UNIVERSIDAD DE MURCIA
FACULTAD DE BIOLOGÍA

Structural and Functional Responses of Mediterranean Riparian Communities to Environmental Filters

Respuestas Estructurales y Funcionales de las Comunidades Riparias Mediterráneas a los Filtros Ambientales

D. Daniel Bruno Collados

2015

UNIVERSITY OF MURCIA

Faculty of Biology
Department of Ecology and Hydrology

Doctoral programme “Biodiversity and Environmental Management”

Structural and functional responses of Mediterranean riparian communities to environmental filters

Respuestas estructurales y funcionales de las comunidades riparias mediterráneas a los filtros ambientales

Dissertation submitted by

Daniel Bruno Collados

to obtain the PhD degree with International Mention

by the University of Murcia

Supervisors / Directores:

Josefa Velasco García
David Sánchez Fernández

Biographical Sketch

I was born on 21 February 1985 in Cartagena (Spain) in the riverside of the Benipila ephemeral watercourse during an intense flash flood which inundated the hospital where I saw the light for first time. Maybe it could be one of the reasons why I have been attracted to Mediterranean rivers and semiarid ecosystems since I was a child.

I studied the degree of Environmental Sciences in the University of Murcia and presented the dissertation "Evaluation of riparian restoration projects in Abarán (Murcia)" in 2008. In that period, I joined the Department of Ecology and Hydrology where I obtained a collaboration grant from the Spanish Ministry for Education and Science.

In 2009 I achieved a M.Sc. in Biodiversity management in Mediterranean ecosystems (Master thesis titled "Biodiversity conservation hotspots and biodiversity surrogates in the Murcia region") and started the Doctorate Program "Biodiversity and Environmental Management" receiving a starting research grant. Afterwards, I obtained a FPU fellowship from the Spanish Ministry for Education and Science (training program for university teachers).

During these years as a PhD student at the University of Murcia (Aquatic Ecology Group) I have been involved in varied research fields such as riparian and aquatic ecology, river restoration, sampling efforts and quality inventories' assessment, environmental modelling, biomonitoring, ecosystem functioning and environmental filters, among others. In addition, I have participated in several sampling campaigns in inland aquatic ecosystems in southern Spain (e.g. Ramsar wetlands, Segura River Basin). I have also taught (with *Venia Docendi* habilitation) in the degrees of Biology and Environmental Sciences, as well as in the B.Sc. Biodiversity Management in Mediterranean Ecosystems in the University of Murcia. More concretely, in the subjects of "Ecology", "Management of protected areas" and "Conservation of aquatic insects and their habitats". Finally, during this period, I enjoyed visitor research fellowships in the University of Lisbon with Maria Teresa Ferreira (Forest Research Center) and in Umeå University with Christer Nilsson (Department of Ecology and Environmental Sciences) which were important to develop this thesis.

Consequently, besides the papers that shape this thesis (which are explained in detail in the General Introduction), I have worked on other research published in peer-reviewed international journals and a book chapter.

- Belmar, O., **Bruno, D.**, Martínez-Capel, F., Barquín, J. & Velasco J. (2013) Effects of flow regime alteration on fluvial habitats and riparian quality in a semiarid Mediterranean region. *Ecological Indicators*, 30, 52–64.

- **Bruno, D.**, Sánchez-Fernández, D., Millán, A., Ros, R.M., Sánchez-Gómez, P. & Velasco, J. (2012) Assessing the quality and usefulness of different taxonomic groups inventories in a semiarid Mediterranean region. *Biodiversity and Conservation*, 21, 1561-1575.

- **Bruno, D.,** Sánchez-Fernández, D., Millán, A., Picazo, F., Carbonell, J.A. & Velasco, J. (2012) Predicting the richness of aquatic beetles and bugs in a semi-arid Mediterranean region. *Limnetica*, 31, 23-36.

- **Bruno, D.**, Picazo, F., Carbonell, J.A., Sánchez-Fernández, D., Abellán, P., Velasco, J. & Millán, A. (2012) Áreas prioritarias para la conservación de la biodiversidad en la Región de Murcia. In: *Los espacios naturales protegidos en la Región de Murcia: estudio de casos desde una perspectiva multidisciplinar* (eds Esteve M.A., Martínez-Paz J. M., Soro B.), pp. 85-109. EDITUM, Servicio de Publicaciones de la Universidad de Murcia, Murcia, Spain.

- Carbonell, J.A., Gutiérrez-Cánovas, C., **Bruno, D.**, Abellán, P., Velasco, J. & Millán, A. (2011) Ecological factors determining the distribution and assemblages of the aquatic hemiptera (Gerromorpha & Nepomorpha) in the Segura river basin (Spain). *Limnetica,* 30, 57-70.

The obtained outcomes have been shown in 7 international scientific congress related to Ecology, e.g. XV AIL Congress (best student poster award), 12thEEF, 8th SEFS, IALE2013, I Iberian Conference on Biodiversity and ASLO2015.

Recently, I have been vice-president (2014) of AJIUM (Association of Young Researchers of the University of Murcia). Currently, I am working as researcher on the LIFE+ RIPISILVANATURA which is focused on the control of invasive alien species in the Segura River as well as the strengthening of riparian habitats.

Funding

The fieldwork of this thesis and both grants as well as stays abroad of D. Bruno, have been funded by the following institutions:

- FPU predoctoral grant from Spanish Ministry for Education, Science and Research (AP2009-0432).
- Predoctoral grant from University of Murcia (Spain).
- Euromediterranean Institute of Water (Spain) through the project 'Hydrological classification of the rivers and streams in the Segura basin and associated macroinvertebrate communities'.
- Aquatic Ecology research group from University of Murcia (Spain).

Table of contents

Resumen General

Salix eleagnos (sarga) ocupando la primera banda riparia en el río Tús (Jaén)

Resumen

Los ecólogos han mostrado desde hace tiempo un interés especial en entender y predecir las respuestas ecosistémicas a los cambios ambientales. En el actual contexto de cambio global, los ecosistemas están experimentando un incremento de la intensidad del impacto humano a nivel mundial, llevando a una pérdida de biodiversidad sin precedentes. Esto resulta especialmente preocupante en los ecosistemas acuáticos continentales, siendo éstos reconocidos como uno de los medios más amenazados a nivel mundial. Sin embargo, en comparación con los ecosistemas terrestres, la biología de la conservación en ambientes acuáticos presenta un déficit en calidad y número de estudios empíricos en los que apoyarse. Desde una perspectiva más aplicada, las técnicas de evaluación ecológica deberían permitir el conocer y entender de manera rápida, mecánica y precisa, las consecuencias de los cambios ambientales sobre la biodiversidad y el funcionamiento de los ecosistemas. Por lo tanto, es necesario avanzar en la detección y predicción de las respuestas biológicas a estresantes múltiples en ecosistemas acuáticos, para guiar con éxito los esfuerzos conservacionistas y la gestión de los recursos naturales en estos ambientes.

