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Title: Functional response of aquatic invertebrate communities along two natural stress gradients (water salinity and flow intermittence) in Mediterranean streams.

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Abstract

Functional trait diversity can provide insight into ecosystem function beyond that provided by species diversity measures. The relationship between functional diversity and natural stressors has received less attention compared to anthropogenic stressors. In this study, we investigated how two natural stressors, water salinity and flow intermittence, affect functional richness and functional redundancy of aquatic invertebrate communities using seven biological traits and 39 modalities. For this purpose, we characterized these functional diversity measures in 22 Mediterranean streams with a gradient of natural salinity and flow intermittence. Our findings showed that both functional richness and functional redundancy decreased with increased stress by water salinity and flow intermittence for all the studied traits but more rapidly for the former, suggesting that water salinity is a stronger environmental stressor than flow intermittence. Our study also described an antagonistic interaction of the two study stressors, in which the net effect of both is less than the sum of their independent effects. This study emphasizes that in saline streams, characterized by lower functional richness and functional redundancy, the loss of any taxon can have a huge impact on community functioning. In particular, the functional singularity of saline intermittent streams makes them extremely sensitive to additional anthropogenic impacts. In the context of future global change scenarios, which predict higher flow intermittence and water salinity, this study gives a better understanding of the functional features of these types of ecosystems.

Keywords: biological traits, functional redundancy, functional richness, freshwater streams, intermittent streams, saline streams

Introduction

Our current understanding of the relationship between biodiversity and functioning of communities and ecosystems and is still limited (Allan et al. 2013; Balvanera et al. 2014; Hodapp et al. 2014), despite its importance for understanding and predicting ecosystem responses to environmental changes. The term biodiversity includes the number, variety and variability of living organisms that inhabit ecosystems, as well as the complex relationships that exist between them. Although species richness and composition (i.e. the most conventional component of biodiversity) have been widely used to evaluate the response of ecosystems to perturbations, the community's functional diversity, based on trait measures of diversity, can be more helpful for explaining ecosystem responses to environmental changes (e.g. climate change, land use changes, hydrological events), and is likely to provide insight into the ecosystem function beyond that provided by species diversity measures (e.g. Charvet et al. 1998; Diaz and Cabido 2001; de Bello et al. 2010; Cadotte et al. 2011; Mouillot et al. 2014). Therefore, functional diversity (i.e. the value and range of functional traits of organisms in a community) is currently viewed as one of the most important parameters to help understand the functioning of communities (Elmqvist et al. 2003).

Species richness and community functional diversity measures (i.e. functional richness and functional redundancy) often correlate positively, where loss of species produced by natural and/or anthropogenic stressors results in loss of functional diversity at the community level (e.g. Guerrero et al. 2014; Gutiérrez-Cánovas et al. 2015). However, the strength, and even the direction that this relationship takes, is largely determined by the degree of functional redundancy in the community (Guerrero et al. 2014), are understood as the number of species with similar functional traits (Rosenfeld 2002; Göthe et al. 2014). Some species can replace the functional role of others (i.e. functional redundancy) and maintain or increase ecosystem resilience (e.g. Gerish 2014). In this context, functional redundancy, which varies among habitats, taxonomic groups and also types of environmental stressors (Gerish 2014), helps us to understand that species loss may not significantly affect a community's resilience.

Many studies have shown how anthropogenic stressors (e.g. habitat loss, land use change, invasive species, overexploitation and pollution) reduce biodiversity and, consequently, functions of communities and ecosystems (e.g. Cardinale 2011; Hooper et al. 2012; Guerrero et al. 2014). This is particularly true in freshwater ecosystems (e.g. Dudgeon et al. 2006), where multiple stressors have vastly altered the structure and functioning of these ecosystems (e.g. Schäfer et al. 2012; Theodoropoulos et al. 2015). In those ecosystems, benthic macroinvertebrates contribute largely to biodiversity, and are important contributors to ecosystem functions, including detritus processing and energy transfer to consumers at higher trophic levels, among other processes (Heino 2005).

The relationship between functional diversity and natural stressors has received little attention. In freshwater ecosystems, water salinity and flow intermittence can be important natural stressors affecting the structure and functioning (e.g. Gutiérrez-Cánovas et al. 2009; Vidal-Abarca et al. 2013; Schriever et al. 2015). These stressors characterize many water courses in the Mediterranean Basin region. In this area, flow intermittence occurs naturally by strong interannual and seasonal hydrological variability, with

recurrent flood and drought events (e.g. Bernal et al. 2013; Bonada and Resh 2013). Moreover, the natural water salinity of such streams is due to catchment lithology (e.g., presence of gypsum and halite-rich evaporite rocks; Gómez et al. 2005) and the balance between rainfall and evapotranspiration (e.g. Haron and Dragovich 2010).

