

# Impacts of environmental filters on functional redundancy in riparian vegetation

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## Summary

1. Understanding and predicting ecosystem responses to multiple environmental pressures is a long-standing interest in ecology and environmental management. However, few studies have examined how the functional features of freshwater biological communities vary along multiple gradients of environmental stress. Furthermore, modelling these functional features for a whole river network constitutes a strong potential basis to improve ecosystem management.

2. We explored how functional redundancy of biological communities (FR, a functional feature related to the stability, resistance and resilience of ecosystems) responds to single and multiple environmental filters. We compared these responses with those of functional richness, evenness and divergence. We used riparian vegetation of a Mediterranean basin, and three of the main environmental filters affecting freshwater communities in such regions, that is drought, flow regulation and agricultural intensity, thus considering the potential effect of natural environmental variability. We also assessed the predictability of FR and estimated it for the entire river network.

3. We found that all functional measures decreased with increasing environmental filter intensity. However, FR was more sensitive to single and multiple environmental filters compared to other functional measures. The best-fitting model explained 59% of the FR variability and included agriculture, drought and flow regulation and the pairwise interactions of agriculture with drought and flow regulation. The parameters of the FR models differed from null model expectations reflecting a non-random decline along stress gradients.

4. *Synthesis and applications.* We found non-random detrimental effects along environmental filters' gradients for riparian functional redundancy (the most sensitive functional index), meaning that increased stress could jeopardize stability, resistance and resilience of these systems. In general, agriculture caused the greatest impact on functional redundancy and functional diversity measures, being the most important stressor for riparian functionality in the study area. Temporary streams flowing through an agricultural, regulated basin had reduced values of functional redundancy, whereas the free-flowing medium-sized, perennial water courses flowing through unaltered sub-basins displayed higher values of functional redundancy and potentially greater stability against human impacts. All these findings along with the predicted basin-wide variation of functional redundancy can assist environmental managers in improving monitoring and ecosystem management.

**Key-words:** drought, flow regulation, functional diversity, functional traits, global change, habitat filtering, land use, Mediterranean rivers, multiple stressors, plant functional groups

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## Introduction

The world's ecosystems are experiencing an increase in human impacts causing an unprecedented biodiversity loss. These changes may alter the functioning of ecosystems and jeopardize the goods and services provided to humanity (Mouillot *et al.* 2013). Consequently, predicting ecosystem responses to multiple human pressures and interacting natural filters has become one of the most challenging tasks for scientists in order to guide conservation efforts and the management of ecological resources.

Traditionally, ecologists have focused on the response of the taxonomic community structure to different types of disturbances. Mitigation of the ecological consequences of environmental change, however, requires a deeper understanding of the relationship between biodiversity and ecosystem functioning (Cardinale *et al.* 2012). During the last decade, there has been a growing development of trait-based approaches to explore the effects of human activity on ecosystem functioning (Clapcott *et al.* 2010; Laliberté *et al.* 2010; Mouillot *et al.* 2013). Thus, as the combination of species traits determines the likelihood that a species can overcome environmental filters (Kraft, Godoy & Levine 2015), a non-random species sorting along environmental gradients is expected (Weiher *et al.* 2011; Mouillot *et al.* 2013).

Trait-based approaches allow the estimation of many components of functional diversity (FD), such as functional richness, evenness, divergence (Mason *et al.* 2005 for a review) and functional redundancy (FR, Fonseca & Ganade 2001; Rosenfeld 2002; Laliberté & Legendre 2010). Among them, FR is one of the most promising functional indices since it relates positively to stability, resistance and resilience of ecosystems (Hooper *et al.* 2005; Guillemot *et al.* 2011). It represents the number of species contributing similarly to an ecosystem function (Walker 1992; Lawton & Brown 1993). Although the notion of redundancy suggests that functionally similar species may compensate for the loss or failure of others, there is evidence that ecosystems need such redundancy to perform their functions efficiently and stably over time (Rosenfeld 2002; Guillemot *et al.* 2011; Biggs *et al.* 2012). In fact, a decrease in FR could be dramatic in non-redundant communities since the loss or replacement of one species would lead to loss of unique traits or functions (Hooper *et al.* 2005), increasing ecosystem vulnerability (Elmqvist *et al.* 2003).

We focus especially on the response of FR (but also considering FD components such as functional richness, evenness and divergence) to the main environmental filters in Mediterranean rivers using riparian trees and shrubs as model organisms. Riparian vegetation is a key component in the functioning of freshwater ecosystems (Hladyz *et al.* 2011) and provides essential functions, goods and services such as organic matter supply (Woodward *et al.* 2012), sediment retention (Tabacchi *et al.* 2000), and food and shelter for numerous animals (Sabo

& Power 2002). Riparian communities are taxonomically well studied and species trait information is usually available, which allows the estimation of functional features. These ecosystems have well-defined, multifunctional and species-rich vegetation that enables the detection of functional responses even to minor impacts (Nilsson & Svedmark 2002; Aguiar *et al.* 2009). However, very few studies have examined how the functional features of freshwater ecosystems vary along gradients of environmental filters (e.g. Clapcott *et al.* 2010; Matsuzaki, Sasaki & Akasaka 2013) and if they can act synergistically to affect ecosystem resilience and stability (Sasaki *et al.* 2015).

