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**Title:** Drivers of plant richness patterns of Mediterranean riparian forests at local and regional scales have bottom-up and top-down effects

**Running title:** plant richness of riparian forests at two scales

Leo M<sup>1</sup> (corresponding author, leo@rjb.csic.es) ORCID ID 0000-0002-1431-5244 & Calleja JA<sup>23</sup> (juan.calleja@gmail.com) ORCID ID 0000-0002-6586-0939

Lara F<sup>4</sup> (francisco.lara@uam.es) ORCID ID 0000-0002-1665-5277

Garilleti R<sup>5</sup> (Ricardo.garilleti@uv.es) ORCID ID 0000-0002-5977-2908

Medina NG<sup>6</sup> (ngmedina@gmail.com) ORCID ID 0000-0003-4702-1610

<sup>1</sup>Real Jardín Botánico (CSIC-RJB), 28014 Madrid, Spain.

leo@rjb.csic.es

<sup>2</sup> Departamento de Biología Animal, Biología Vegetal y Ecología, Botánica, Universidad Autónoma de Barcelona, 08193 Bellaterra, Spain.

<sup>3</sup> CREAF, Cerdanyola del Vallès 08193, Spain.

<sup>4</sup> Departamento de Biología (Botánica), Universidad Autónoma de Madrid, 28049 Madrid, Spain.

<sup>5</sup> Departamento de Botánica y Geología, Universidad de Valencia, 46100 Burjasot, Spain.

<sup>6</sup> Department of Botany, Faculty of Science, University of South Bohemia, Na Zlate stoce 1, 370 05 České Budějovice, Czech Republic.

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## **Abstract**

### **Question**

It has been long recognized that community species richness depends on factors operating at different spatial scales. Most frequently, across-scale studies have focused on the impact of regional factors on local richness (top-down effects) while very few have analyzed the importance of local factors on regional richness (bottom-up) and even fewer have tried to integrate effects on both directions.

Our objectives were to reveal the key factors shaping plant species richness of the Mediterranean riparian forests and to test whether empirical models based on top-down or bottom-up relationships are able to explain the spatial scaling of richness.

### **Location**

Southern half of Spain, SW Europe.

### **Methods**

We designed two models integrating relationships between biotic and abiotic variables at two spatial scales, local and regional. Then, we faced our models with the observed richness of 689 riparian woody communities by using structural equation modeling.

### **Results**

Local scale richness depended mostly on local climate, lithology and sediment textures. Regional species richness was driven by climate, lithology and water regime.. In the top-down model, regional to local effects were driven mostly by the influence of regional richness on local richness. However, we also detected several bottom-up effects linking local climate, abiotic habitat and vegetation structure with the regional richness. In the bottom-up model, results were very similar adding an effect of regional climate on local richness.

## Conclusions

Local, regional and across-scales factors are crucial to understand species richness of Mediterranean riparian forests. Some factors are inherent to riparian habitats whereas others are already known as relevant for upland habitats.

We provide support for the top-down models relying on the concepts of species pool and environmental filtering. However, we also stress that local scale processes influence regional species richness. Bottom-up effects should not be underestimated when studying the spatial scaling of biodiversity.

**Keywords:** *community; diversity; modeling; riverbank; scales; SEM; southwestern Europe; species pool.*

**Nomenclature:** Castroviejo et al. (1986–2018).

## Introduction

The notion of ecological communities as hierarchical entities influenced by factors acting at several spatial and temporal scales has been increasingly recognized over the past decades. However, empirical analyses of the network of relationships involved have proven challenging. One of the main difficulties is the wide range of scales involved that spans from local to regional or even coarser scales (Macarthur and Levins, 1967; Leimar et al., 2013). Likewise, the number of factors that affect the structure of communities can be very high and include: i) local abiotic habitat characteristics such as lithology, soil texture or disturbances (e.g. Keddy, 1992; ii) local biotic interactions (HilleRisLambers et al., 2012), or small scale dispersal and population dynamics (Hubbell, 2001); and iii) factors varying at larger scales such as changes in climate, major geological events, etc. (Ricklefs, 1987). All these factors and scales meet at

intermediate or regional scales so that studies that span hundreds of kilometers offer a unique opportunity to understand the relative importance of each one of these factors (Harrison & Cornell, 2008).

Partly because diversity analyses that integrate several scales are still scarce, there is little consensus regarding which processes dominate. For many years, communities were seen as bottom-up entities dominated by local scale factors with an uppermost influence of biotic interactions (Macarthur & Levins, 1967; Leimar et al., 2013), but in the last decades there has been an increasing trend towards highlighting the importance of the regional control over local communities (see for example Ricklefs, 2008 and Rolls et al, 2018). A widely accepted example of this regional control is the species pool hypothesis (Zobel, 2016), where large-scale factors and processes determine the number of species in a region (the regional species pool) that is filtered by intermediate and small-scale factors and processes to build the local communities (Keddy, 1992; Harrison & Cornell, 2008). Thus, the concept of species pool can be used to integrate the effects of the factors at several scales and enables an empirical -and to some extent easy- evaluation of the hierarchical nature of the communities and the factors that influence them (Harrison & Cornell, 2008; Medina et al., 2018; Jiménez-Alfaro et al., 2018).

The spatial structure of the communities and their connectivity are key factors influencing the nature of the relationships across scales. For example, if we assume a top-down hierarchy the ability of species in the species pool to colonize all the suitable sites will be limited in fragmented localities immersed in a heterogeneous or adverse matrix (Butaye et al., 2002; Harrison et al., 2006) Riparian communities are good examples of fragmented ecosystems (Naiman et al., 2005; Johnson et al., 2016) since they occur in the inter-phase between water and land and function as islands within an