El efecto del cambio global podría ser especialmente acusado en zonas con clima árido y semiárido, ya que las condiciones de estas áreas se volverán incluso más extremas a corto plazo. En consecuencia, la pérdida de biodiversidad biológica resulta particularmente preocupante en el área mediterránea, que es además, uno de los puntos calientes de biodiversidad del planeta. Las cuencas mediterráneas presentan un especial interés para los estudios ecológicos, ya que muestran amplios gradientes ambientales (tanto naturales como antrópicos), ideales para testar la influencia de diferentes tipos de filtros ambientales en las comunidades biológicas.

Aunque las riberas fluviales son frecuentemente ignoradas en estudios limnológicos, estas áreas de transición entre los ecosistemas acuáticos y terrestres son parte integral de los ecosistemas fluviales, afectando tanto a la estructura como al funcionamiento de los mismos. La vegetación riparia cumple funciones esenciales (ej. fijación de suelo, aporte de materia orgánica) y provee de valiosos bienes y servicios ecosistémicos (ej. materias primas, depuración de agua, recarga de acuíferos, mitigación del impacto de riadas). Además, son comunidades muy diversas y taxonómicamente bien conocidas. Así, las riberas fluviales son un ejemplo paradigmático de zonas interesantes desde el punto de vista biológico pero con un alto grado de impacto humano, especialmente en el Mediterráneo donde el paisaje circundante presenta fuertes presiones antrópicas.

En este contexto, esta tesis tiene como objetivo explorar las respuestas estructurales y funcionales de las comunidades riparias a filtros ambientales, tanto naturales como antrópicos que afectan y amenazan los ecosistemas fluviales mediterráneos, y en particular a la sequía, los usos del suelo y la alteración hidrológica. La presente tesis contribuye a un mejor conocimiento y predicción sobre el efecto de los estresantes naturales y antrópicos en la diversidad, calidad ecológica y funcionalidad de las comunidades riparias y acuáticas, de cara a mejorar las aproximaciones actuales de evaluación ecológica y la gestión de los ecosistemas fluviales. Las plantas leñosas constituyen el núcleo de esta investigación ya que además de tener un rol esencial en las áreas mediterráneas, tienen una notable persistencia y estabilidad (larga vida), así como alta sensibilidad a las presiones humanas, lo que las hace buenas candidatas para ser usadas como un indicador de perturbación.

Todos los estudios que componen esta tesis han sido llevados a cabo en la Cuenca Hidrográfica del Segura, una cuenca de carácter mediterráneo situada en el sureste de la península Ibérica (Mediterráneo occidental) que presenta un marcado gradiente ambiental. El clima oscila desde subhúmedo en las zonas montañosas del noroeste con ríos que presentan caudales medios relativamente altos y estables, al semiárido en las tierras bajas del sureste donde los cursos fluviales muestran caudales medios bajos y variables. Un gradiente de perturbación humana está también presente desde las boscosas cabeceras escasamente pobladas a los tramos fluviales bajos con vegetación arbustiva, ciudades densamente pobladas, fuerte regulación de caudales y cultivos de regadío como principal actividad económica en su cuenca vertiente. Pese a las numerosas áreas actualmente impactadas por la agricultura, (45.2 % de la superficie de la cuenca) o la alteración hidrológica (150 presas > 2 m de altura), la Cuenca del Segura todavía alberga un número importante de ríos con buen estado ecológico, lo que permite evaluar el impacto humano en las comunidades biológicas. Finalmente, estudiar una cuenca con este carácter semiárido en un contexto mediterráneo podría resultar útil para anticipar futuros escenarios en otras cuencas europeas actualmente de carácter más templado, como consecuencia del cambio climático en curso.

La presente tesis está estructurada en cuatro capítulos que tratan diferentes atributos (diversidad, calidad y funcionalidad) de las comunidades riparias mediterráneas y sus relaciones con los filtros ambientales. Primeramente, en el Capítulo 1, se exploran las similitudes y diferencias en los patrones de composición y diversidad taxonómica entre especies riparias de naturaleza leñosa y herbácea, usando para ello un amplio conjunto de filtros ambientales como variables explicativas. Tras encontrar una notable convergencia en los patrones de riqueza riparia, pero una mayor significación para la vegetación leñosa, el Capítulo 2 se centra en el efecto de diferentes tipos de presiones humanas (agricultura y alteración hidromorfológica) a diferentes escalas espaciales sobre la condición ecológica y la diversidad de la vegetación leñosa, en comparación con las comunidades de macroinvertebrados estrictamente acuáticos. Por otro lado, es bien conocido que las aproximaciones basadas en rasgos funcionales muestran ventajas claras sobre los métodos taxonómicos convencionales para predecir las respuestas biológicas a las condiciones ambientales (ej. mejor comparabilidad entre taxones, menor influencia biogeográfica, conexión con el funcionamiento del ecosistema). En consecuencia, el objetivo del Capítulo 3 fue explorar la respuesta funcional de la vegetación leñosa a los filtros ambientales (en especial de la redundancia funcional que se compara con otras medidas de diversidad funcional). Finalmente, en el Capítulo 4, se testa el uso de la redundancia funcional como herramienta de evaluación ecológica (pues resultó ser el índice funcional más sensible a la alteración en el capítulo previo), y se compara con otros índices tradicionales de seguimiento y evaluación.