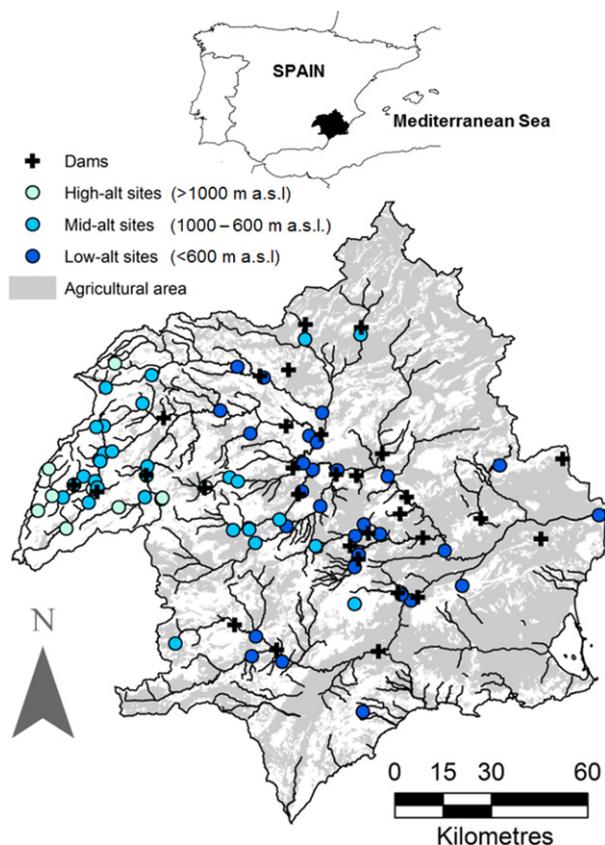
We used a data base of woody riparian plants from a semi-arid Mediterranean catchment (Segura River) to explore how the main environmental filters (i.e. predictable seasonal drought, agriculture and flow regulation), as well as their interactions, may impact the FR (and other FD indices) of riparian communities. As it is probable to find a relationship between environmental filters and functional measures simply as a consequence of an underlying taxonomic richness gradient (Villéger, Mason & Mouillot 2008), we also check for non-randomness of the empirical response patterns. Finally, we forecast the values of FR for the whole river network as a basis for ecosystem management. We expect that environmental filters would reduce the value of measures of functional features and that FR response should be predictable from large-scale geographical variables. Modelling FR in entire basins in response to environmental filters could assist decision-makers in setting goals and designing strategies for conservation and restoration of riparian ecosystems.

## Materials and methods

### STUDY AREA

The Segura River basin (SE Spain, Fig. 1) is highly heterogeneous (Bruno *et al.* 2014a), making it ideal to represent other areas with Mediterranean or semi-arid climates around the world. The climate ranges from sub-humid in the mountains in the north-west, where the rivers have relatively stable flows and high discharges, to semi-arid in the south-eastern lowlands where streams show more variable flows and lower mean discharge, featuring intermittent streams subject to variable summer drought (Belmar, Velasco & Martinez-Capel 2011).

The intense expansion of agricultural land (currently 52.1% of the entire basin; Fig. 1), especially the parts irrigated during the last 25 years, resulted in a reduction of natural and semi-natural areas, now representing 45.2% of the basin extent. As a consequence, there is an intense flow regulation, leading to widespread hydromorphological alterations. In contrast to the areas currently impacted by agriculture or hydrological alterations, this basin still holds an important number of rivers with a good ecological status, the study of which allows an assessment of human impacts on biological communities (Bruno *et al.* 2014b).



**Fig. 1.** Geographical location of the study area showing the 71 sampling sites classified by elevation (alt), the agricultural area and the main dams.

#### SAMPLING SITES

We selected 71 freshwater river reaches with varying land-use intensity, flow regulation and flow persistence accounting also for the natural environmental variability through elevation in the Segura basin (Fig. 1). Each locality was sampled once between 2010 and 2012 during late spring and summer along 500-m long reaches at both riversides, as this period is the most suitable for single surveys (Ferreira & Aguiar 2006). Within these 500-m long reaches, we noted the presence of woody riparian species, from the low-water margin up to the natural bankfull limit through ten transects, thus obtaining a list of species for each locality. We estimated the species abundance in a semi-quantitative way, that is three abundance classes according to species dominance (dominant, frequent and present).

#### FUNCTIONAL TRAITS

We used a wide set of biological traits in order to capture the entire range of functions and responses of the riparian plants recorded. We gathered a total of 30 continuous, semi-continuous and categorical biological effect and response traits to characterize the functional features of the species recorded (Lavorel & Garnier 2002; Cornelissen *et al.* 2003; Appendix S1, Supporting information). Functional effect traits are those biological features that directly influence a specific function of the ecosystem (e.g. primary productivity, nutrient cycling) while the response traits change according to the abiotic and biotic environment (e.g. resource availability,

climatic conditions and disturbance regime; Díaz & Cabido 2001). Species-specific mean trait values were compiled from 59 online trait data bases and scientific publications (Table S1.3 in Appendix S1). The final trait data set is found in Appendix S2.