unsuitable matrix. Besides, they are highly diversified communities that harbor unique  
floras affected by local and regional factors plus historical ones (Johnson et al., 2016).  
However, they are frequently characterized as communities mostly influenced by local  
factors (*i.e.* river water regime, geomorphology, sediment texture) and with little  
influence of factors acting at broader scales such as macroclimate (Gasith & Resh,  
1999; Naiman et al., 2005). These features have led to the notion of riparian  
communities as azonal vegetation (Walter, 1985) and riparian habitats as biogeographic  
islands (Warner & Hendrix, 1984). In the Mediterranean region, riparian environments  
have more marked island character than in more humid regions due to the steep  
microclimatic contrast between the riparian environment and the surrounding up-lands  
(Dan Moore et al., 2005), showing clear floristic discrepancies (Sabo et al., 2005;  
Calleja et al., 2016). However, in very dry Mediterranean zones the prolonged water  
shortage linked to the summer drought promotes temporal or ephemeral water regimes  
that reduce the contrast between the local and regional climate and diminish the  
composition differences between riparian and up-land communities (Tabacchi et al.,  
1996; Salinas & Casas, 2007). The water shortage plays a key role on riparian species  
richness and composition as it acts as a stressor for hydrophilic species as well as a  
positive driver for xeric up-land species (Gasith & Resh, 1999; Sabo et al., 2005; Salinas  
& Casas, 2007). Thus, Mediterranean riparian habitats are complex systems where the  
impact of some local factors may counteract or favor the effect of other factors acting at  
broader scales (Bendix & Stella, 2013). Despite the general interest of riparian  
communities as study system and their relevant contribution to the richness of any  
territory (Sabo et al., 2005), few multi-factorial studies have focused on plant richness  
of riparian communities across spatial scales (Tabacchi et al., 1996; Sarr & Hibbs,

2007). This knowledge gap is even more pronounced in the Mediterranean context (Stella et al., 2013).

The aim of the present work is to understand the spatial variation in the local and regional richness of vascular plant species in riparian woody communities within the southern half of the Iberian Peninsula (Western Mediterranean). This is a diverse Mediterranean setting that encompasses different regional and local climates, water regimes, riverbed sizes, lithology, human perturbations, etc. Our specific aims are to reveal: 1) which are the key environmental drivers of the local and regional richness of vascular plant species of riparian woody communities under Mediterranean climates; and 2) to what extent top-down and bottom-up models provide valid frameworks to explain the observed richness patterns. Here, the top-down model assumes that the regional species pool limits local species richness (H1) while the bottom-up model assumes that the local richness builds-up the regional species pool (H2). In both models regional species richness is derived from the local studied sites of a region and is considered as a fair proxy of the regional species pool (Cornell & Harrison, 2014).

To address these questions, we proposed and evaluated two *a priori* models based on a comprehensive framework built on the concepts of species pool and environmental filtering (Fig. 1, Appendix S1). This model reflects our working hypotheses about the putative factors (climate, lithology, hydric regime, channel width, riverbank textures, conservation status, etc.) influencing richness at two scales, local and regional, in the basis of our prior knowledge on ecological requirements, structure, dynamics, and composition of riparian woody communities (Lara et al., 2007; Garilletei et al., 2012) and other previous works (e.g. Lite et al., 2005; Renöfält et al., 2005; Salinas & Casas, 2007; Biswas & Mallik 2010).

## Methods

## Study area

The study encompasses the southern half of Spain (southern Iberian Peninsula), a vast area of more than 250,000 km<sup>2</sup> (Fig. 2) and rough topography with remarkable altitudinal differences (sometimes 2000 m in less than 30 kilometers). The climate is Mediterranean but with nuances (oceanic, continental, montane) depending on the distance to the coast and altitude. Hence, there are notable differences in temperatures, rainfall and summer water deficit (from 1 up to 7 months).

Water courses exhibit different sizes and geomorphologies: from narrow gullies to valleys over 1 km width, channel widths varying from 0.5 to 50 m wide, that can have or not sediments (rocks, gravel, sand, clays or mixed). Lithology and the resulting soil pH vary from acid to calcareous, including salty ones. The hydric regime is also very heterogeneous with a large proportion of temporary or even ephemeral rivers and streams. Extreme floodings can be common in natural rivers but they are much reduced in big and continuous rivers by the presence of dams and levees (Sabater et al., 2006).

The riparian vegetation in the Mediterranean area thrives not only on the banks but also in the fluvial bed, especially in discontinuous or ephemeral water courses (Appendix S7; Salinas & Casas, 2007; Garilletei et al., 2012). The riparian vegetation comprises tree and shrub communities and hosts an extraordinary array of woody and herbaceous plants belonging to several floristic elements (Mediterranean, Temperate, Irano-Turanian, Cosmopolitan). This is a consequence of the environmental heterogeneity and biogeographic position of Spain, in the interface between European and African continents (Garilletei et al., 2012). The conservation status of riparian systems is uneven, becoming very poor outside the mountainous areas because of multiple human pressures, especially agrarian ones (Sabater et al., 2006; Garilletei et al., 2012). In general, continuity and richness of riparian communities decreases in parallel



to land use intensity which, in turn, is inversely related to topographic irregularity (Corbacho et al., 2003). However, there are still areas that support well conserved riparian communities (Garilletei et al., 2012).

### **Data collection**

We sampled 689 with riparian woody communities in the western Mediterranean watercourses (Fig. 1) dominated by: *Alnus glutinosa*, *Salix* sp. pl., *Fraxinus angustifolia*, *Populus alba*, *Betula* sp. pl., *Nerium oleander*, *Flueggea tinctoria*, *Tamarix* sp. pl., *Erica* sp. pl., *Prunus lusitanica*, *Vitex agnus-castus*, *Rhododendron ponticum*, *Ulmus minor*, and *Ziziphus lotus* (Garilletei et al., 2012). We selected representative stands with diverse conservation status but discarding sites where the native tree and shrubs layers had been removed by humans or recently (< 5 years) affected by extreme floods. We conducted fieldwork campaigns in three consecutive years (2005 – 2007) from spring to early summer adjusting the sampling date to the local flowering season (April – July). All the studied sites were embedded in landscape mosaics with predominance of active and abandoned forest and agrarian farms plus natural upland forests and shrublands. Urban systems were discarded.

The studied communities were growing at riverbanks or on emerged riverbeds of natural channels, with diverse hydric regimes (continuous or temporal) from sea level up to 1900 m a.s.l. In each locality, we identified all terrestrial and epiphytic vascular plants until the number of species stabilized, within an area of approximately 500 m<sup>2</sup>.