A continuación, se muestra un resumen más detallado de la aproximación, objetivos, resultados y conclusiones de los cuatro capítulos:

El **Capítulo 1** describe los patrones de riqueza y composición de especies tanto de la vegetación riparia de carácter leñoso como herbáceo e identifica las principales variables ambientales que los conforman. Se exploraron una amplia variedad de variables (climáticas, geológicas, topográficas, hidromorfológicas y de usos del suelo) con efecto potencial en las comunidades riparias. Entre ellas, las hidromorfológicas y los usos del suelo afectaron fuertemente a la composición y diversidad de ambos tipos de vegetación riparia. Por el contrario, la riqueza de especies leñosas estuvo principalmente condicionada por el caudal y la forma del valle mientras que la riqueza de las herbáceas resultó ser más dependiente de las características del sustrato. Tanto la composición como la riqueza de especies mostraron un patrón longitudinal siguiendo el gradiente ambiental en la cuenca, aunque éste fue más evidente para las leñosas que para las herbáceas. Por lo tanto, en el estudio de las comunidades riparias mediterráneas, resultaría adecuado considerar especies leñosas y herbáceas de forma conjunta, o incluso seleccionar solamente uno de los grupos riparios (preferiblemente leñosas).

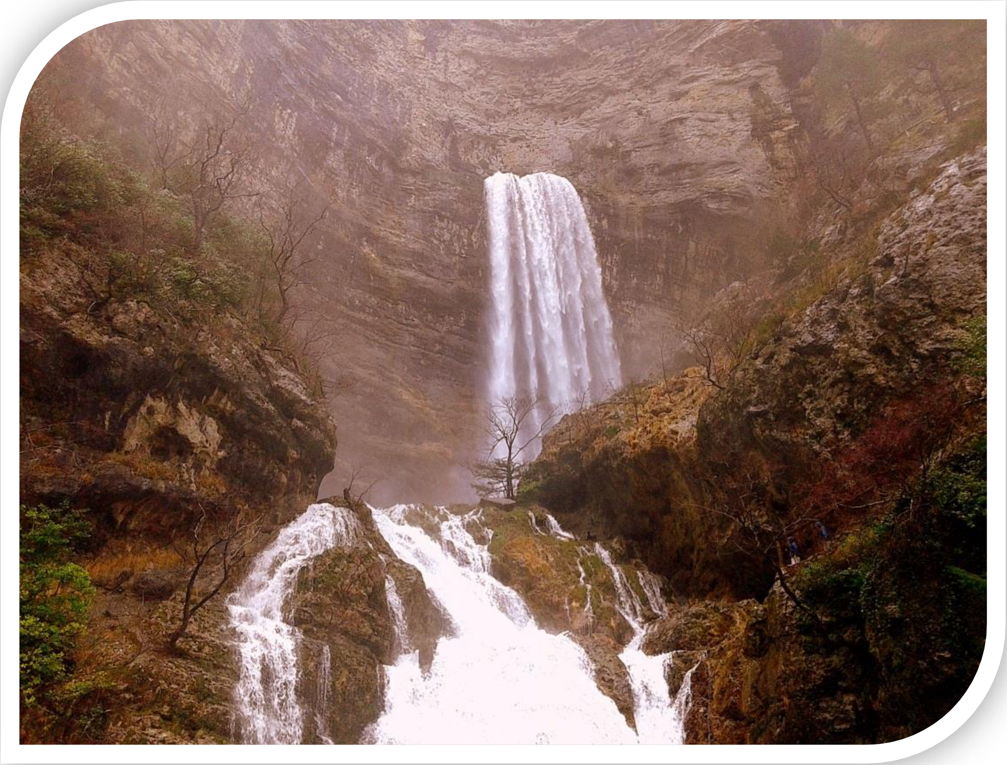
El **Capítulo 2** se centra en la vegetación leñosa y en las principales presiones humanas que afectan a las comunidades de agua dulce en los ríos mediterráneos, es decir, la intensificación de los usos del suelo (representada por el uso de suelo agrícola) y la alteración hidromorfológica. Se evaluaron y compararon las respuestas de las comunidades riparias y de macroinvertebrados acuáticos a tales presiones, teniendo en cuenta que estas respuestas biológicas podían variar dependiendo de la escala espacial considerada y los indicadores usados para detectarlas. Las presiones humanas influenciaron negativamente tanto a las comunidades acuáticas como riparias, independientemente de la escala espacial utilizada (tramo fluvial o cuenca vertiente), la naturaleza de la presión (agricultura o alteración hidromorfológica) o el tipo de indicador biológico utilizado (condición ecológica y diversidad). La agricultura fue la perturbación con mayor efecto sobre las comunidades riparias mientras que la alteración hidromorfológica lo fue para las comunidades acuáticas. La extensión e intensidad de la agricultura y la alteración hidromorfológica en la cuenca vertiente (aguas arriba) tuvo un efecto al menos comparable o incluso mayor que las mismas perturbaciones presentes en el propio tramo de estudio. Finalmente, los índices de condición ecológica fueron más sensibles a las presiones humanas que la riqueza de especies.

En el **Capítulo 3** se explora cómo la redundancia funcional de las comunidades riparias (un atributo funcional relacionado con la estabilidad, resistencia y resiliencia de los ecosistemas) responde a los principales filtros ambientales en las cuencas mediterráneas (sequía, alteración hidrológica y agricultura) y sus interacciones. La respuesta de la redundancia funcional fue comparada con otras medidas de diversidad funcional (riqueza, uniformidad y divergencia funcional). Los valores de todos los índices funcionales descendieron al incrementarse la intensidad del estrés ambiental, especialmente como respuesta a la intensificación agrícola, la presión ambiental más importante para la funcionalidad riparia en el área de estudio. Sin embargo, la redundancia funcional fue más sensible que otras medidas funcionales a los filtros ambientales tanto individuales como múltiples, mostrando un descenso no aleatorio a lo largo de los gradientes de estrés. La redundancia funcional fue predicha y proyectada espacialmente para toda la red fluvial usando variables geográficas de amplia escala obtenidas por SIG, lo que constituye una herramienta útil potencial para el seguimiento y la gestión medioambiental a nivel de cuenca.