#### FUNCTIONAL INDICES

We constructed matrices of taxon counts by site and traits by taxon to estimate the functional features of riparian communities. The estimation of the functional components is in continuous evolution so there are a variety of methodologies to estimate FR and a lack of consensus about them. Thus, FR was obtained for each sampling site from two different approaches: (i) considering FR as the average number of species per functional group (FG; Rosenfeld 2002; Laliberté *et al.* 2010) and (ii) as the difference between taxonomic (using the Gini-Simpson diversity index) and FD (using Rao's quadratic entropy) (Pillar *et al.* 2013; data comparing both methods are available in Appendix S3). To define FGs, we used the approach proposed by Díaz & Cabido (2001), which considers FGs as sets of plants that have traits with similar functional effects on the dominant ecosystem processes. Thus, the selection of FGs must represent different life strategies with a clear ecological significance (Naiman, Décamps & McClain 2005). First, species were classified into FGs by means of Ward's clustering method based on the effect-trait dissimilarity matrix, which was estimated using Gower dissimilarity index. Given that Ward's clustering method requires a Euclidean distance, we checked that the Gower effect-trait dissimilarity matrix met this criterion by ensuring that the eigenvectors of a double-centred matrix obtained through a principal component analysis were positive. We defined FGs with a suite of coadapted characteristics to environmental conditions of channel and riparian zones that guarantee a minimum number of six species to allow further statistical analyses. Secondly, after calculating both FR measures and running the models for them (see below), we focused on the most sensitive FR approach, which fulfilled models' assumptions and showed a non-random response to stress. Although similar qualitative results were obtained when comparing both FR measures, we retained the FR estimated as the average number of species per FG since it showed a better performance in response to environmental filters (see Appendix S3 for further details).

We calculated the three primary components of FD (richness, evenness and divergence *sensu* Mason *et al.* 2005) to compare their response with those obtained using FR. First, we estimated three Gower dissimilarity matrices using the all traits by taxon, response traits by taxon and effect traits by taxon. Functional richness (FRic) was estimated as the hypervolume enclosing the functional space filled by the community (Villéger, Mason & Moullot 2008). The functional space was built using the six first axes of a principal component analysis based on the all-traits dissimilarity matrix. The number of axes retained to estimate the hypervolumes was decided following the method proposed in Maire *et al.* (2015). This variable was standardized by its maximum, ranging from 0 to 1. Functional evenness (FEve) was calculated using the method of the minimum spanning tree in a functional space based on all-traits dissimilarity matrix (Villéger, Mason & Moullot 2008). Functional divergence (FD<sub>is</sub>) was measured as the abundance-weighted functional dispersion of the response traits (i.e. response diversity). To quantify this metric for each community, we estimated the weighted mean distance to the weighted community centroid (Laliberté & Legendre 2010).

## ENVIRONMENTAL FILTERS

Changes in land use and flow regulation are globally recognized as the most important anthropogenic stressors impacting aquatic and riparian ecosystems (Nilsson & Berggren 2000; Allan 2004), and particularly in Mediterranean and semi-arid areas as the study area (Bruno *et al.* 2014b). We used the percentage of agricultural land at basin scale as a surrogate for land-use intensity. It was calculated after delineating the catchment for each sampling point using the ArcGIS software (v 9.2) (ESRI, Redlands, CA, USA) and the analysis toolkit NetMap (Benda *et al.* 2007), taking as a base the available layers (1 : 25 000) of the Occupation Information System of Soil in Spain. The dam regulation index was estimated using the methodology described in Falcone, Carlisle & Weber (2010) and adapted from Belmar *et al.* (2013). This method uses the number of dams and their regulatory capacity (hm<sup>3</sup>) in the drainage area associated with each sampling site. Sites were assigned from 0 to 8 points for each variable based on their percentile value within the data range. Then, those points were added to provide an index that potentially ranged from 0 (minimum flow alteration) to 16 (maximum flow alteration).

Drought duration (days per year without water flow) was used as a surrogate for the natural hydrological stress to which semi-arid rivers are normally subjected. This filter sorts the regional species pool, leaving species that have developed adaptations to drought (Peñuelas, Lloret & Montoya 2001). Drought duration was estimated at reach scale using the data from the Integrated System for Rainfall–Runoff Modelling (SIMP) (Belmar, Velasco & Martínez-Capel 2011). The SIMPA is a soil moisture balance model where precipitation, soil and aquifer storages are considered, used in Spain, for water resources assessment (Ministry for the Environment 2004) and hydrological classifications (Bejarano *et al.* 2010; Belmar, Velasco & Martínez-Capel 2011). The site-specific values of the environmental filters are shown in Appendix S2.