More knowledge about how these natural stressors affect freshwater insect communities has accumulated in the last decade. Many studies on aquatic invertebrate communities have reported that flow intermittence and water salinity lead to reduced biodiversity (e.g. Williams et al. 1990; Gallardo-Mayenco 1994; Morais et al. 2004; Sánchez-Montoya et al. 2009a; García-Roger et al. 2011; Bogan et al. 2013), modifying the trophic structure of aquatic communities (Muñoz and Prat 1994; Bogan and Lytle 2011). However, very few studies have documented functional trait variation along these natural stressors in freshwater ecosystems. Recently, Schriever et al. (2015) reported that drying events reduce functional diversity in desert streams, and Gutiérrez-Cánovas et al. (2015) documented that both community functional richness and functional redundancy diminished along an increasing salinity gradient. Despite the recent progress made in separately understanding the role of water salinity and flow intermittence shaping functional diversity of aquatic invertebrates, interactions among those two natural stressors, which may generate complex effects that mitigate or amplify the direct single effect of each stressor (see Statzner and Bêchet 2010; Jackson et al. 2015), have not yet been explored in freshwater ecosystems.

The primary objective of this study was to investigate how two natural long-term stressors, water salinity and flow intermittence, affect functional richness and functional redundancy of aquatic invertebrate communities in Spanish Mediterranean streams. Firstly, we studied the relationships among taxonomic richness with functional diversity and functional redundancy. Secondly, we analyzed the effect of the two natural stressors on functional diversity measures in different types of biological traits to describe the potential functional pattern in distinct trait types. Finally, the net effect of this stressor pair on the functional diversity of aquatic invertebrate communities was studied. To approach these aims, we characterized functional diversity measures in Mediterranean streams that exemplify a gradient of natural salinity (from freshwater to hypersaline) and flow intermittence (from perennial to intermittent). We expected functional richness and functional redundancy to be negatively related to increasing water conductivity (i.e. salinity) and increasing dry period (i.e. flow intermittence) due to specialized taxa that persist with the filtering effect of these natural stressors.

Material and methods

Study area and environmental data processing

The study was carried out in the Segura River Basin (southeast Spain). The Segura River flows from northwest to southeast and drains a basin of 14,432 km² (see Vidal-Abarca et al. (1992), Mellado-Díaz et al. (2002) and Robles et al. (2004) for a general description). Climate ranges from sub humid Mediterranean (average annual rainfall >1000 mm, average annual temperature 13°C) in the north/northwest of the catchment to semiarid Mediterranean (<300 mm and 18°C) (CHS 2007) in the south/southeast area. In mountain headwaters, calcites, dolomites and shales are the predominant geology, whereas the lithology of the plains is characterized by the predominance of gypsum and Miocene salt-rich

marls. Both intermittent and ephemeral streams are mainly restricted to the southern half of the Segura Basin, in areas of low altitude (Belmar et al. 2011).

Twenty-two streams were selected in this study (Fig. 1). Drainage areas ranged from 14 km² to 2344 km², and the altitude of sampling sites ranged from 60 to 1050 masl. (Table 1). The salinity gradient of selected streams ranged from electrical conductivity of 190 $\mu\text{S cm}^{-1}$ to $> 55,000 \mu\text{S cm}^{-1}$. According to Arribas et al. (2009) and Millán et al. (2011), we classified the streams whose average electrical conductivity reached 2500 $\mu\text{S cm}^{-1}$ as saline. The flow intermittence of selected streams was characterized using field data according to the number of dry days per year: 0 days, 1-30 days, 31-90 days, 91-180 days and > 181 days. We classified streams whose number of dry days per year was > 0 days as intermittent. Considering the above criteria, the 22 selected streams were classified into four different typologies according to salinity and flow intermittence: fresh-permanent streams (F-P; n=11), fresh-intermittent streams (F-I; n=3), saline-permanent streams (S-P; n=3) and saline-intermittent streams (S-I; n=5) (Table 1).

We also analyzed the relationship between land-use intensification on taxonomic richness, functional richness and functional redundancy in order to justify that the selected study sites did not undergo an intense level of land intensification. To calculate the percentage of different land uses, firstly a digital terrain model (DTM 30 x 30 m; Centro Geográfico del Ejército, Ministerio de Defensa, Spain, 2005) and Arc/Info software (version 9.0, ESRI, Redlands, California, USA, 2005) were used to delimit and calculate the water drainage area as a new polygon for all the sampling sites. Secondly, the percentages of intensive and extensive agriculture, urban zones, burnt area and natural land use were calculated by intersecting the Corine Land Cover 2000 Programme (Spain, Scale 1:100.000, Instituto Geográfico Nacional, Centro Nacional de Información Geográfica) with the water drainage area (Appendix 1).