### **Scales and variables**

We gathered a series of biotic and abiotic variables at two spatial scales: local and regional (Table 1). The local scale was defined as the riparian reach where the plant vegetation was sampled, usually 50 m along the watercourse. To delimit the regions, we

combined hydrological basin boundaries and a biogeographic sectorization based on riparian flora and communities (Garilleti et al., 2012). We first used the function *r.watershed* (GRASS version 7.0) in QGIS that yields a polygon map depicting drainage basins. Basins were used to define regions because they function as physical and biological entities (Naiman et al., 2005). We remodeled the basins with the biogeographic sectorization (Garilleti et al., 2012) and thus we obtained 31 regions (Fig. 2). The area of the regions varied from 834.64 to 23031.88 km<sup>2</sup>, therefore the local/regional area ratio is far from the threshold (> 0.01) established to avoid artifact correlations between local and regional richness (Hillebrand & Blenckner, 2002).

At the local scale, richness was estimated as the number of species observed in each relevée. We initially gathered 13 explanatory variables but after a preliminary analysis of the correlation between them, we retained the seven variables that had Spearman correlation values below 0.8 (Table 1). In order to ease analysis and interpretation, variables were grouped in broader categories. Local abiotic habitat grouped lithology of the sampled area, textures of soils and riverbed width. The remaining variables were the continuity of the hydric regime, local vegetation structure (shrub or forest), community width and local conservation status. Additionally, we considered four climatic variables from WorldClim database (Hijmans et al., 2005) that showed a Spearman correlation among them below 0.8 grouped as local climate: annual mean temperature, mean temperature of the warmest quarter, mean annual precipitation, and mean precipitation of the warmest quarter.

Regional richness was calculated as the sum of all species observed in the localities within each region (Fig. 2), thus avoiding the overestimation of the regional species richness caused by the inclusion of species from other habitats (Hillebrand & Blenckner, 2002; Zobel, 2016; Harrison & Cornell, 2008). In order to evaluate the

influence of the estimation biases in the size of the regional species richness due to sampling intensity differences, we estimated maximum expected richness with Chao (Gotelli & Colwell, 2001) and bootstrap estimators by using the vegan package (Oksanen et al., 2015). The actual richness values were always above 80% of the estimated richness, so we performed the analysis with the recorded species richness. In addition, for each region, we used seven explanatory variables (Table 1): regional lithology, regional hydric regime, regional conservation status, and the variance of the same four climatic variables already considered at local scale and enclosed within the composite variable regional climate. At a regional scale the climatic range of each basin was calculated using the climatic mean data from the 689 studied sites plus a pull of 5376 additional ones provided by Spanish Hydrological Authorities, we calculated the variance of all the climatic stations within each basin as a measure of heterogeneity in climatic conditions.

### **Structural equation modeling**

We used dummy (0/1) variables for categorical variables and we centered and scaled the quantitative ones according to Grace and Bollen (2008). We used the method described in Diniz-Filho et al. (2008) in order to avoid bias due to spatial autocorrelation in the residuals assuming that including spatial dependence parameters makes the models more resistant to misspecification due to missing spatially structured variables. To do so, we gathered the first 30 spatial filters calculated from a short-distance connectivity matrix per each scale. Based on these spatial filters, we built several eigenvectors and selected the minimum number per each scale that maximized the explained spatial autocorrelation: 3 for the regional scale and 1 for the local one (Diniz-Filho *et al.*, 2008). The eigenvectors were included in the model as explanatory variables of richness at local and regional scales. To calculate the eigenvectors, we used

four packages of R 3.2.1. (R Development Core Team, 2014): *vegan* (Oksanen et al., 2015), *fossil* (Vavrek, 2012), *letsR* (Vilela & Villalobos, 2015), and *ape* (Paradis et al., 2004) (Supplementary Material 8).

We built two a priori models. First a top-down model (see Fig. 1, H1) and then an alternative bottom-up model in which the relationship between local and regional richness was reversed (Fig 1, H2). We evaluated the relationships between the local and regional richness with the selected biotic and abiotic predictors using structural equation modeling (SEM, Grace, 2006) in AMOS (SPSS Inc., Chicago, IL, USA). To facilitate the interpretation, we grouped the variables in broader categories (i.e., the four local scale climate variables were grouped in a broader variable called local climate, Fig. 1, Table 1). We did this by using composite variables. Composite variables are conceptual variables created to represent unmeasured concepts, they are calculated by creating an empty variable and bringing together the paths of the component variables to the composite. Then a path is created between the composite and the response, this path coefficient provides a summary of the joint effect of the component variables on the response (Grace, 2006). The overall fit of the model was tested with the  $\chi^2$  goodness-of-fit test. As our *a priori* model did not accurately fit the data, we added paths sequentially until we obtained a satisfactory fit (Grace, 2006). We also removed some variables with negligible effect on local and regional species richness: conservation status at regional and local scales; local hydric regime and community width at local scale (Fig. 3).

## Results

We recorded from 5 to 119 species per relevée and a total of 1964 species in the whole area. Regional species richness varied between 91 and 736 species. Overall, the top-down model fitted the data well ( $\chi^2 = 49.93$ , p-val = 0.16), explaining almost a third

of the variance of richness at the local scale ( $R^2 = 0.27$ , Fig. 3) and half the variance of the regional richness ( $R^2 = 0.49$ , Fig. 3). The bottom-up (H2) model had a very similar overall fit ( $\chi^2 = 49.64$ , p-val = 0.17), also explaining a comparable proportion of variance (local richness  $R^2 = 0.25$ ; regional richness  $R^2 = 0.52$ ). Most of the paths of the environmental variables were similar in the two models; for simplicity results and discussion of their effects are based in the top-down model. The paths that have substantial changes are described in the results below and a full report of both models can be found in Supplementary Material S2 to S6 (top-down model) and S9 to S13 (bottom-up model).

In the top-down model, local richness was positively and directly affected by regional richness (0.20, Fig. 3). Conversely, in the bottom-up model local richness positively and directly affected the regional richness (0.14, Supplementary Material 13). Besides, in the bottom-up model the relationship between climate and local richness was strongly significant and with a significant effect (0.25), being absent in the top-down model. The relationship between local vegetation and local richness, which was small in the top-down model (0.09), was also absent in the bottom-up one.