## DATA ANALYSIS

The relationships between FR and the interacting environmental filters were tested using linear mixed-effect models (LME), assuming a Gaussian distribution of the dependent variables. The models included a fixed part with an intercept and the stressor slopes, along with a random intercept that accounts for environmental variability. Accordingly, LMEs produce two  $R^2$  (goodness-of-fit), the marginal  $R^2$  associated with the fixed effects (those produced by environmental filters) and the conditional  $R^2$  that represents the fixed effects plus the random effects (those caused by environmental filters and variability together). Environmental variability was considered as a three-level factor representing elevation typology (high altitude: elevation > 1000 m a.s.l., mid-altitude: 1000 ≥ elevation > 600 m a.s.l., lowlands: elevation ≤ 600 m a.s.l.) since it summarizes well the natural environmental gradients occurring in the study area (Díaz, Alonso & Gutiérrez 2008). We tested the significance of simple and quadratic coefficients for each  $z$ -standardized (mean = 0, SD = 1) filter as well as the pairwise-filter interaction terms to look for potential combined effects. Before their standardization, drought duration was log-transformed and percentage of agricultural land use was arcsine square-root-transformed to improve linearity against response variables. LMEs were performed using a backward-stepwise procedure retaining the model that minimizes the Bayesian information criteria (BIC). Normality, homoscedasticity and spatial autocorrelation of the

model residuals (Moran's  $I$  test; ArcGIS 9.2) were also assessed. When either normality or homoscedasticity was not met, alpha was set to 0.01. In case neither of these assumptions was met, alpha was set to 0.001. In addition, we examined the statistical relationship between FR and the items that shape it (i.e. species richness and number of FGs) through ordinary least squares.

A relationship between functional features and environmental filters can be found simply as a result of an underlying taxonomic richness gradient (and its response to stress) due to sampling effect (Villéger, Mason & Mouillot 2008) and not due to niche-based sorting. Thus, we also checked for non-randomness of the FR model coefficients by using null models. To assess the non-randomness of the observed trends, empirical parameters should be distinct from a null distribution of simulated parameters. We randomly reassigned traits to each species (999 runs) to re-examine their relationships with the stressors. For randomizations, we kept the same trait combinations, richness gradient and taxon frequency of occurrence. For each simulation, we used the same model and procedure as for the empirical data (i.e. we calculated FR and re-examined its relationship with the same predictors to obtain the simulated intercepts and slopes for each relationship). We examined the null model's statistical significance using an exact two-tailed test to calculate the probability that the observed value was significantly ( $\alpha = 0.05$ ) larger or smaller than the simulated distribution. These same analyses (LME and null models) were also conducted with the three FD measures (FRic, FEve and FDis). Finally, we followed a similar null model approach to test whether the relationship between FR and species richness was different from what is expected by chance.

Finally, using the best-fitting model obtained for FR, we forecasted their values for the entire river network. Thus, rivers were divided into homogeneous reaches characterized by an absence of tributaries and defined by 409 fluvial nodes in which FR was predicted. The predictive power of the final model was estimated by a jackknife cross-validation procedure. Thus, the mean error percentage of all sampling sites was used as a measure of model reliability. All statistical analyses were performed in the R statistical software (libraries: 'ade4', 'boot', 'car', 'FD', 'MuMIn', 'nmlr' and 'vegan'; R Development Core Team 2013). See R code and FR functions used in Appendix S2.

## Results

A total of 63 woody riparian species were recorded and classified into five FGs representing different life strategies and effects with a clear ecological significance on ecosystem functioning. Among them, we identified two groups of phreatophytes mainly differing in life form (FG1: shrubby phreatophytes; FG2: arboreal phreatophytes), both strongly associated with watercourses. Drought-adapted riparian species showing special leaves, roots and structural features formed FG3, and riparian evergreen shrubs formed FG4. Lianas and climbers typical for well-developed and humid riparian systems shaped FG5 (see Fig. S1.1 and Table S1.2 in Appendix S1 for details).

Generally, we found that community functional measures significantly decreased with increasing environmental filters (Fig. 2). Droughts and especially agriculture caused the strongest effects on the functional features used. The

responses of FR and functional richness (FRic) were similar, being the most sensitive indices. The best model for FR (minimum BIC) showed a higher percentage of explained deviance ( $R^2 = 0.59$ ) than the best-fitting model for the FD components ( $R^2 < 0.4$ , Table 1). The FR model included agriculture, drought and flow regulation as well as the interactions of agriculture with the two latter (Table 1). Conditional  $R^2$  and marginal  $R^2$  displayed the same values in the best-fitting mixed-effect models for all functional indices (i.e. the combination of the different environmental filters resulted more explicative). On the other hand, conditional  $R^2$  was higher than marginal  $R^2$  in some mixed-effect models only when considering each environmental filter alone (Appendix S4).

Null models revealed that stressors caused non-random changes in FR. All terms were significant ( $P < 0.05$ ), and empirical slopes were significantly lower for all environmental filters, and significantly higher for the interactions among them and the intercept (Fig. S4.2). Nevertheless, excluding FEve, FD measures did not produce significant null models ( $P < 0.05$ ) so their observed responses to environmental filters were actually a direct consequence of taxonomic diversity reduction (see Appendix S4 for details about the null models).