Invertebrate data

Between 2001 and 2010, 131 aquatic invertebrate samples were collected (Table 1). At each site, the taxonomic composition was obtained by pooling up to seven samples collected in different seasons during the study period. This approach has proved adequate to represent the mean annual community, even when a single season was used (Bonada et al. 2007, Gutiérrez-Cánovas et al. 2015). We collected aquatic invertebrates following the PRECE protocol (Jaimez-Cuellar et al. 2004), where a multi-habitat semi-quantitative kick-sampling was applied. Invertebrate samples were collected from all habitats using a hand net (250-400 μm) and preserved in 90% ethanol. At least 200 individuals per sample were randomly picked and identified at the genus level in the laboratory, except for some dipterans (identified to families, subfamilies or tribes), Hydrachnidia, Tricladida, Oligochaeta and Nematoda. Large uncommon individuals were picked individually.

Functional richness and functional redundancy

We used presence/absence data to minimize sampling error. We used seven biological traits and 39 modalities (Appendix 2). The trait information of each taxon was obtained from Tachet et al. (2010) and Bonada and Dolédec (2011), and from Picazo et al. (2012) for Coleoptera in particular, who described the averaged affinity of each genus to each category. An affinity score (1-5) of each taxon was assigned to each

trait category by a fuzzy coding approach (Chevenet et al. 1994). Each taxon was characterized by the affinity values of the different modalities of each biological trait used. To compensate for anomalies detected in the affinity values allocated to taxa, we transformed the affinity values of the biological traits used to a binary scale (1=presence/ 0=absence) (Schmera et al. 2012). Taxa that played an identical functional role (i.e. characterized by identical affinity values at each modality of the used biological traits) were considered to be functionally redundant and constitute the same functional unit (see Schmera et al. 2012). A taxon was considered functionally distinct when at least one of the affinity values differed. We identified 82 different functional roles for feeding habits, 141 for food, 15 for life cycle duration, 33 for the potential number of reproduction cycles per year, 64 for reproduction, 67 for dissemination and 45 for resistance forms (Appendix 2). Functional richness was calculated as the number of functional roles, and functional redundancy as the difference between taxonomic richness and functional richness.

Statistical analysis

Firstly, Pearson's correlations were performed to test the possible influence of human impacts (land use) on taxonomic richness, functional richness and functional redundancy. Secondly, we tested the linear and saturating (curvilinear) relationships among taxonomic richness, functional richness and functional redundancy by comparing the fit of linear ($y = a + bx$) and logarithmic ($y = a + b \cdot \ln(x)$) regressions. Models with the highest adjusted R^2 and the lowest AIC (Akaike's information criterion) were determined to represent the best fit. A positive linear relationship with slope = 1 indicates that new species were incorporated into the community, which results in new ecological functions. On the contrary, a positive slope, but < 1, indicated that some species shared functional traits. A curvilinear response between taxonomic and functional richness indicated that at low taxonomic richness, the community rapidly aggregated new functions. Where an asymptote was reached at a higher level of taxonomic richness, redundancy was suggested (e.g. Beche and Stazner 2009; Schriever et al. 2015).

We assessed the relationships between functional richness and functional redundancy and conductivity (log) and intermittency (log number of dry days per year) using linear and quadratic regressions for each studied trait. The best model was chosen according to the highest adjusted R^2 and the lowest AIC. Boxplots of the four sampling sites groups (F-P, F-I, S-P and S-I) for seven types of studied biological traits were drawn. Kruskal–Wallis non parametric ANOVA and Tukey's HSD post-hoc tests were used to detect possible differences among site groups. All statistical analyses were performed in SPSS, version 19.0 (Chicago, USA).

Results

We obtained low Pearson's correlation values for almost all correlations among taxonomic richness, functional richness and functional redundancy, and different land uses (Appendix 3). Moreover, a non-significant correlation among taxonomic richness, functional richness and functional redundancy with irrigated agriculture was found, showing that land use did not seem to act as a strong stressor in the 22 selected streams.

Relationships between taxonomic richness, functional richness and functional redundancy

Positive and significant correlations (always $P < 0.001$) between taxonomic richness and functional richness, between taxonomic richness and functional redundancy, and between functional richness and functional redundancy for all the studied traits (Table 2) were found. Taxonomic richness exhibited a significant linear relationship with functional richness for the traits that related to feeding (food and feeding habits) and to dispersal. On the contrary, a saturating relationship (logarithmic relationship) between taxonomic richness and functional richness showed a better fit than the linear one for the other traits (Table 3; Appendix 4a). According to the saturation curves, the number of taxa required to obtain maximum trait richness ranged from 403 for trait “reproduction” to 34 for trait “number of reproductive cycles per year” (Table 3). For this latter trait, 82 % of the sites (i.e. 18 sites) had enough taxonomic richness to achieve trait saturation. However, only one site had the necessary taxonomic richness (i.e. 121 taxa, sampling site 2) to achieve “food” trait saturation (115 taxa; Table 3). Taxonomic richness exhibited a strong positive linear relationship with functional redundancy for all the studied traits (Table 3; Appendix 4b), indicating the existence of functional redundancy in the studied streams.