En el **Capítulo 4** se testa la aplicabilidad de la redundancia funcional como herramienta para la evaluación y seguimiento ecológico, comparándola con índices convencionales de biomonitoreo (taxonómicos y de calidad ecológica). Concretamente, se evaluaron tanto las respuestas de estos índices a los filtros antrópicos (alteración hidrológica y superficie agrícola) considerando el estrés natural subyacente (sequía), así como su capacidad para discriminar entre diferentes categorías de intensidad de perturbación humana. Aunque todos los índices mostraron respuestas significativas a los filtros ambientales, la redundancia funcional fue la más explicativa y sensible, siendo el único índice capaz de detectar impactos humanos de baja intensidad tanto en ríos permanentes como temporales. Además, en base a los valores de redundancia funcional riparia previamente obtenidos, se establecieron distintas categorías de impacto funcional (referencia, moderado, alto), tanto para los ríos permanentes como temporales del área de estudio. Usando los valores límite de estas categorías de impacto y el mejor modelo de redundancia funcional, se obtuvo un mapa del impacto humano para toda la red fluvial, lo que puede ayudar a los gestores a establecer objetivos y diseñar estrategias para la conservación y restauración a amplia escala. La redundancia funcional puede ser considerada como un buen indicador para evaluar y monitorear el impacto de las perturbaciones humanas en las funciones ecosistémicas. Su integración como una herramienta complementaria en los programas de seguimiento y evaluación puede ayudar a anticipar cambios en la cantidad y estabilidad de las funciones ecosistémicas que desempeñan las comunidades biológicas.

En resumen, se puede concluir que las comunidades riparias mediterráneas experimentan cambios en la composición de especies conforme los filtros ambientales se intensifican, tornándose menos diversas y reduciéndose la calidad, diversidad funcional y redundancia funcional de los hábitats riparios. Esto puede comprometer la capacidad de las riberas fluviales para hacer frente a nuevas perturbaciones (baja resistencia y resiliencia) así como la cantidad y calidad de los bienes y servicios que aportan. Las cabeceras fluviales fueron las áreas más favorables para las comunidades riparias y acuáticas debido a la ausencia de presiones humanas y condiciones ambientales más benignas. En general, la agricultura y la alteración hidromorfológica parecen ser las presiones humanas que más afectan a las comunidades riparias y fluviales, respectivamente. En concreto, la superficie agrícola en la cuenca vertiente ejerció un efecto mayor en la diversidad taxonómica, calidad y funcionalidad de las comunidades riparias. Por lo tanto, la planificación hidrológica y de usos del suelo a escala de cuenca resultan complementos esenciales a las medidas tradicionales de conservación y restauración a nivel local si queremos preservar los ecosistemas fluviales con éxito. Aunque la riqueza taxonómica, la calidad riparia y los índices de diversidad funcional parecen responder claramente a los impactos antrópicos, la redundancia funcional resultó ser más sensible que los otros índices. Además, mostró una reducción dirigida (no aleatoria) en respuesta al incremento de los filtros ambientales, aportando así, información complementaria (a la riqueza de especies) sobre como las comunidades biológicas responden al estrés. Finalmente, su respuesta puede ser predicha para cuencas fluviales completas o áreas administrativas grandes utilizando variables geográficas y de amplia escala obtenidas a través de SIG, y actualmente disponibles para la mayoría de regiones. Los gradientes de estrés natural subyacentes, que influencian los patrones taxonómicos y funcionales en ríos mediterráneos, deben ser tenidos en cuenta a la hora de evaluar las comunidades riparias en estas áreas. De hecho, los valores de referencia para la redundancia funcional difirieron según la temporalidad del río. En este sentido, la redundancia funcional fue el único índice biológico capaz de detectar desde perturbaciones menores a grandes impactos tanto en ríos permanentes como temporales. En consecuencia, la redundancia funcional se perfila como una herramienta útil y complementaria a ser incorporada en el seguimiento y evaluación del estado de los ecosistemas, ya que muestra claras ventajas sobre los índices taxonómicos y de calidad tradicionalmente usados en el biomonitoreo de los mismos.

General Abstract



Source of Mundo river (Albacete)

General Abstract

There is a long-standing interest among ecologists in understanding and predicting ecosystem responses to environmental changes. In the current context of global change, the world's ecosystems are experiencing an increase in human impact intensity leading to an unprecedented biodiversity loss. This is especially worrying in inland aquatic ecosystems, as they have been recognised as one of the most threatened habitats in the world. Nevertheless, in comparison with terrestrial ecosystems, aquatic conservation science is still lagging in quality and quantity of empirical studies. From a more applied perspective, bioassessment techniques should allow an early, precise and mechanistic understanding of the consequences of environmental changes on the relationship biodiversity – ecosystem functioning. Accordingly, to guide conservation efforts and the management of natural resources, it is necessary to move forward in the detection and prediction of aquatic ecosystems responses to multiple environmental stressors.

The effect of global change could be especially dramatic in arid and semiarid areas, whose climatic conditions will become even more extreme in the short term. Thus, the loss of freshwater biodiversity is of particular concern in the Mediterranean Basin, one of the Earth's biodiversity hotspots. Mediterranean river basins have also a particular interest for environmental sciences, as they provide wide environmental gradients (both natural and anthropogenic), making them an ideal scenario to test the influence of different types of environmental filters on biological communities.

Although frequently overlooked in limnological studies, riparian zones, as transitional areas between aquatic and terrestrial ecosystems, are an integral part of freshwater ecosystems conditioning both the structure and functioning of rivers. Riparian vegetation provides essential functions (e.g. soil fixation, organic matter supply) and services (e.g. clean water, recharge aquifers, mitigate flash flood impacts). Besides, these communities are diverse and taxonomically very well-known. Riparian zones are the paradigm of biologically interesting yet highly impacted ecosystems, particularly in the Mediterranean

basins, as they are surrounded by a landscape subjected to high anthropogenic pressures and impacts.

In this context, this thesis aims to explore the structural and functional responses of riparian communities to natural and anthropogenic environmental filters that affect and threaten Mediterranean river ecosystems, specially drought, land use intensification and hydromorphological alteration. It contributes to a better knowledge and prediction about the effect of natural and anthropogenic stressors on the diversity, ecological quality and functionality of riparian and aquatic communities in order to improve bioassessment and environmental management. Besides having an essential role in Mediterranean areas, woody riparian plants constitute the core of this research since they are long-lived, stable and sensitive to human pressures, which make them a good candidate to be used as suitable indicator of disturbance.

All the studies that compose this thesis have been carried out in the Segura river basin. It is a Mediterranean watershed located in the south east of the Iberian Peninsula (West Mediterranean) with marked environmental gradients. The climate ranges from sub-humid in the northwestern highlands, where rivers have relatively stable flows and high discharges, to semiarid in the southeastern lowlands, where streams show more variable flows and lower mean discharges. An anthropogenic disturbance gradient is also present, from sparsely populated forested headwaters to lowland rivers with a predominantly shrubby landscape, densely populated cities, intense flow regulation and irrigated agriculture as the main human activity. Despite the areas currently impacted by agriculture (45.2 % of the basin extent) or hydrological alterations (150 dams > 2 m height), 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. Finally, studying such a semi-arid basin in a western Mediterranean context could be useful to anticipate changes in biological communities in other most temperate European watersheds as a consequence of climate change.