Species richness was positively related to FR and the richness of the different FGs, except for FG3 and FG4 that showed a weak, flat response (Fig. 3). Nevertheless, null model results showed that FR increased more than expected by chance as taxonomic richness rose (Appendix S4). More concretely, empirical intercept was lower in comparison with the simulated distribution ( $Z$ -score =  $-2.78$ ,  $P = 0.005$ ), whilst the empirical slope was significantly higher (i.e. species richness,  $Z$ -score =  $4.72$ ,  $P = 0.003$ ). Finally, species richness and FR showed humped relationships with the number of functional groups (FGR, Fig. 3). FGR peaked at medium–high values of species richness and FR and consequently at low–moderate anthropogenic stress intensity (Fig. S4.3 in Appendix S4). The best obtained model was applied to forecast the FR values for the river stretches of the entire river network. There was a clear FR gradient, decreasing from headwaters to lowlands (Fig. 4). The model showed a mean error percentage of 36.3% without any geographical concentration of high residuals.

## Discussion

All environmental filters led to reductions in FR, thereby decreasing ecosystem resistance and resilience to future disturbances. The FD components chiefly declined in response to agriculture, the most important stressor in the study area. However, only FR showed a non-random reduction in response to increased stress or species loss, with the exception of functional evenness, which although less sensitive, also experienced a non-random decline in response to stress. Natural environmental variability (i.e. associated to elevation gradient) exerted an inconspicuous

influence on the spatial distribution of FD indices in comparison with the effect of multiple stressors (Table 1).

Our results for single stressors are similar to those observed in previous studies, where FR decreased along single anthropogenic impact gradients for plants (Laliberté *et al.* 2010), birds (Huijbers *et al.* 2015), soil microbes and invertebrates (Salminen, van Gestel & Oksanen 2001), and aquatic invertebrates (Gutiérrez-Cánovas *et al.* 2015). However, one of the main novelties of this study was in revealing non-random effects between combined environmental filters on riparian vegetation. The decrease in FR following species loss was greater than expected by chance and particularly evident at high species richness as derived from the relationships among FR, FG and species richness (Fig. 3). The reduction in FR could be associated with a loss of richness within some FGs (mainly FG1, FG2 and FG5), likely as a consequence of different response diversity or trait combinations of the species within each FG. Thus, the random loss of one species might not affect ecosystem functioning in functionally redundant communities, as its function could be compensated for by the remaining species of the same FG if they are capable of expanding to fill the gap (Fonseca & Ganade 2001). In particular, different responses of functionally equivalent species to environmental change increase response diversity (Elmqvist *et al.* 2003), enhancing the capacity of ecosystems to resist impacts (Mori, Furukawa & Sasaki 2013).

It is worth noting that FR can be partitioned into intrinsic and extrinsic redundancy. We mainly focus here on intrinsic redundancy, which results from the patterns of functional similarity among species. On the other hand, extrinsic redundancy (or lack thereof) can result from non-random compositional change with respect to functional traits (Petchey *et al.* 2007). Thus, although we have detected that FR increases more than expected by chance as taxonomic richness rises, further studies will allow us to explore extrinsic redundancy which is also a key variable in functional ecology with direct applications to management.

Although both (intrinsic) FR and FD measures decreased as stressors intensified, FD components seem to be less affected by environmental stressors, helping to mitigate the effect of stressors in redundant communities (i.e. the reduction of FD was minimal in redundant places, Appendix S5). Agriculture, drought and flow regulation (in order of importance) reduced FR and the FD components, suggesting that general functional response is similar irrespective of whether the impact had natural (drought) or anthropogenic origin (agriculture and flow regulation), as found by Gutiérrez-Cánovas *et al.* (2015). However, some differences depending on the nature and source of stress can be observed. In general, agriculture caused the greatest impact on all functional measures, probably due to its multiple effects on the riparian community, such as direct destruction of riparian forest (Allan & Flecker 1993), higher nutrient loading due to fertilization (Monteagudo, Moreno & Picazo 2012), and water abstraction for irrigation (Belmar *et al.* 2013). The traits