Relationship between functional richness and functional redundancy with water salinity and flow intermittence

Functional richness decreased when both conductivity (log) and flow intermittency (log number dry days) increased for all the studied traits (Fig. 2a and b). However, this decrease was more marked with increasing conductivity than flow intermittence. Similarly, the functional redundancy for all the studied traits dropped sharply with increasing conductivity (Fig. 2c). Conversely, functional redundancy decreased with increasing intermittency flow, but only for the traits related to reproductive strategies (life-cycle duration, number of reproductive cycles per year and reproduction) and dispersal, but not for resistance type or for traits related to feeding strategies (Fig. 2d).

For functional richness and functional redundancy, the boxplots revealed a strong gradient of all the studied traits from the Fresh-Permanent groups to the Saline-Intermittent ones (Fig. 3a, b). According to the Kruskal-Wallis analysis, significant differences existed for functional richness between the Fresh-Permanent and Saline-Intermittent groups for all studied traits. In addition, “dispersal” “feeding habits” and “food” traits between Fresh-Permanent and Saline-Permanent also showed significant differences (Fig. 3a). For functional redundancy, significant differences were detected between Fresh-Permanent and the two hydrological types of saline streams for the majority of the studied traits (Fig. 3b).

Discussion

Water salinity and flow intermittence can act as strong environmental filters (*sensu* Mayfield et al. 2010) and shape the biodiversity of aquatic ecosystems (e.g. Millán et al. 2011; Boersma et al. 2014; Gonzalez et al. 2015) by affecting both taxonomic and trait composition of aquatic communities (e.g. Gallart et al. 2012; Kefford et al. 2012). These two stressors occur naturally in water courses distributed worldwide, particularly in arid and semiarid regions, and co-exert strong selective pressures on the evolution of traits for the resistance and resilience of biota to survive both dry periods and high salinity.

The study of natural stressors in aquatic ecosystems is expected to be problematic especially in Mediterranean areas, with a long-standing history of intense flow regulation, agricultural development and

pollution (e.g. Sánchez-Montoya et al. 2009a; Cooper et al. 2013), in which anthropogenic stressors could obscure functional patterns in response to natural stressors. For this reason, we first checked the influence of land use of the studied streams on functional measures. Our findings showed that there were only weak correlations between the studied metrics and land uses, supporting that the obtained results reflect mainly the effect of the studied natural stressors on the functional diversity of aquatic invertebrate communities. In addition, previous studies by Sánchez-Montoya et al. (2007, 2009b) in the same study area reported the lack of effects of other environmental factors related to climate, geology and morphology on reference macroinvertebrate communities in the studied streams, as well as no seasonal and interannual variation in those communities.

In our study, aquatic invertebrate communities with a large number of taxa (with higher taxonomic diversity) showed higher functional richness and functional redundancy than communities with fewer taxa. According to other studies (e.g. Bêche and Stazner 2009; Schmera et al. 2012), the positive correlation found between taxonomic and functional richness suggests the existence of functional redundancy in stream communities, regardless of the number of species and types of stream studied.

The type of relationship between taxonomic and functional richness can help us understand how communities respond to environmental stress (Schriever et al. 2015). In our study, the type of such a relationship depended on the particular biological trait. A linear relationship between taxonomic and functional richness for the traits related to feeding strategies (Appendix 4a) suggested the presence of more taxa specialists in aquatic ecosystems under high environmental stress. On the contrary, the taxonomic and functional richness curves for the traits related to reproductive strategies and dispersal (Appendix 4a) indicated that functional richness reached saturation; i.e. adding new taxa to the community does not involve adding new combinations of traits.

Trait saturation was relatively rare in our study, and this finding is similar to that described by other authors (Bêche and Stazner 2009; Schmera et al. 2012; Schriever et al. 2015). It should be noted that only one site (sampling site 2; Table 1) had enough taxonomic richness to achieve “food” trait saturation, and only trait “number of reproductive cycles per year” had the necessary taxon richness to achieve saturation (34 taxa; Table 3) at 18 sampling sites. We found no saturation of functional richness for this latter trait at four sampling sites (one F-P, one S-P and two S-I; Table 1), all of which presented a low taxonomic richness level.

Generally, in our study, the two studied natural stressors similarly constrained the functional features of aquatic invertebrate communities. The functional richness for all the studied traits decreased with the increased stress of water salinity and flow intermittence. However, the degree of the responses differed from one stressor to another. Functional richness decreased more rapidly with increasing conductivity than dry period duration (Fig. 2a, b). These results suggest that water salinity is a stronger environmental stressor than flow intermittence (Vidal-Abarca et al. 2013), imposing a threshold above which only physiological adaptations allow species to survive (e.g. Millán et al. 2011).

When we considered the different fit models in our study for each type of trait (linear or quadratic), the 50% reduction in functional richness for all the studied traits occurred at the same level of water salinity (conductivity > 33 mS /cm (~ 20 g/l)), indicating a similar sensitive of all the types of biological traits to a gradient of water salinity. This finding agrees with that reported by Williams et al. (1990) who found that

biodiversity rapidly decreased as salinity increased to 10 g/l, but decreased more gradually thereafter. This effect has been also documented by Arribas et al. (2009), who differentiated among three kinds of saline streams according to their different macroinvertebrate communities: low saline streams (3-20 g/l), medium-high saline streams (>20-100 g/l) and very high saline streams (>100 g/l). Unlike water salinity, the 50% of the reduction for flow intermittence is detected at different values, ranged from >90 dry days (for feeding habits and food traits) to >270 (for trait life cycle duration), suggesting that the effect of dry period on functional diversity depended on the type of traits.