The current thesis is structured in four chapters that address different aspects (diversity, ecological quality and functionality) of riparian Mediterranean communities and their relationships with environmental filters. First, in Chapter 1, the similarities and differences in taxonomic diversity patterns between woody and herbaceous riparian species are explored, using a wide set of environmental filters as explanatory variables. After finding a notable convergence in richness riparian patterns but a greater significance for woody vegetation, Chapter 2 is focused on the effect of various types of human pressures (agriculture and hydromorphological alteration), at different spatial scales, on the ecological condition and diversity of woody riparian plants compared with strictly aquatic macroinvertebrate communities. On the other hand, as it is well-know that trait-based approaches show clear advantages over conventional taxonomic methods to predict biological changes in response to environmental conditions (e.g. better inter-taxon comparability, lower biogeographical influence, mechanistic links to environmental change and ecosystem functioning), the objective of Chapter 3 was to explore the functional response of riparian woodlands (using both functional diversity and redundancy measures) to environmental filters. Finally, in Chapter 4, the use of functional redundancy (it was found as the most sensitive functional index in the previous chapter) as a tool for bioassessment is tested and compared with traditional biomonitoring indices.

Next, a detailed summary of the approach, objectives, results and conclusions of the four chapters is presented:

Chapter 1 describes the composition and richness patterns of both woody and herbaceous riparian vegetation, and identifies the main environmental variables shaping them. We explored a wide variety of variables (i.e. climatic, geologic, topographic, hydromorphologic, land use) with potential effect on riparian communities. Among them, hydromorphology and land use variables strongly affected species composition and diversity for both riparian life forms. On the other hand, woody species richness was mainly influenced by flow conditions and valley shape, whereas herbaceous one was more dependent

on substrate features. Both composition and richness showed a longitudinal pattern following the environmental gradient in the basin, although patterns were clearer for woody than for herbaceous species. Thus, in Mediterranean basins, considering species of both groups jointly or even selecting only one of them (preferably woody ones) could be suitable when studying Mediterranean riparian communities.

Chapter 2 focuses on riparian woodlands and the main human pressures that affect freshwater communities in Mediterranean rivers, i.e. land use intensification (using agriculture as surrogate) and hydromorphological alteration. The responses of riparian and aquatic macroinvertebrate communities to such pressures were assessed and compared taking into account that these biological responses could also vary depending on the spatial scale considered and the indicators used as response variable. Human pressures negatively influenced both riparian and aquatic communities, regardless of the spatial scale considered (basin or reach), the nature of the human pressure (agriculture or hydromorphological alteration) or the type of indicator used (ecological condition or biodiversity). Agricultural land use was the most important disturbance for riparian communities, whereas hydromorphological alteration had a clearer effect on aquatic communities. The extent and intensity of agriculture and hydromorphological alteration upstream (basin scale) had an effect at least comparable to or even greater than that occurring just at the reach scale. Finally, ecological condition indices were more sensitive to human pressures than species richness.

Chapter 3 explores how functional redundancy of riparian communities (a functional feature related to the stability, resistance and resilience of ecosystems) responds to the main environmental filters in Mediterranean basins (i.e. drought, flow regulation and agriculture) and their interactions. Besides, its response is compared with those of different functional diversity measures (i.e. functional richness, evenness and divergence). All functional indices decreased with increasing environmental filter intensity, especially in response to

agriculture, the most important stressor for riparian functionality in the study area. However, functional redundancy was more sensitive than the other functional measures to single and multiple environmental filters and displayed a non-random decline along stress gradients. Functional redundancy was predicted from coarse-grain and remote (SIG) environmental variables for the entire river network, constituting a potential useful tool for biomonitoring and environmental management at basin level.

Chapter 4 tests the applicability of functional redundancy as a tool for bioassessment, comparing it with traditional (taxonomic and ecological status) biomonitoring indices. Concretely, both the response of these indices to anthropogenic environmental filters (hydrological alteration and agriculture) considering the underlying natural stress gradients (e.g. drought), and their ability to discriminate between different categories of human alteration were assessed. Although all indices (functional redundancy, species richness and riparian quality index) showed significant negative responses to environmental filters, functional redundancy was the most explicative and sensitive one, being the only index able to detect subtle human impacts in both perennial and intermittent rivers. In addition, taking the values of functional redundancy as a base, we established different categories of functional disturbance (reference, moderate and high), both in perennial and intermittent rivers of the study area. Using the threshold values of these categories and the best-fitting functional redundancy model, we obtained a human impact map for the entire river network, which can assist decision-makers in setting goals and designing strategies for conservation and restoration at wide scale. Functional redundancy can be used as a meaningful indicator to evaluate and monitor the impact of human disturbances on ecosystem functions. Its integration as a complementary tool in bioassessment programmes can help to anticipate changes in the amount and stability of ecosystem functions provided by biological communities.

In summary, it can be concluded that as the intensity of environmental filters increased, riparian communities change in species composition, turning less diverse, and reducing habitat quality, functional diversity and redundancy. This jeopardises their ability to face new disturbances (low resistance and resilience) as well as the amount and quality of the goods and services provided by these ecosystems. Headwaters were the most favourable areas not only for riparian communities but also for aquatic ones due to the absence of anthropogenic pressures and milder environmental conditions. In general, agriculture and hydromorphological alteration seemed to be the most important anthropogenic pressures for riparian and aquatic communities, respectively. In particular, the extent of agriculture upstream exerted the stronger effect on species diversity, quality and functionality of riparian communities. Accordingly, land use and hydrological planning at basin scale seem essential complements to traditional conservation and restoration measures at reach scale, in order to successfully preserve rivers ecosystems. Although taxonomic richness, riparian quality and functional diversity indices seem to respond clearly to such anthropogenic impacts, functional redundancy proved to be more sensible than the other indices. In addition, it shows a non-random reduction in response to increased environmental filters, providing complementary information to species richness on how biological communities respond to stress. Finally, its response can be predicted from large-scale geographic variables for entire river catchments of large administrative areas. Underlying natural stress gradients (e.g. drought), which influence taxonomic and functional patterns in Mediterranean basins, must be considered when assessing riparian communities in these areas. In fact, reference values for functional redundancy differed depending on flow permanence. Functional Redundancy was the only biological index able to detect from minor to large human impacts in both perennial and intermittent rivers. In conclusion, functional redundancy can be considered as a useful complementary tool for bioassessment and environmental management, since it shows clear advantages over traditional taxonomic and ecological status biomonitoring indices.