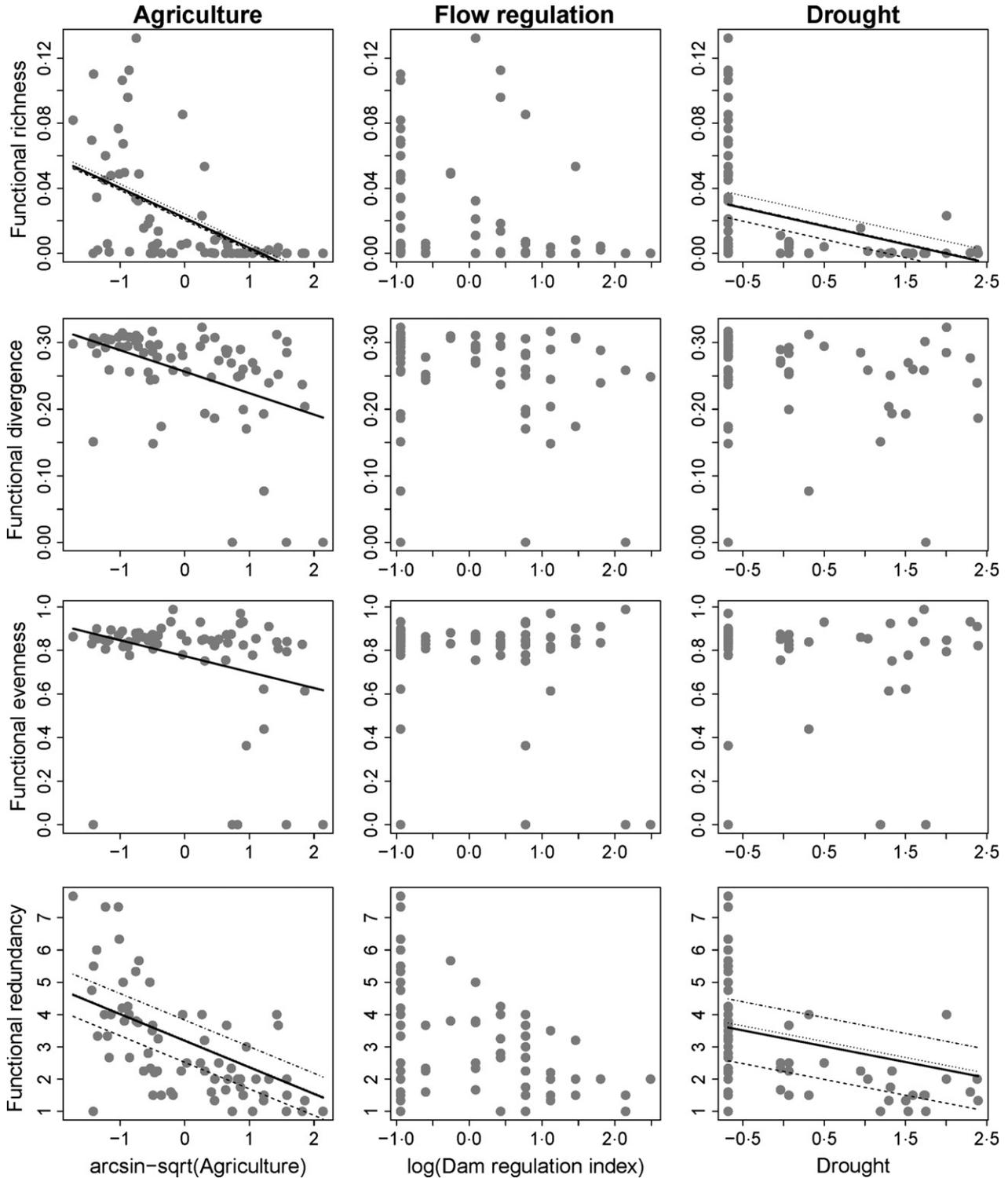


Fig. 2. Plots showing the response of functional redundancy and three measures of functional diversity to single environmental filters estimated through mixed-effect models. The solid line represents the fitted models for each single stressor, dashed lines represent the fitted model for the lowland rivers, dotted lines show the fitted model for the mid-altitude rivers, and dashed-dotted lines display the fitted model for the high-altitude rivers.

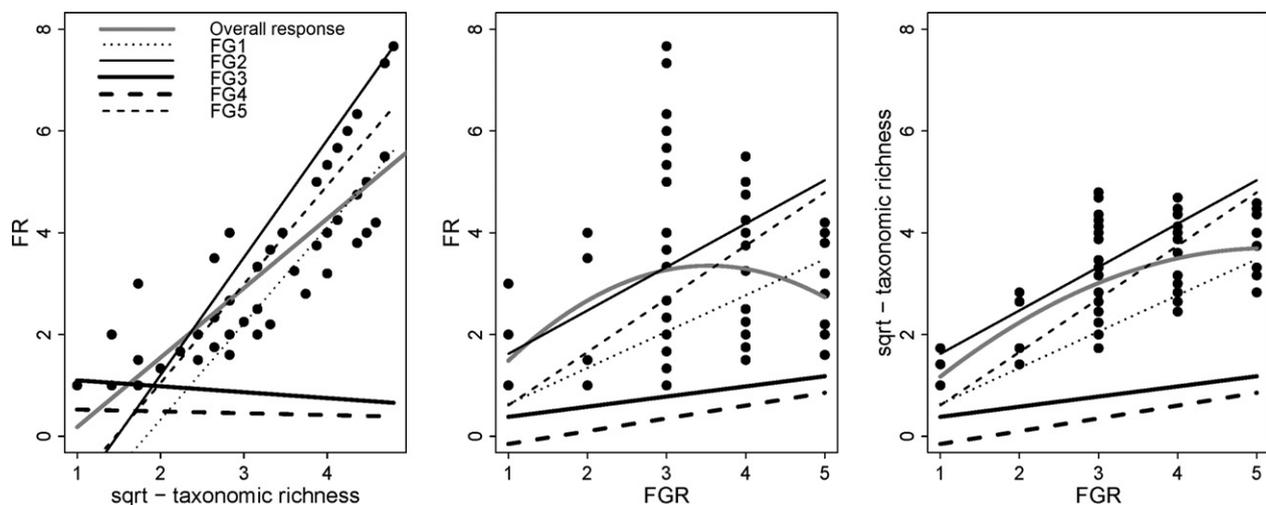
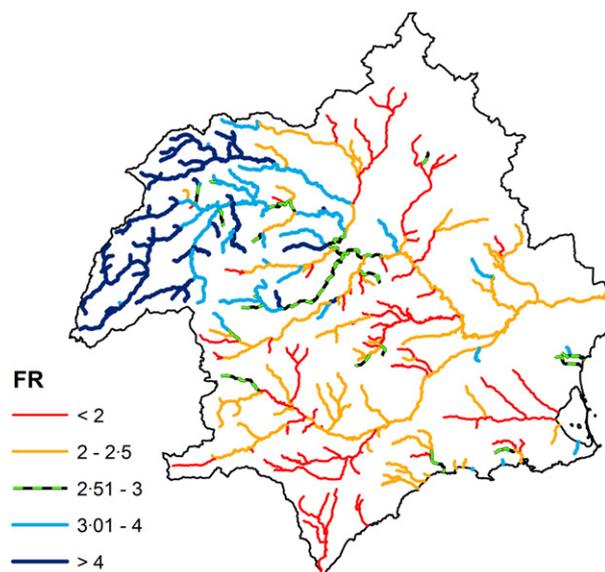
most disfavoured by agriculture include high species woodiness, slow growth, large lateral extension, sexual reproduction and short-term persistent seed bank (Kleyer 1999). Flow regulation modifies abiotic features and homogenizes habitat conditions (Belmar *et al.* 2013),