Similarly, functional redundancy decreased with an increased gradient of both stressors. For the traits related to resistance forms, feeding habits and food (Figure 2d), reduction stopped at a high level of flow intermittence, and even recovered in the case of food. Although the quadratic relationship existed for feeding habits and resistance form, it showed increased functional redundancy when the number of dry days increased (Fig. 2d). Moreover, we found no significant differences among the four stream groups studied for the “food” trait (Fig. 3b). This result suggests that some functional role of species (e.g. food) may vary along an environmental gradient (e.g. increased flow intermittence), which is in accordance with Wellnitz and Poff (2001).

It is commonly assumed that functional redundancy may offer ecosystem function resilience to environmental variation (e.g. Petchey et al. 2007; Bêche and Statzner 2009; Boersma et al. 2014). Nevertheless, the low level of functional redundancy found mainly in intermittent and saline streams in the current work, and in many other studies (e.g. Micheli and Halpern 2005; Petchey et al. 2007; Guerrero et al. 2014; Schriever et al. 2015), could indicate that its role for maintaining community functioning, especially resilience, is smaller than expected (Gerisch 2014).

As far as we know, the current study is a first attempt to describe the combining effects of two natural long-term stressors (water salinity and flow intermittence) on the functional features of aquatic insect communities. The interaction between stressors can generate complex effects, which can mitigate or amplify the direct single effect of each stressor (Sala et al. 2000). Our study indicates an antagonistic interaction of the two studied stressors (Fig. 3), in which the net effect of the two stressors was not as strong as the sum of their independent effects. Recently, Jackson et al. (2015) have revealed that the net effects of stressor pairs in freshwater ecosystems were frequently more antagonistic than synergistic, additive or reversed. Theoretically, such a response may indicate that the negative influence of each stressor affects the same set of species in a community (Jackson et al. 2015). This agrees with the knowledge of how water salinity and flow intermittence affect aquatic insect communities which, in both cases, produces loss of the taxa that belong to the Ephemeroptera, Plecoptera, Trichoptera and Odonata groups (water salinity: Millán et al. 2011; flow intermittence: Lake 2003; Sánchez-Montoya et al. 2009a). As a result, aquatic communities in saline and intermittent streams are characterized by the predominance of Heteroptera, Coleoptera and Diptera taxa (Mellado-Díaz et al. 2008), which present behavioral and physiological adaptation to survive in water courses that withstand these two natural stressors.

The fact that saline streams have lower functional richness and functional redundancy for the large majority of studied traits compared to freshwater stream types indicates that in such ecosystems, which house communities with a high percentage of specialist taxa, loss of any taxon can have a huge impact on the functioning of the community and ecosystem (Walter 1992). In particular, the functional singularity of

saline intermittent streams makes them extremely sensitive to additional anthropogenic impacts, despite their high conservation value (Millán et al. 2011).

In the context of future global change scenarios, which predict higher flow intermittence and water salinity in riverine ecosystems, this study implies a need for better understanding of the functional features of these types of ecosystems.

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Table 1. Main characteristics of the studied streams, number of samples used in this study and typology according to average electrical conductivity and intermittency as number of dry days per year (* F-P = fresh-permanent; F-I = fresh-intermittent; S-P = saline-permanent; S-I = saline-intermittent) (Hydrological type: 0 = 0 dry days; 1 = 1-30 dry days; 2 = 31-90 dry days; 3 = 91-180 dry days; 4 = > 181 dry days).