General Introduction

Segura river in Almadenes canyon (Murcia)

General Introduction

One of the most serious environmental problems is undoubtedly the acceleration in the rate of species extinction associated with human activities, as it involves an irreversible loss of biological information, threatening also the amount and stability of goods and services provided by ecosystems (Sala *et al*., 2000; Chapin *et al*., 2002). Consequently, understanding and predicting ecosystem responses to ongoing environmental changes is one of the most urgent and exciting challenges for ecologists. From a more applied perspective, it is also imperative to improve the methods to detect, assess and predict the impacts of environmental stressors on natural systems.

Rivers have experienced intense and long-standing human pressures which have caused these habitats to become recognised as some of the most threatened in the world (Saunders *et al*., 2002). In fact, declines in biodiversity are far greater in aquatic than in terrestrial ecosystems (Sala *et al*., 2000). The main impacts on inland aquatic ecosystems are caused by activities such as water overexploitation, flow regulation, agricultural and urban pollution, habitat alteration, riparian deforestation and the introduction of exotic species (e.g. Dudgeon *et al*., 2006). Although freshwater ecosystems are scarce compared with other habitats (covering just 0.8% of the global surface) they host a disproportionally high amount of species (reaching almost 10% of all described species), being considered as hotspots of biodiversity (Strayer & Dudgeon, 2010). Thus, it seems necessary a deeper understanding about the processes and relationships between environmental filters, spatial heterogeneity and riverine communities (Bonada & Resh, 2013; Cooper *et al*., 2013; Garófano-Gómez, 2013) in order to improve conservation policies and minimise the anthropogenic detrimental effects. However, in comparison with terrestrial ecosystems, aquatic science is still lagging in quality and quantity of these empirical studies as well as in systematic conservation planning (Abell, 2002). In addition, climate change is expected to synergistically affect aquatic ecosystems (Moss *et al*., 2009) rising global temperatures and increasing the frequency and intensity of droughts and extreme flow events in some regions (Milly *et al*., 2005). This environmental change is expected to drastically alter the structure and functionality of inland aquatic systems, even promoting their disappearance, especially in arid areas that could turn even more naturally extreme in the short term (Sala *et al*., 2000).

Accordingly, further research is particularly urgent in regions such as the Mediterranean Basin, where climate change models predict a pronounced alteration in precipitation seasonality and an increase in aridity and river intermittency (e.g. Bonada *et al*., 2007; Giorgi & Lionello, 2008) and where the long history of substantial human impacts on fluvial systems has been well-documented (Hooke, 2006). The landscape in this region has been subjected to strong human influences for centuries, which has led to the progressive loss of riverine species and habitats (Tierno de Figueroa *et al*., 2012). Therefore, the historical anthropogenic pressure coupled with the ongoing process of aridification associated to climate change (Sala *et al*., 2000; Filipe *et al*., 2012) has resulted in a critical situation for Mediterranean biodiversity. Despite all these constraints, Mediterranean region stills holds unique and diverse ecological communities, being one of the world's biodiversity hotspots (Myers *et al*., 2000). In sum, rivers in Mediterranean areas can be considered as an ideal scenario to study the influence of environmental filters on aquatic ecosystems, as they harbour highly interesting biological communities subjected to wide gradients of natural and anthropogenic stress.

Most of the studies relating environmental filters to biological communities in rivers have been developed using macroinvertebrates and fish as model organisms (Resh, 2008; Friberg *et al*., 2011), while other components such as riparian vegetation has been frequently overlooked (Ferreira & Aguiar, 2006). However, riparian zones, as transitional areas between aquatic and terrestrial ecosystems, are an integral part of freshwater ecosystems (Ward *et al*., 2002) influencing both the structure (e.g. aquatic communities' composition and richness) and functioning (e.g. aquatic primary production) of freshwater ecosystems (Sabater *et al*., 2000), through different mechanisms such as shading, organic matter supply or providing habitat for aquatic biota (Gregory *et al.,* 1991). Thus, aquatic and riparian communities are mutually interdependent in terms of ecological processes.

Riparian woodlands are among the most fragile of all ecosystems (Nilsson & Grelsson, 1995), and particularly in Mediterranean areas, where riparian zones are the paradigm of biologically interesting yet highly impacted ecosystems (Ferreira *et al*., 2005). In this spatial context, the lushness of riparian trees and shrubs contrasts with the surrounding arid landscape where vegetation is scarce (Fig. 1). These areas support unique ecological communities, constitute a refuge for many species (Brinson & Verhoeven, 1999) and host a large proportion of the regional species pool in a highly populated, fragmented and agriculturally dominated landscape (Allan & Flecker, 1993; Aguiar & Ferreira, 2005; Stella *et al*., 2013). Mediterranean riparian woodlands are essential at regulating microclimate (they reduce solar radiation, temperature, wind and increase humidity), enhancing productivity (strongly limited by water availability in terrestrial adjacent ecosystems), reducing erosion (woody species have in general more complex root systems which is especially important to minimise the physical impact of Mediterranean typical flash floods), acting as a true corridor (in a scarcely vegetated landscape), improving water quality (which is very important at buffering the negative effect of agriculture, i.e. diminishing the amount of sediments, nutrients and pesticides that reach the river course) and increasing water quantity (favouring water infiltration and having a reduced evapotranspiration in comparison with exotic herbaceous species in these regions, e.g. *Arundo donax*) and biodiversity (riparian areas constitute a refuge for deciduous species, absent from conventional Mediterranean forests; Velasco, 2008). Consequently, riparian deforestation in Mediterranean areas could affect the numerous ecosystem functions and services they are sustaining in a greater extent than in more temperate ones. Woody riparian plants are long-lived, stable and sensitive to human pressures, which makes them a good candidate to be used as a suitable indicator of disturbance (Nilsson *et al*., 1991; Bejarano *et al*., 2012; Villarreal *et al*., 2012).