affecting reproduction, recruitment, dispersal opportunities, succession and fragmentation of the riparian community (Jansson, Nilsson & Renöfält 2000; Nilsson & Berggren 2000). Drought sorted out woody riparian communities, favouring sclerophyllous and evergreen shrubs

**Table 1.** Results of mixed-effect models showing the best-fitting model equation, *P*-values (significant coefficients in bold type), marginal ( $R^2_m$ ) and conditional ( $R^2_c$ ) goodness-of-fit for the different functional diversity indices

Index	Model equation	(A)	(F)	(D)	A*F	A*D	F*D	$R^2_m$	$R^2_c$
FRic	$y = 0.017 - 0.016A - 0.009D + 0.01A*D$	< 0.001	ns	<b>0.03</b>	ns	<b>0.018</b>	ns	0.37	0.38
FDis	$y = 0.253 - 0.032A$	< 0.001	ns	ns	ns	ns	ns	0.21	0.21
FEve	$y = 0.809 - 0.074A - 0.097A*F + 0.091D*F$	<b>0.004</b>	ns	ns	<b>0.002</b>	ns	< 0.001	0.28	0.28
FR	$y = 2.66 - 0.624A - 0.642D - 0.475F + 0.506A*D + 0.354A*F$	< 0.001	< 0.001	< 0.001	<b>0.002</b>	<b>0.002</b>	ns	0.59	0.59

A, agriculture; F, flow regulation; D, drought; ns, non-significant coefficient; FR, functional redundancy. Pairwise interactions are noted with an asterisk.

**Fig. 3.** Plots relating functional redundancy (FR), taxonomic richness and number of functional groups (FGR). Single results for each functional group (FG) are also shown.**Fig. 4.** Predicted functional redundancy (FR) values for riparian communities in the entire river network of the Segura basin.

(Aguar & Ferreira 2005). Drought-adapted species usually have long roots, low seed buoyancy, low canopy, little specific leaf area or small and thick leaves (Cornwell &

Ackerly 2009; Douma *et al.* 2012). In addition, the regional persistence of drought could have helped some species to tolerate flow regulation, which might partially explain its lower impact on FD measures. In fact, the strong flow regulation by dams leads to a terrestrialization of riparian and river communities favouring the occurrence of opportunistic, terrestrial and drought-adapted species (Catford *et al.* 2014). Although these two disturbances differ in periodicity, timing and origin, both alter the flow regime and the water supply for riparian vegetation.

The interactions between agriculture and the other stressors were not surprising since several links exist among them in the study area. Large agricultural surfaces in areas with long drought periods produce high water demands that have triggered massive dam construction and other hydraulic infrastructures. The combination of high nutrient loading, clearing of river banks and reduction of the water-table may favour similarly opportunistic, drought-adapted and generalist species (e.g. *Arundo donax* L., see Quinn & Holt 2008) leading to a simplification of ecosystem structure and function. Given these complementary effects, the management of anthropogenic pressures should be addressed in a holistic way considering also the underlying natural stress such as the Mediterranean drought in the study area.

Conservation and biomonitoring efforts have been traditionally focused on taxonomic features (such as species presence, abundance and rarity), ignoring other ecosystem properties (Cadotte, Carscadden & Mirotchnick 2011). However, functional features are linked to ecosystem functioning (Hooper *et al.* 2005) or community assembly (Weiher *et al.* 2011), which allows explaining, in some cases, non-random patterns, as observed here. Their use has several advantages, such as better intertaxon and inter-region comparability (McGill *et al.* 2006). Accordingly, we feel that this kind of measures should be incorporated in conservation prioritization and ecosystem management in order to have a broader perspective of the response of biological communities to different environmental stressors. In particular, FR informs about the species playing similar roles (Lawton & Brown 1993), and consequently, the likelihood of losing particular ecosystem functions as a result of biodiversity reduction (Naem & Wright 2003). In our case, restoration efforts might be focused on those river reaches showing slightly or moderately reduced FR values, as a first step to recover the integrity of the riparian functioning, within a context of cost-effective management (i.e. restoring greatly damaged places could be less efficient). Particularly, phreatophytes (both arboreal and shrubby) as well as lianas and climbers seem to be the most affected FGs, suggesting that their recovery is essential to reach a better riparian functionality across the study area. Thus, FR could provide additional and complementary information to taxonomic diversity on how communities respond to stress. Besides, quantifying community functional responses to increasing intensity and frequency of anthropogenic impacts is required to further evaluate the loss of ecosystem services associated with biodiversity erosion in the current context of global change (Cardinale *et al.* 2012).