Stream	X_UTM	Y_UTM	Altitude (m.a.s.l.)	Order	Drainage basin (km ²)	n° samples	Average (± SD) Conductivity (µS/cm)	Hydrological type (dry days)	Type *	Taxonomic Richness
1. Río Segura	5346	42246	1020	3	196.0	7	333.20 (74.25)	0	F-P	110
2. Río Madera	5345	42258	1020	2	100.5	7	406.40 (64.59)	0	F-P	121
3. Río Taibilla	5557	42219	950	2	79.5	7	710.31(101.72)	0	F-P	110
4. Chorros Río Mundo	5492	42565	1040	1	16.4	7	251.86 (66.91)	2	F-I	75
5. Río Mundo at Ayna	5815	42675	650	4	485.6	7	499.04 (91.50)	0	F-P	98
6. Río Mundo at Casas del Río	6175	42439	330	4	2388.0	4	600.13 (165.84)	0	F-P	32
7. Río Quípar	5975	42104	710	3	443.6	7	1772.66 (378.88)	0	F-P	84
8. Fuente Caputa	6314	42166	410	1	11.6	7	2136.46 (593.71)	0	F-P	79
9. Río Pliego	6319	42091	200	4	277.6	3	4470.67 (425.54)	2	S-I	50
10. Río Corneros	5972	41761	650	3	551.2	7	1604.86 (465.13)	0	F-P	93
11. Rambla Puerto Cadena	6616	41975	350	2	11.2	7	2515.86 (214.61)	1	F-I	51
12. Rambla Salada at Periquitos	6660	42215	140	2	42.0	7	55145.71 (18793.44)	0	S-P	30
13. Rambla Majada	6460	41635	60	1	18.8	6	9072.00 (1869.82)	0	S-P	65
14. Rambla Reventón	6421	41682	136	1	12.0	7	20921.43 (4829.59)	0	S-P	51
15. Rambla Garruchal	6701	41023	100	2	11.6	5	11429.00 (4015.46)	3	S-I	50
16. Río Argos	5901	42151	780	4	233.6	7	1074.70 (134.32)	0	F-P	112
17. Río Chícamo	6749	42367	340	1	170.4	7	2623.14 (299.71)	3	S-I	47
18. Río Zumeta	5488	42302	720	4	355.0	3	350.67 (39.50)	0	F-P	99
19. Rambla Rogativa	5676	42216	1105	1	47.2	7	784.00 (142.81)	4	F-I	46
20. Arroyo Blanco	5684	42245	1050	1	23.0	4	647.50 (82.73)	0	F-P	60
21. Rambla Salada at Los Valientes	6635	42216	123	1	38.0	4	32311.25 (2558.23)	3	S-I	17
22. RamblaReventón	6455	41666	92	1	14.0	4	31300.00 (80200.00)	2	S-I	27

Table 2. Pearson's correlation (r) between taxonomic richness and functional richness, between taxonomic richness and functional redundancy and between functional richness and functional redundancy, for all the studied traits. P -value in all the cases is <0.0001 .

		Functional Richness							Taxonomic Richness
N=22		Life-cycle duration	N° reproductive cycle per year	Reproduction	Dispersal	Resistance form	Feeding habits	Food	
Taxonomic Richness		0.864	0.945	0.948	0.980	0.929	0.975	0.987	
Functional Redundancy	Life-cycle duration	0.845	0.940	0.942	0.976	0.925	0.976	0.987	0.999
	N° reproductive cycle per year	0.852	0.921	0.940	0.975	0.918	0.969	0.980	0.998
	Reproduction	0.825	0.922	0.897	0.954	0.881	0.965	0.971	0.991
	Dispersal	0.837	0.930	0.919	0.950	0.902	0.967	0.972	0.993
	Resistance form	0.847	0.927	0.917	0.964	0.886	0.961	0.975	0.995
	Feeding habits	0.871	0.927	0.939	0.970	0.903	0.937	0.968	0.991
	Food	0.836	0.860	0.878	0.909	0.846	0.900	0.898	0.957

Table 3. Relationships between functional and taxonomic richness, and functional redundancy and taxonomic richness, which indicate either a linear or a saturating relationship. The logarithmic relationship between functional richness and taxonomic richness for feeding habits and food traits was not significant. Parameters a and b (\pm SE) that correspond to $y = a + bx$ (linear) and $y = a + b \ln(x)$ (logarithmic) (SE = standard error).

		Functional Richness		Functional Redundancy
		Linear (N=22)	Logarithmic (N=22)	Linear (N=22)
Life-cycle duration	R^2	0.747	0.808	0.999
	AIC	70.57	64.48	70.57
	a	6.716 \pm 0.578	-4.122 \pm 1.635	-6.716 \pm 0.578
	b	0.059 \pm 0.008	3.626 \pm 0.395	0.941 \pm 0.008
	P	<0.000	<0.000	<0.000
	Max trait richness	140 taxa	194 taxa	
Number reproductive cycle per year	R^2	0.892	0.905	0.996
	AIC	91.31	88.56	91.31
	a	9.575 \pm 0.925	-18.225 \pm 2.826	-9.575 \pm 0.925
	b	0.159 \pm 0.12	9.416 \pm 0.683	0.841 \pm 0.012
	P	<0.000	<0.000	<0.000
	Max trait richness	147 taxa	34 taxa	
Reproduction	R^2	0.900	0.937	0.982
	AIC	115.82	105.47	115.82
	a	11.422 \pm 1.615	-40.023 \pm 4.151	0.712 \pm 1.615
	b	0.288 \pm 0.022	17.333 \pm 1.002	0.288 \pm 0.022
	P	<0.000	<0.000	<0.000
	Max trait richness	261 taxa	403 taxa	
Dispersal	R^2	0.960	0.949	0.987
	AIC	104.12	109.22	104.12
	a	8.863 \pm 1.238	-53.115 \pm 4.520	-8.863 \pm 1.238
	b	0.360 \pm 0.017	21.095 \pm 1.092	0.640 \pm 0.017
	P	<0.000	<0.000	<0.000
	Max trait richness	161 taxa	295 taxa	
Resistance form	R^2	0.863	0.912	0.989
	AIC	109.04	99.3	109.04
	a	7.703 \pm 1.385	-29.647 \pm 3.608	-7.703 \pm 1.385
	b	0.207 \pm 0.018	12.552 \pm 0.871	0.793 \pm 0.018
	P	<0.000	<0.000	<0.000
	Max trait richness	180 taxa	384 taxa	
Feeding habits	R^2	0.950		0.983
	AIC	109.59		109.59
	a	10.601 \pm 1.402		-10.601 \pm 1.402
	b	0.365 \pm 0.019		0.635 \pm 0.019
	P	<0.000		<0.000
	Max trait richness	357 taxa		
Food	R^2	0.974		0.916
	AIC	119.84		119.84
	a	7.030 \pm 1.770		-7.030 \pm 1.770
	b	0.653 \pm 0.024		0.347 \pm 0.024
	P	<0.000		<0.000
	Max trait richness	115 taxa		