Fig. 1. The exuberance of riparian forests contrasts with the semi-arid shrubby landscape in Mediterranean areas.

Although many authors have studied the influence of single stressors on riparian and aquatic communities, the effect of multiple simultaneous environmental filters has been scarcely tested (Gutiérrez-Cánovas *et al.*, 2015). However, this is important as the intensity of the stressor effect can vary acutely depending on if it acts in combination or alone. The study of multi stressors effects on natural ecosystems constitutes a major issue in ecological research (Breitburg *et al.*, 1999; Vinebrooke *et al.*, 2004), especially in Mediterranean ecosystems, where multiple natural (e.g. drought, salinity) and anthropogenic pressures usually co-occur and interact. Accordingly, bioassessment and biomonitoring tools are performed to measure the impact of anthropogenic stress in ecosystems by using a set of sensitive biological indicators under undisturbed conditions as a reference, to be compared with impaired sites in order to quantify the human-induced deviation from the reference conditions. For naturally benign ecosystems, conventional bioassessment can easily detect the effect of human stressors (e.g. Bonada *et al.*, 2006; Friberg *et al.*, 2011). However, detecting signs of degradation in naturally-stressed ecosystems is much more complicated, because they share some similarities with anthropogenically-stressed ecosystems such as low diversity or dominance of stress-tolerant species (e.g. Elliott & Quintino, 2007; Gutiérrez-Cánovas *et al*., 2015).

The effects of environmental stressors can vary depending on the spatial scale analysed and the indicator used to estimate the responses of biological communities. Despite the limitations of taxonomic approaches to predict and generalise the effects of environmental change (McGill *et al.,* 2006), biomonitoring efforts have been mainly focused on taxonomic features (species occurrence or abundance), ignoring other facets of biodiversity, such as functional components. During the last decade, theoretical and empirical studies have demonstrated the utility of functional measures to explore the effects of human activity on biodiversity (Clapcott *et al*., 2010; Laliberté *et al*., 2010; Mouillot *et al*., 2013). Although this new knowledge has not been translated to biomonitoring (McGill *et al*., 2006), the incorporation of functional measures to conventional tools supposes a great opportunity of improving river management in a cost-effective way. Therefore, holistic bioassessment approaches that consider different aspects of biodiversity (composition, diversity, quality and functionality) should allow an early, precise and mechanistic understanding of the consequences of environmental changes on the relationship biodiversity – ecosystem functioning (Chapin *et al*., 2002; Hooper *et al.,* 2012).

Objectives and thesis structure

The main goal of this thesis is to study the structural and functional responses of riparian communities to the environmental filters that affect and threaten Mediterranean rivers in order to improve bioassessment techniques and environmental management. This thesis focuses on the Segura River basin and follows a holistic approach considering different types of environmental filters, taxonomic, structural and functional indicators and also including both riparian and aquatic communities. Woody riparian vegetation constitutes the core of this research, although herbaceous riparian vegetation and aquatic macroinvertebrates are also considered for comparative purposes in some chapters.

More specifically, the aims of this thesis are to:

1) Describe the composition and richness patterns of riparian vegetation in a semi-arid Mediterranean basin and the environmental factors (climate, geology, topography, hydrogeomorphology and land use) that best explain both woody and herbaceous riparian patterns (*Chapter 1*).

2) Assess the influence of the main anthropogenic disturbances (agriculture and hydromorphological alteration) at different spatial scales (basin and reach) on the biodiversity and ecological condition of both Mediterranean riparian and strictly aquatic communities (*Chapter 2*).

3) Explore how functional redundancy and other measures of functional diversity (functional richness, functional divergence and functional evenness) of riparian communities respond to single and multiple environmental filters in a Mediterranean basin, and to predict the response of the most sensitive functional measure for the entire river network (*Chapter 3*).

4) Test the usefulness of functional redundancy in ecosystem bioassessment comparing its response with other usual taxonomic and ecological quality biomonitoring tools, along the main gradients of natural (i.e. drought) and anthropogenic stress (i.e. flow regulation and agriculture) in a Mediterranean basin (*Chapter 4*).

This thesis is structured in four chapters, corresponding to four scientific articles. Chapters 1 and 2 have already been published in international peer-reviewed journals indexed in SCI, while chapter 3 has recently been resubmitted for publication and it is currently under second review. Finally, chapter 4 is in preparation to be submitted. The four articles on which this thesis is based are:

Chapter 1 Bruno, D., Belmar, O., Sánchez-Fernández, D. & Velasco, J. (2014) Environmental determinants of woody and herbaceous riparian vegetation patterns in a semi-arid Mediterranean basin. *Hydrobiologia*, **730**, 45–57.

Chapter 2 Bruno, D., Belmar, O., Sánchez-Fernández, D., Guareschi, S., Millán, A. & Velasco, J. (2014b) Responses of Mediterranean aquatic and riparian communities to human pressures at different spatial scales. *Ecological Indicators*, **45**, 456–464. Also outlined by *Science for Environment Policy*, journal edited by the European Commission DG Environment (Issue 390, 2014).

Chapter 3 Bruno, D., Gutiérrez-Cánovas, C., Sánchez-Fernández, D., Velasco, J. & Nilsson, C. (under second review) Impacts of environmental filters on functional redundancy in riparian vegetation. *Journal of Applied Ecology.*

Chapter 4 Bruno, D., Gutiérrez-Cánovas, C., Velasco, J. & Sánchez-Fernández, D. (to be submitted) Functional redundancy as a tool for bioassessment: a test using riparian vegetation. *Science of the Total Environment.*

Study area

The Segura River basin (SE Iberian Peninsula) is a Mediterranean watershed located in one of the most arid zones of Europe (Fig. 2). Despite its relatively small size (18,870 km^2), it presents a strong climatic and altitudinal gradient from NW to SE. Therefore, as in other Mediterranean regions, the basin is characterised by scarce and unevenly distributed water resources. Climate ranges from wet (<1,000 mm mean annual precipitation) and cold (<10°C mean annual temperature) in the northwestern mountains (<2,000 m) to dry (<200 mm) and hot (>18°C) in the lowlands (CHS, 2007). Accordingly, there is a gradient from perennial rivers characterised by relatively large and stable flows to intermittent streams featuring variable and discontinuous flows (summer drought) and lower mean discharges (Belmar *et al.*, 2011). Regarding geology, mountain headwaters are dominated by calcites and dolomites with varied karstic relief, whereas the plains are characterised by the dominance of limestone as well as Miocene and Triassic marls made up of continental and frequently marine sediments. This geological diversity adds physical heterogeneity to the river courses and generates high variability in natural water salinities.