### **Environmental factors influencing richness at local scale**

Local richness was significantly and directly related to local abiotic habitat, local climate, and local vegetation structure, and with hydric regime at regional scale (Fig. 3). The local abiotic habitat had a significant positive effect on local richness (0.34). Carbonated and mixed soils (lithology) and gravel and sandy soils (texture) increased the local richness while saline and clay soils showed lower richness with respect to that of riparian communities growing on acid or/and rocky ones (Table 2, Appendix S5). The local climate also played an important role but with a negative effect (-0.30, Fig. 3). Within local climate, the mean temperature of the warmest quarter had a negative effect

(-0.48) on local richness while the annual mean temperature (0.44) and, in much lesser extent, the annual precipitation (0.11), showed a positive influence (Table 2). Local vegetation also showed a small, positive effect (0.09) in the top-down model but a non-significant effect in the bottom-up one showing that shrub communities were – if at all – only slightly richer than the tree-dominated ones (Fig. 3, Table 2, Appendix S5). In contrast, several local-scale variables included in the *a priori* model (Fig. 1) had non-significant effects on local richness: community width, local hydric regime, riverbed width and local conservation status.

Local richness was also affected by the regional hydric regime. This implies that a larger percentage of continuous rivers in the region increases local richness (Fig. 3, Table 2, Appendix S5). In the bottom-up model, there was also a direct effect of the regional climate on the local richness (0.25, Appendix 13) that did not exist in the top-down model.

#### **Environmental factors influencing richness at regional scale**

Regional richness was directly influenced by three variable groups measured at the regional scale: climate, regional lithology, and hydric regime. Unexpectedly, the regional richness also directly depended on three factors of the local scale: climate, abiotic habitat and vegetation structure (Fig. 3).

Regional climate showed a significant effect on regional richness (0.71). Within it, the variance of the annual mean temperature stood out for its strong positive effect (0.90, Table 2). The variances of the annual precipitation and precipitation of the warmest quarter also showed a positive effect on regional richness, opposed to the negative effect of the variance of the mean temperature of the warmest quarter (Table 2).

The regional lithology showed a significant but negative influence on regional richness (-0.37) (Fig. 3). Regions dominated by carbonated lithology hosted relatively poor communities. Conversely, the regional hydric regime showed a positive effect on regional species richness. Thus, a higher proportion of rivers with continuous hydric regime was related to richer communities at the regional scale.

Three local scale variables showed an unforeseen direct influence on regional richness. Local climate showed a positive effect (0.34, Fig. 3): higher local annual temperatures and summer precipitations correlated with larger regional richness (Table 2). Conversely, local abiotic habitat and local vegetation structure showed a negative effect on regional richness (-0.18 and -0.17 respectively, Fig. 3, Appendix S5): saline soils and most of the textures showed lower richness than acid and rocky soils. In turn, shrubby communities contributed less than those dominated by trees to the regional richness (Table 2, Appendix S5).

The model also supported indirect relations between local and regional richness with local and regional variables. Local and regional climates and the regional lithology showed links with regional hydric regime (-0.97, -0.49 and 0.61 respectively, Fig. 3). Likewise, the regional hydric regime, local climate plus local abiotic habitat (-0.28, 0.28 and 0.34, respectively, Fig. 3) affected local vegetation, which subsequently also had effects on richness at both regional and local scales.

## **Discussion**

The model (Fig. 3) provides a useful framework to understand the variability of plant richness in Mediterranean riparian forests at local and regional scales. Our results showed that regional richness depends strongly on the variability of the regional abiotic factors (mostly climate but also hydric regime and abiotic habitat) while local richness depended mainly on local abiotic habitat and local climate, as it has been reported in

previous works on non riparian (e.g. Zellweger et al., 2016; Jimenez-Alfaro et al., 2018) and riparian habitats (e.g. Renöfält et al., 2005), including the riparian communities of several semi-arid regions (Tabacchi et al., 1996). We found that both our initial hypotheses, (H1, top-down relationship between richness at regional and local scale and H2, bottom-up relationship) are compatible with the empirical data. In fact, both models show very similar overall fit values and therefore we are not able to discern between the two. The inability to discriminate between the two might be just a statistical limitation of our data. However, it might also be indicating that both processes are operating simultaneously. If this is true, it implies there is a positive feedback loop in which, provided enough time, regionally rich floras tend to enhance richer local floras and at the same time locally rich floras build-up larger regional pools. Although our dataset does not allow discerning between the two process, time sequence data can provide insight on the underlying mechanism. This is so because as a direct consequence of the positive feedback loop, rich locations should show an increase in their species numbers with time, an increase that will be significantly larger than the trends observed in less rich locations.

Even if we cannot discriminate which is the most adequate model, our results strongly suggest the existence of a regional control over local richness in the studied riparian communities. In the one hand, the top-down link (H1) has a slightly larger effect than the bottom-up link (H2). In the other, there is always a regional effect on the local richness that is independent of the framework employed. In the top-down model, regional abiotic conditions indirectly influence local richness via regional richness, as in Jiménez-Alfaro et al. (2018). In the bottom-up model, the effect of the regional factors occurs directly on the local richness. All in all, we have shown that local factors alone are not enough to explain the local richness patterns since regional factors also exert a



significant effect on local richness. A pattern also shown in a wide range of regions and ecosystems (e.g. Cornell & Lawton, 1992; Hillebrand & Blenckner, 2002; Kristiansen et al., 2011), including riparian communities from temperate zones (e.g. Renöfält et al., 2005).

In the Mediterranean riparian communities analyzed here, regional climate shows the largest indirect effect on local richness through regional richness (Fig. 3). This implies that local communities in the regions (basins) with large climate heterogeneity will be relatively richer compared to localities with similar local conditions in less heterogeneous regions. This result contrasts with the common view of riparian communities as a type of azonal vegetation *i.e.* relatively independent of the regional processes (Walter, 1985). However, it is consistent with empirical evidences suggesting that both species composition and richness of riparian forests depend significantly on a wide range of factors acting beyond the local level (Tabacchi et al., 1996; Sarr & Hibbs, 2007). The current results have implications that go beyond the context of the riparian communities. When studying diversity patterns, we need models including bidirectional relationships across scales or tests which allow discriminating which relationship (bottom-up or top-down) is dominant. Ignoring this fact can lead to biased conclusions, and the undermining of important processes.