Although FR and other FD indices can be useful in conservation ecology and environmental management, there are some methodological considerations. The grouping of taxa in FGs may result in a loss of information in comparison with continuous measures. On the other hand, this approach is interesting to explore further to understand how environmental filters may modify particular ecosystem functions and services provided by biological communities. Thus, each FG and even each species within the same FG may respond differently to the same stressor. Otherwise, accounting for intraspecific variability enables more accurate measures of multidimensional functional overlap (Gutiérrez-Cánovas *et al.* 2015), but gathering such data could be costly in comparison with the data quality improvement. Finally, functional measures could depend on the number and nature of traits used for its computation, as species are more likely to have non-overlapping functional niches (low FR) in a functional space when using single or few functional traits (Rosenfeld 2002).

This is one of the first studies predicting a whole community functional measure for an entire administrative

area, which may help to improve ecosystem biomonitoring and management (Devictor *et al.* 2010; Matsuzaki, Sasaki & Akasaka 2013; Sasaki *et al.* 2014). In a changing environment, this measure provides three major advantages: (i) valuable information on how river ecosystems respond to human and natural environmental stressors, which can help managing the current increase of multiple stressors across the river network, (ii) assessment of stressors' effects on functional features from the descriptive to the predictive (being the assessment framework of broad-scale applicability across ecological domains) and (iii) the geographical distribution of sites that potentially could show more stability, resistance and resilience, and vice versa.

#### CONCLUDING REMARKS

Functional redundancy proved to be more sensible than other FD measures to impacts of the most important stressors in Mediterranean rivers as well as the interactions between them. FR can be considered as an ecologically-sound measure able to detect non-random responses to single and multiple stressors. According to the FR gradient found across the catchment, temporary streams flowing through an agricultural, regulated basin had reduced values of FR. On the other hand, free-flowing medium-sized, perennial water courses flowing through unaltered sub-basins displayed higher values of FR and potentially greater stability against human impacts. Thus, undisturbed conditions held more diverse communities, where redundant species may ensure ecosystem functioning when response diversity is high. Our study reveals that the response of FR can be predicted for entire river networks, constituting a potential tool to detect more impacted river reaches and improve their conditions through restoration measures, as well as to conserve the reaches with better functional conditions.

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#### Data accessibility

All data (functional traits and indices, species abundances per site and environmental variables) and R scripts used to produce this manuscript are available in Appendix S2.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Effect and response functional traits information.

**Table S1.1.** Effect and response traits considered to characterize the functional features of the woody riparian species.

**Table S1.2.** Functional group description based on distinctive functional effect traits.

**Table S1.3.** Data sources used to obtain the functional trait values.

**Fig. S1.1.** Dendrogram resulting from classifying riparian species according to their similarity in the functional effect traits.

**Appendix S2.** R code and data files.

**Appendix S3.** Details about functional redundancy estimations.

**Table S3.1.** Results of the linear mixed-effect models relating the divisive and additive estimations of FR with individual stressors.

**Table S3.2.** Results of the null models for the models relating the divisive and additive estimations of FR with individual stressors.

**Table S3.3.** Results of the linear mixed-effect models for the best-fitting models relating the divisive and additive estimations of FR with multiple stressors.

**Table S3.4.** Results of the null models for the best-fitting models relating the divisive and additive estimations of FR with multiple stressors.

**Fig. S3.1.** Values of the divisive (FRa) and additive (FRb) estimations of FR across the study area.

**Fig. S3.2.** Plots showing the response of FRa and FRb to single environmental filters.

**Appendix S4.** Linear mixed-effect models, null models and residuals' assumptions.

**Table S4.1.** Results of linear mixed-effects models for single environmental stressors.

**Table S4.2.** Null model results for the individual significant stressors for each functional index.

**Table S4.3.** Null model results for the best-fitting models for each functional index.

**Fig. S4.1.** Plots showing the residuals' normality and homoscedasticity of the best-fitting model for FR.

**Fig. S4.2.** Results of null models for each model parameter of functional redundancy's best-fitting model.

**Fig. S4.3.** Best-fitting model for FGR in response to environmental filters.

**Appendix S5.** Spatial pattern of the functional diversity and redundancy indices and their pairwise relationships.

**Table S5.1.** Spearman correlations between functional indices.

**Fig. S5.1.** Spatial pattern of FR and FRic.

**Fig. S5.2.** Spatial pattern of FEve and FDis.

**Fig. S5.3.** Relationships between functional indices.