparian sections, the woody species are able to take advantage of a stable, well-drained substrate directly adjacent to the river (Everson & Boucher 1998). Moreover, bedrock can provide an anchoring medium for the establishment of certain species unable to find a firm rooting medium on the alluvium (van Coller 1993), while woody debris offers elevated sites for those species unable to survive on water-logged soil (Fetherston et al. 1995).

The downstream changes in plant species number observed in our study were consistent with results from other authors (Vannote et al. 1980; Statzner & Higler 1985; Nilsson et al. 1989; Tabacchi et al. 1990; Ferreira & Moreira 1999; van Looy et al. 2006). Most of these studies predict a maximum of plant species richness in the central section of river systems, where maximum environmental heterogeneity and intermediate level of disturbance occur. If the disturbance is neither too weak nor too strong, the potential species richness is likely to be high, consistent with the Intermediate Disturbance Hypothesis (Nilsson et al. 1989). By contrast, in Rio Santa Lucia only one plot in the upper part of the course had a low number of species, while the peak of richness was not only in the medium part but also in the upper one. This happened because this river (and generally Mediterranean rivers) is short, small, and does not include (or includes only a small part of) the headwater section, which is often ephemeral and was not flowing during the study period (Salinas & Casas 2007). In Santa Lucia River, only one plot corresponds to the headwater, while the subsequent plots already belong to the intermediate-sized stream section. As hypothesized by Huston (1999), regional patterns of species richness along environmental gradients may result, to a large extent, from very local processes, and, conversely, regional processes may produce local-scale emergent gradients. Although the species richness of plants varies considerably along riparian corridors (Planty-Tabacchi et al. 1996), and the explanation for species richness along rivers still remain controversial, a deeper knowledge of plant distribution may help to identify functional stretches in terms of the creation of biodiversity hotspots.

Bedrock-alluvial transition and discontinuity

As the classification and ordination analyses already showed, the peak in β-turnover occurring between plots in correspondence of the bedrock/alluvial transition (where more than 70% of species changed) indicated a strong discontinuity in species distribution. These high values of turnover index may reflect rapid and ecologically significant changes in the environment in the transition between the two lithological types.

Other significant discontinuities also appeared between: (i) sites 1 and 2, due to the difference in environmental features (headwater vs. intermediate-sized stream), (ii) the plots of the lowest stretch of the river, where new floristic elements appeared probably due both to higher human impact, that have indirectly determined a magnification of between-sites variability along the altitudinal-longitudinal dimension, and to a pronounced increase in salinity towards the mouth, as reported for other Mediterranean rivers (see Gasith & Resh 1999; Aguiar et al. 2001; Corbacho et al. 2003; Salinas & Casas 2007).

Some authors also emphasize the discontinuity in the longitudinal changes of riparian vegetation composition, with high species turnover between reaches of the rivers (Tabacchi et al. 1990; van Looy et al. 2006). In accord with Malanson (1993), van Coller et al. (1997) and Rosales et al. (2001), we found that the transition between bedrock and alluvial zones generates the highest floristic discontinuity. Geology is important in terms of reaction (acidic vs. basic soils), limiting the plant species that can be harbored in an area, but also in terms of morphology, influencing landform types (incised valleys vs. level lands). Moreover, the transition between high and low altitudinal gradients causes a decrease in both the depth and speed of the water, with a consequent increase in sedimentation downstream and significant variations in the width of the fluvial bed. In addition, in the lower sections of rivers, flatter landscapes allow the presence of agricultural activities and urban centers next to the riparian strip, features that become the main factors responsible for riparian corridor alteration (Décamps et al. 1988; Salinas et al. 2000; Corbacho et al. 2003), as found in many streams of the Mediterranean basin (Di Castri 1991; Gasith & Resh 1999; Aguiar & Ferreira 2005). Finally, as proposed by other authors (e.g. Kalliola & Puhakka 1988), vegetation distribution along floodplains can be highly patchy in relation to the heterogeneous nature of sedimentary patterns.

Conclusions

Our analyses confirmed that the degree of bedrock/alluvial influence is an integral component to the patch structure of a river and strongly influences vegetation distribution patterns. Riparian plant species patterns and fluvial geomorphic forms and processes linked to the bedrock/alluvial transition turned out to be closely integrated environmental phenomena in this Mediterranean river, even along strongly human altered stretches. Given their deep influence, it would be important to identify strong environmental discontinuities along rivers, since they are indicative of present and ongoing species distribution trends, while simultaneously reflecting a diverse array of river bed morphologies and fluvial dynamics.

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