Despite the fact that we successfully explained up to 30% of the variability in local richness and 50% of the variability in regional richness, there is still a high proportion of unexplained variability left. The incorporation of new or more accurate predictors such as water and flow regimes (Lite et al., 2005; Renöfält et al., 2005; Rolls et al., 2018), explicit past and current connectivity (Johnson et al., 2016), plus historical factors and their lag effects on plant richness and its contemporary drivers (Ricklefs, 1987; Lindborg & Eriksson 2004) will likely improve the fit of the model. However,

note that if random processes linked to the population dynamics of the species are responsible for the unexplained variability (Chase & Myers, 2011) improving the description of the environment will not entail lower proportions of unexplained variability.

#### **Richness at local scale**

The few previous works analyzing the impact of climatic gradients on riparian species richness have used altitude as a surrogate of climate (Tabacchi et al., 1996; Salinas & Casas, 2007) so that the individual effects of precipitation and temperatures on Mediterranean riparian communities have seldom been evaluated. Our model shows that local climate exerts an overall negative effect on local species richness of Mediterranean riparian communities (Fig. 3). More specifically, our model reveals that a proportion of the species colonizing riverbanks avoid localities with low temperatures (frost, prolonged cold winters) as upland flora does (Benayas et al., 2002). Likewise, high summer temperatures have a detrimental influence on species richness since many deciduous broadleaved and mesic species demand not only wet soils but also humid air (Lara et al. 2007; Salinas & Casas, 2007; Stella & Battles, 2010; Garilleti et al., 2012). On the contrary, precipitation exerts a positive effect on local richness as it can partially mitigate the water stress linked to very warm and dry Mediterranean summers (Salinas & Casas, 2007). Basic and well-drained soils (gravel and sand textures) show relatively high richness in Mediterranean environments, a pattern consistent with other studies in riparian and upland vegetation (Nilsson et al., 1994; Gould & Walker 1997; Hérault & Honnay, 2005; Chytrý et al., 2003; Bendix & Stella, 2013). Many species are limited by nutrient availability in too acid or salty soils (Gould & Walker 1997; Dubuis et al., 2013). Likewise, the most hygrophilous species are constrained by the poor infiltration and minimum drainage of clay soils and/or rocky soils (Bendix & Stella 2013).

The model shows that the structure of the riparian communities (local vegetation in Fig. 3) also influences the species richness at local scale, yet in an unexpected way. In European cold temperate forests, a greater vertical complexity of tree-dominated communities is linked to a wider range of life-forms that enhances species richness (Zellweger et al., 2016). Our opposite result must be analyzed within the Mediterranean context. Riparian shrub-dominated communities can host as many life-forms as forested communities (Garilleti et al., 2012), and provide an environment of heterogeneous luminosity that minimizes the stressful combination of dense shady environments (*i.e.* broad-leaved tree canopies) plus the typical Mediterranean drought (Valladares & Pearcy, 2002; Pulido et al., 2008).

Unexpectedly, riparian community width and channel width fail as surrogates of environmental heterogeneity that triggers species richness, unlike in non Mediterranean regions (Lite et al., 2005; Naiman et al., 2005; Hupp & Rinaldi, 2007; Kuglerová et al., 2015). In Mediterranean temporary watercourses, the riparian vegetation grows on riverbeds which implies the lack of environmental gradients (eg. soil moisture) along the horizontal axis across the riparian habitat regardless of the size of the river channel and the amplitude of the riparian community (Salinas & Casas, 2007; Garilleti et al., 2012). Likewise, continuous rivers with wide channels (*e.g.* Genil, Guadalquivir or Segura rivers) usually entail detrimental environmental characteristics for plant diversity: clay and silt or salty riverbanks plus hot and dry climates (Salinas et al., 2000; Salinas & Casas, 2007). All these features (alone or combined) preclude the described positive input of the arrival of different species' propagules at wide channels from its tributaries (Kuglerová et al., 2015).

The negligible effect of the local hydric regime can be partially explained by the ability of a number of phreatophytes species to cope with temporal water shortages

within semiarid regions (Busch et al., 1992). Additionally, riparian communities of temporary watercourses show a composition shift whereby the loss of riparian specialist species is compensated by others more xerophytic, usually up-land plants (Tabacchi et al., 1996; Renöfält et al., 2005; Salinas & Casas, 2007).

Finally, conservation status is also unrelated to local species richness. Disturbed riparian communities may compensate the partial loss of the original inhabitants by acting as an ecological sink for opportunistic species (Hérault & Honnay, 2005) that colonize wet riparian habitats to withstand the critical Mediterranean summer drought (Tabacchi et al., 1996; Salinas & Casas, 2007; Garilleti et al., 2012).

### **Richness at regional scale**

Our study provides the first empirical evidence of the key role of climatic heterogeneity on the regional species pool of Mediterranean riparian communities. Although it was known that these factors were crucial at the local scale, we provide evidence of their relevance also at the regional scale highlighting the extent to which species richness of riparian communities in Mediterranean environments is constrained by regional factors. Besides, our model shows for the first time the key role of regional hydric regime for the regional richness of the Mediterranean riparian communities. A greater proportion of riparian reaches with continuous river flow favors a greater regional richness linked to the concomitant connectivity among distant localities and the increase of suitable habitats for a number of riparian (hydric and mesic) species (Johansson et al., 1996; Naiman et al., 2005; Rolls et al., 2018). In contrast, river basins dominated by temporal or ephemeral watercourses lack many hydrophilic species (Tabacchi et al., 1996; Salinas & Casas, 2007; Rolls et al., 2018).

Related to the regional abiotic habitat, we confirmed greater regional species richness in regions with heterogeneous or acid bedrocks as observed in previous studies

(e.g. Pausas et al., 2003). Additionally, the relative abundance of heterogeneous or acid soils in the Mediterranean regions may favor species richness since many hygrophilous taxa, like ferns, can thrive in dry areas but only on acid rocks (Moreno Saiz & Lobo, 2008). Conversely, the prevalence of basic rocks (limestones, clay, marls, gypsum) in Mediterranean regions with summer drought may entail a higher water stress that inhibits high water-requirement species (Salinas et al., 2000; Stella et al., 2013 and references therein).