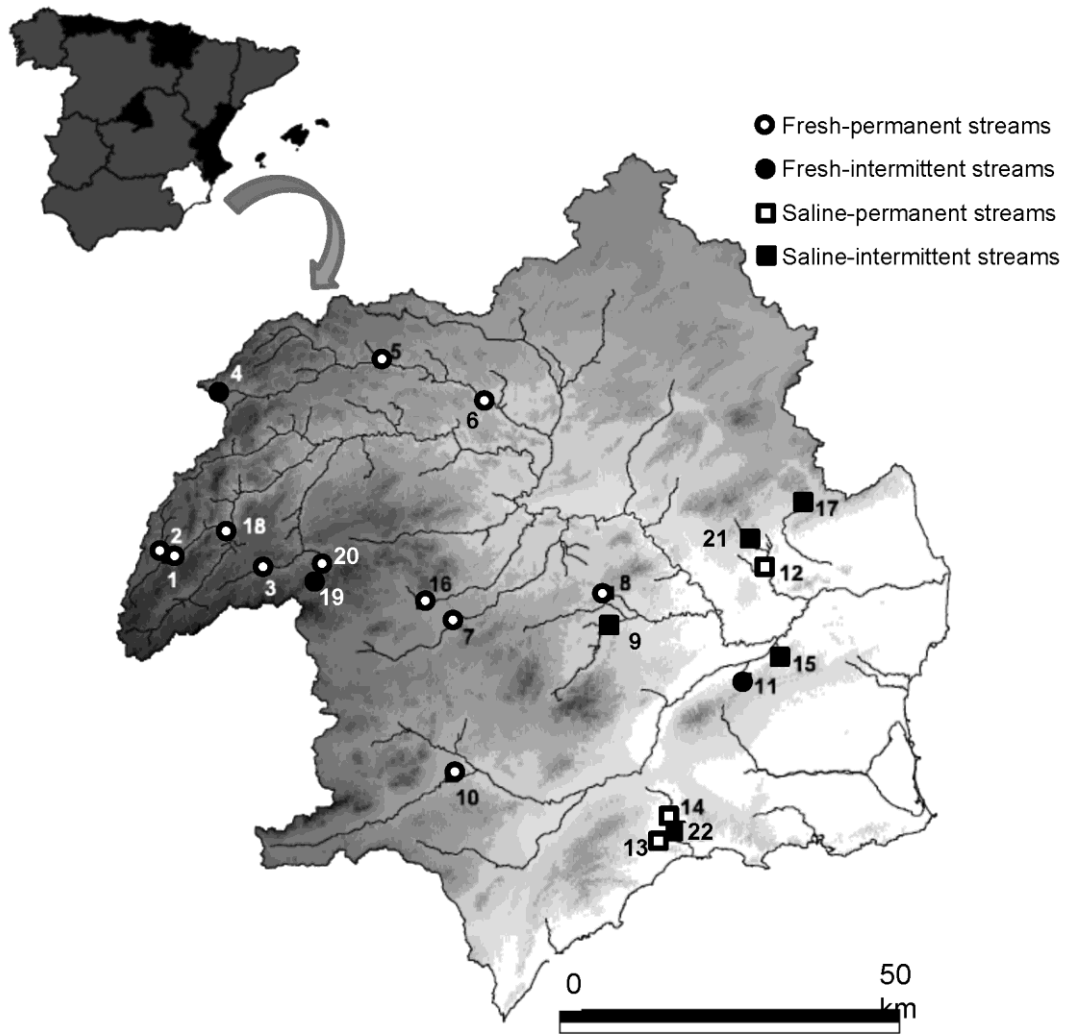


Figure 1. Location of the studied streams in the Segura River Basin and typology according to average electrical conductivity and intermittency (for further data of the sampling sites, see Table 1).