Our results do not agree with antagonistic relationship between perturbation level and species richness as suggested by Gamez-Virues *et al.* (2015). The compensation phenomena suggested at the local scale might play the same role at the regional scale since the effect of perturbations on species richness shows no spatial scale dependence (Mayor et al., 2015). However, the effects of past perturbations including fragmentation on current plant richness have not been considered (Lindborg & Eriksson, 2004).

#### **Drivers across scales**

We have found that species richness patterns depend on a complex network of interactions among factors across scales. In our a priori model, the only relationship proposed across scales was between the regional and the local richness. This relationship is confirmed but new relationships across scales have arisen. From the local to the regional scale, local climate and local abiotic habitat influence the regional hydric regime. Likewise, local climate, local abiotic habitat plus local vegetation structure affect the regional richness. The three latest ones might be crucial when studying diversity relationships across scales, yet they are often excluded from general models (e.g. Jiménez-Alfaro et al., 2018). These unexpected but significant bottom-up relationships imply that models including only relationships among factors at the same scale and top-down frameworks may draw inaccurate results (Huston, 1999).

The model reveals positive but also negative bottom-up relationships. Firstly, warm and wet local climates seem to increase the regional richness. This local climatic combination is uncommon in the Iberian Peninsula Mediterranean context but favors an enrichment of the regional species pool as happens in the SW corner of Spain and nearby mountainous areas (Rodríguez-Sánchez et al., 2008). Secondly, the dominance at local scale of saline soils or any of the sediment texture types decreases the regional species richness due to their stressful effect (e.g. saline soils) or because of reduction in environmental heterogeneity (Pausas et al., 2003; Bendix & Stella, 2013). This latest relationship can be understood through a metacommunity perspective since a low environmental heterogeneity leads to a reduced regional richness (see Harrison & Cornell 2008). However, the presence of environmental discrepancies among local sites within the same region (i.e. these warm and wet local climates embedded into the dry, arid Mediterranean region) promotes the coexistence of locally incompatible species and therefore, increases the regional species richness (Harrison & Cornell, 2008).

The model also incorporates some top-down relationships. Even if the model reflects a regional control over local processes, this control can be channeled through the regional richness (see the top-down model, H1) or through other regional variables (both H1 and H2). Thus, the regional climate seems to be a significant driver of local richness operating both directly (H2, bottom-up model) or indirectly (H1, top-down model) through the regional richness (Harrison & Cornell, 2008; Medina et al., 2014) or through the regional hydric regime (H1 and H2), especially in semi-arid regions (Tabacchi et al., 1996). Likewise, the regional hydric regime directly increases local richness but also exerts an indirect influence through the local vegetation structure. These evidences point out the challenge of integrating the effects of the regional factors and those of the factors operating simultaneously at different scales and also across

scales (Harrison & Cornell, 2008; Medina et al., 2014; Rolls et al., 2018), which will let us detect both direct and indirect effects, which may be playing an essential role in the ecosystem functioning.

In order to disentangle the complex relationships of communities and even ecosystems, there has been an important effort to develop general, theoretical frameworks that support the inclusion of different scales (Cornell & Lawton, 1992; Hillebrand & Blenckner, 2002; Zobel, 2016; Rolls et al., 2018). However, we still lack empirical studies to test these frameworks and therefore evaluate its usefulness to describe communities or ecosystems (Harrison & Cornell, 2008). The results of the top-down model (H1) provides empirical evidence of the generality of the theoretical frameworks, which assume top-down relationships and/or relationships among environmental variables and richness occurring at the same scale (Whittaker et al., 2001). However, our dataset is also compatible with a bottom-up framework (H2), suggesting that both bottom-up and top-down processes may be operating simultaneously and stressing the importance of these often undermined local scale processes and their influence on species richness at the regional scale and across scales. These bottom-up relationships should not be underestimated when attempting to explain richness patterns or the spatial scaling of biodiversity. Our study joins an increasing body of knowledge where explicitly addressing processes acting at small scales and across scales effects are gaining importance (Medina et al., 2018), nuancing the general top-down models predominantly used in ecological studies (Ricklefs, 1987; Whittaker et al., 2001).

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#### **Author contributions (optional):**

M.L., J.A.C. and N.G.M. conceived the research idea, J.A.C., F.L. and R.G. collected field data, M.L. and N.G.M. performed statistical analyses, M.L., J.A.C. and N.G.M. wrote the paper; all authors discussed and commented on the manuscript.

#### **Data accessibility:**

The original species richness data are available upon official request to the public institution that supported field works, CEDEX (<http://vegetacionderibera.cedex.es/>).

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## **Supporting information to the paper**

**Appendix S1.** Description of the a priori model represented in Figure 1.

**Appendix S2.** Model Fit Summary.

**Appendix S3.** Correlation between two variables in the model and the respective estimated value.

**Appendix S4.** Squared multiple correlations ( $R^2$ ) of every response variable of the model.

**Appendix S5.** Regression weights of the variables without composite variables.

**Appendix S6.** Regression weights with composites variables.

**Appendix S7.** Illustrations of studied riparian plant communities on continuous and temporary rivers and ephemeral streams.

**Appendix S8.** R code employed to calculate the eigenvectors.

**Appendix S9.** Model Fit Summary.

**Appendix S10.** Correlation between two variables in the model and the respective estimated value.

**Appendix S11.** Squared multiple correlations ( $R^2$ ) of every response variable of the model.

**Appendix S12.** Regression weights of the variables without composite variables.

**Appendix S13.** Regression weights with composites variables.



814 TABLE 1: Variables included in the *a priori* model, subsequent analysis, and final  
815 model. Composite and simple variables included in the final model are in bold.

Scale	Composite variable	Simple variable	Abbreviation	Description
LOCAL	<b>Local Abiotic Habitat</b>	<b>Local Lithology</b>	<b>Lit</b>	Estimated in the field considering the first 1 m depth of exposed riverbank (first terrace level) or riverbeds (in the case of discontinuous or ephemeral watercourses). Four categories: 1: $\geq 75\%$ of the sampled area consist of siliceous rocks or sediments; 2: $\geq 75\%$ carbonated; 3: two or more lithology types surpass 25% of the sampled area; 4: $\geq 75\%$ saline rocks or sediment
				Estimated in the field Four categories: 1: $\geq 75\%$ of the sampled area consist of rocks and/or blocks; 2: $\geq 75\%$ gravel and/or sands; 3: $\geq 75\%$ clays, 4: two or more texture types surpass 25% of the sampled area
		Local Riverbed Width	Rbed Width	Measured in the field (m), river channel in bankfull

			Binary variable, measured in the field.
	Local Hydric Regime	Local Hydric Regime	Continuous or discontinuous river flow during the spring-summer season (April-August)
	<b>Local Vegetation Structure</b>	Local Vegetation	Estimated in the field. 2 categories: 1: tree dominated community; 2: shrub community formed by multi-stem woody species growing below 4 m height
	Community Width	Community Width	Measured in the field, perpendicular to the river channel (m) comprising the area covered by the riparian community growing on one of the two riverbanks and/or the riverbed
	Local Conservation Status	Local Conservation Status	Measured in the field. 5 categories: (from high to low conservation level): 5: continuous forests (c.f.), no anthropogenic perturbations; 4: c.f. but partially affected by slight human perturbations; 3: c.f. with slight anthropogenic perturbation affecting all the studied area; 2: forest with gaps due to anthropogenic perturbations; 1: fragmented forest due to anthropogenic perturbations
<b>Local Climate</b>	<b>Annual Mean Temperature</b>	AMT	Annual mean temperature

REGIONAL	<b>Mean Temperature of the Warmest Quarter</b>	MeanTWarmQ	Mean temperature of the warmest quarter
	<b>Annual Precipitation</b>	AP	Annual precipitation registered
	<b>Precipitation of the Warmest Quarter</b>	PWarmQ	Precipitation of the warmest quarter
	<b>Regional Lithology</b>	Regional Lithology	1: $\geq 75\%$ of sampled communities (within each region) grow on riverbeds dominated by acid rocks ( $\text{pH} < 7$ ); 2: basic and acid rocks occur separately in $> 25\%$ of sampled communities (within each region); 3: $\geq 75\%$ of sampled communities (within each region) grow on riverbeds dominated by basic rocks ( $\text{pH} > 7$ )
	<b>Regional Hydric Regime</b>	Regional Hydric Regime	% of river sectors (associated to the sampled riparian communities) with a continuous hydric regime in each region
	<b>Regional Conservation Status</b>	Regional Conservation Status	Mean conservation value of all studied communities within each region

<b>Regional Climate</b>	<b>Annual Mean</b>		
	<b>Temperature</b>	AMT Var	Variance of the annual mean temperature per region
	<b>Variance</b>		
	<b>Variance of</b>		
	<b>the Mean</b>		
	<b>Temperature</b>	MeanTWarm	Variance of the mean temperature of the
	<b>of the</b>	Q Var	warmest quarter per region
	<b>Warmest</b>		
	<b>Quarter</b>		
	<b>Variance of</b>		
	<b>the Annual</b>	AP Var	Variance of the annual precipitation per region
	<b>Precipitation</b>		
	<b>Variance of</b>		
	<b>the</b>		
	<b>Precipitation</b>		
	<b>of the</b>	PWarmQ Var	Variance of the warmest quarter per region
	<b>Warmest</b>		
	<b>Quarter</b>		

TABLE 2: Correlation scores of variables forming composite and their influence on the local and regional richness of the top-down model. The Standardized Estimate shows the correlation score of the exogenous variable with the endogenous variable ( $R^2$ ). Asterisks show the significance of the relationship (\*\*>0.01 - <0.05; \* >0.05 - <0.1). The effects of the composite variables on the local and regional richness are shown in figure 3.

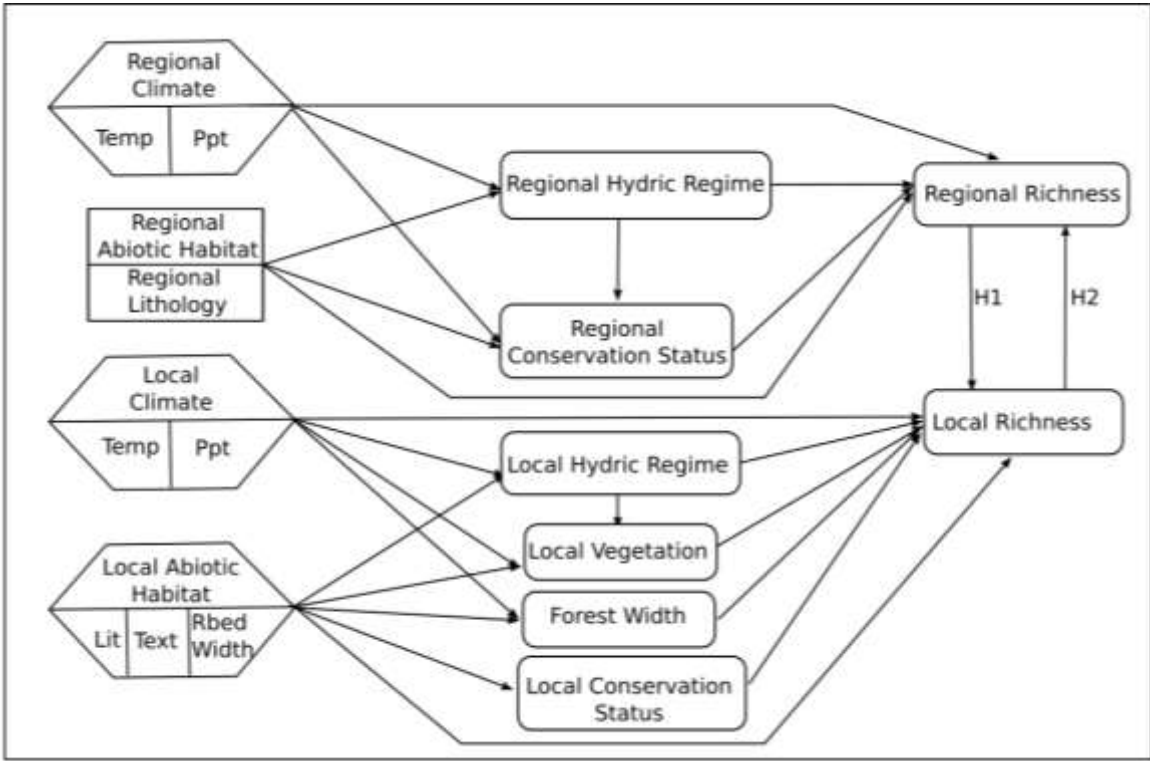
Composite variable	Exogenous variable	Endogenous Variable	Standardized Estimate	p
Local Climate	AMT	Local Richness	0.44	**
		Regional Richness	0.30	***
	MeanTWarmQ	Local Richness	-0.48	**
	AP	Local Richness	0.11	**
		Regional Richness	-0.05	
	PWarmQ	Local Richness	0.08	
		Regional Richness	0.37	***
	Lithology: carbonated	Local Richness	0.27	***
		Regional Richness	0.09	
	Lithology: mixed	Local Richness	0.12	***
		Regional Richness	-0.001	
	Lithology: saline	Local Richness	-0.03	
		Regional Richness	0.06	*
Abiotic Habitat	Texture: gravel/sands	Local Richness	0.14	***
		Regional Richness	-0.15	***
	Texture: clays	Local Richness	-0.14	***