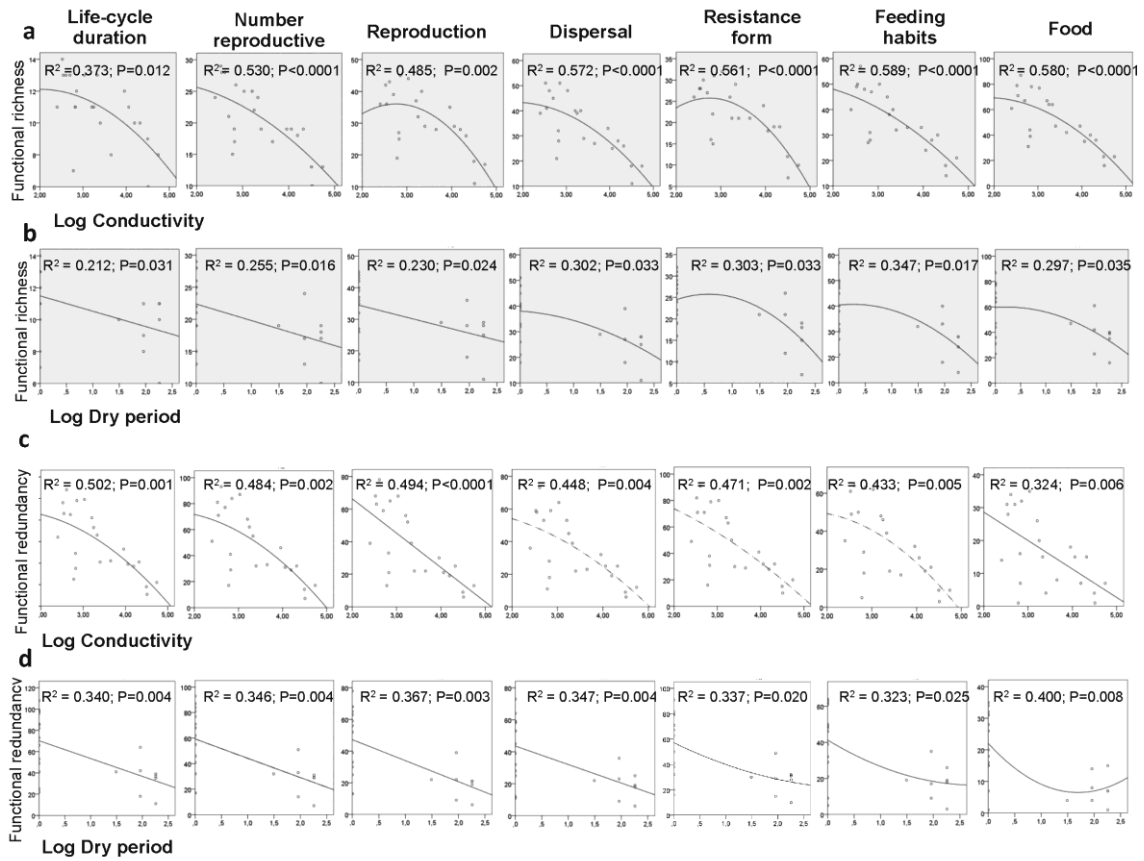


Figure 2. Relationships between functional richness and log conductivity (a); functional richness and log number dry days (b); functional redundancy and log conductivity (c) and functional redundancy and log number dry days (d). The best fit (linear: L or quadratic: Q) function is presented with an adjusted R^2 and P -value. Each point represents one stream site.

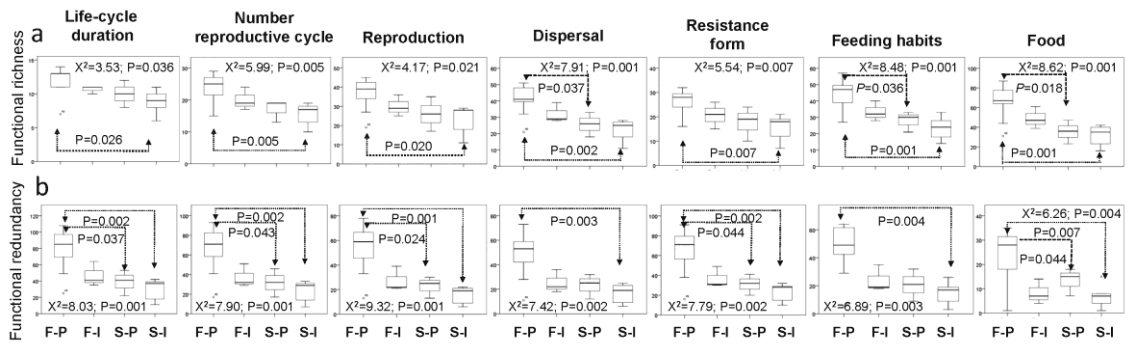


Figure 3. Boxplots of the seven biological traits in the four stream types defined according to water conductivity and flow intermittence. The median values (central line), 25th and 75th percentile values, and maximum and minimum are shown. Results of Kruskal-Wallis tests are given in each plot. Also post-hoc comparisons are indicated when differences were significant.