Regional Climate	Texture: mixed	Regional Richness	-0.18	***
		Local Richness	-0.02	
		Regional Richness	-0.12	***
	AMT Var	Regional Richness	0.90	***
	MeanTWarmQ Var	Local Richness	0.02	
		Regional Richness	-0.44	***
	AP Var	Local Richness	0.19	***
		Regional Richness	0.46	***
	PWarmQ Var	Local Richness	-0.10	
		Regional Richness	0.31	***

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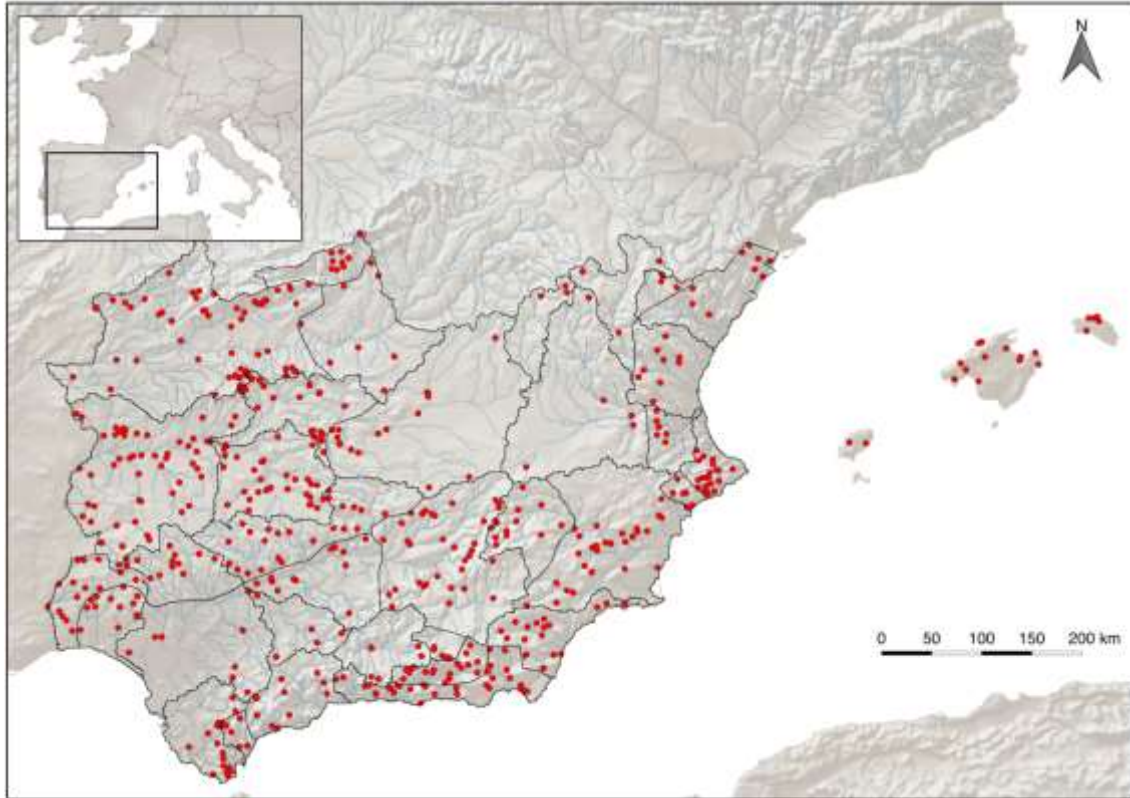
FIGURE 1. *A priori* model containing all target variables and relations. Composite variables are represented with hexagons and include the simple variables in the lower part. The single simple variables are shown within quadrates. Arrows indicate the direction of influence between variables. All these influences are set within one scale (either regional or local) except the relationships between regional and local richness. H1 refers to a top-down framework, whereas H2 reflects a bottom-up one. Labels Temp and Ppt refer to climatic variables included at both scales (see Table 2).



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836 FIGURE 2. The study area, located in the southern half of Spain. Regions are depicted by

837 the black lines. Red points correspond to the 689 sampled sites.



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FIGURE 3. Path diagram depicting all significant ( $p < 0.1$ ) paths among variables at Regional and Local scales in the top-down model. Yellow boxes contain the response variables of interest. Hexagon-shaped variables show composite variables, with the name of the composite in the upper part and the simple variables included in the lower part. Numbers above the boxes refer to the amount of explained variance ( $R^2$ ) of the variable. Blue paths indicate positive relationships and red paths indicate negative ones. The numbers in the paths are the standardized path coefficients and arrow thickness is proportional to coefficient size. Asterisks show the significance of the relationships (\*\* $< 0.01$ ; \* $> 0.01 - < 0.05$ ; \* $> 0.05 - < 0.1$ ). Labels Temp and Ppt refer to climatic variables included at both scales (see Table 2).