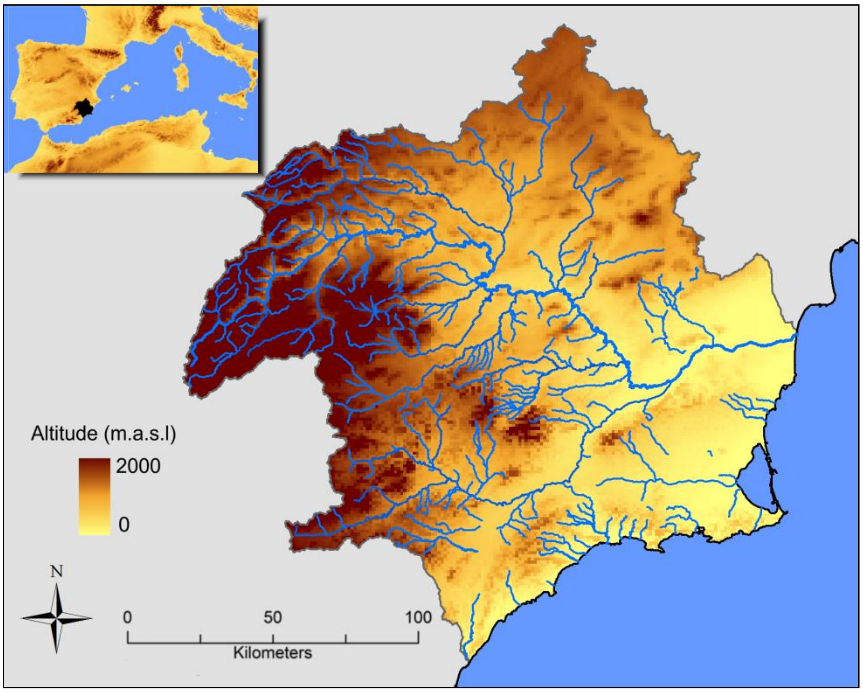


Fig. 2. Geographic location of the Segura River basin in Iberian Peninsula and western Mediterranean basin showing the altitudinal gradient and the watercourses in the study area.

This environmental natural gradient is coupled with an anthropogenic disturbance gradient (also NW–SE). The basin ranges from sparsely populated forested (Mediterranean conifer forests) headwaters to lowland rivers with densely populated cities, irrigated lands, intense flow regulation and a predominantly shrubby landscape in their watersheds. The intense expansion of agricultural land (the main land use occupying 52.1% of the entire basin), especially irrigated during the last 25 years, resulted in a reduction of natural and semi-natural areas, now representing 45.2% of the basin extent and mainly located in the headwaters. Comparatively, artificial land use occupies a little extent in the basin (2.1% estimated from Corine land cover 2000). The water supply for irrigation is responsible for 90% of water demands in the study area, and therefore constitutes the main anthropogenic pressure on stream flows (CHS, 2007). Furthermore, water demands exceed largely the water resources of the basin (Gil-Olcina, 2000) thereby producing a structural deficit that has been accentuated in recent decades by a decreasing trend in precipitation. As a consequence of such intense pressure, there is an intense flow regulation and overexplotation on running waters, leading to widespread hydromorphological alterations. The Segura basin has a great regulatory capacity (770 hm^3, over 90% of the natural input) provided by 24 large (10 m height; Grindlay *et al.*, 2009) and 121 medium dams (higher than 2 m; CHS, 2007). Therefore, with an average of a big dam every 50 km of channel, it is one of the most regulated river networks in Spain and Europe (Ministry for the Environment, 2004; CHS, 2007). In contrast to the areas currently impacted by agriculture and/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 (Fig. 3). The high environmental diversity due to natural and human influence makes this basin an ideal candidate to be utilised as a Mediterranean pilot basin to represent other areas under semiarid climates around the world, as they involve a wide range of conditions that can be present in most Mediterranean basins. In addition, studying such a semiarid basin in a western Mediterranean context may help to anticipate changes in temperate European watersheds as a consequence of climate change.

Fig. 3. River reaches with different ecological condition (from undisturbed to very highly disturbed) in the Segura river basin.

All of these environmental features result in a great variety of riparian communities (Fig. 4; Alcaraz *et al*., 1997). The upper sector is characterised by common species in Europe (*Salix* spp., *Fraxinus* spp., *Crataegus* spp., *Corylus* spp.). The midlands are a transitional area presenting a mixture of European and North African flora (*Salix* spp., *Fraxinus* spp., *Populus* spp., *Tamarix* spp., *Nerium oleander*), which constitute a singular occurrence in the Iberian Peninsula. Finally, the high thermal, hydrological and osmotic stress in the lowland rivers and streams form a barrier for most European riparian species that leads to the exclusive presence of Mediterranean and North African species (*Tamarix canariensis*, *Tamarix boveana*, *Tamarix africana*, *Nerium oleander*, *Phoenix dactylifera;* Ríos, 1994).

Fig. 4. Environmental gradient and diversity of riverine communities in the study area. Riparian transition from typically European taxa (*Fraxinus* spp., *Populus* spp., *Salix* xpp.) in the headwaters (upper images) to Mediterranean and North African ones in the lowlands (*Tamarix* spp., *Nerium oleander*, *Phoenix dactylifera*).

References

Abell, R. (2002) Conservation biology for the biodiversity crisis: A freshwater follow-up. *Conservation Biology*, **16**, 1435–1437.

Aguiar, F.C. & Ferreira, M.T. (2005) Human-disturbed landscapes: effects on composition and integrity of riparian woody vegetation in the Tagus River basin, Portugal. *Environmental Conservation*, **32**, 30–41.

Alcaraz, F., Ríos, S., Inocencio, C. & Robledo, A. (1997) Variation in the riparian landscape of the Segura River Basin, SE Spain. *Journal of Vegetation Science*, **8**, 597–600.

Allan, J.D. & Flecker, A.S. (1993) Biodiversity conservation in running waters. *BioScience*, **43**, 32–43.

Bejarano, M.D., González del Tánago, M., Garcia de Jalón, D., Marchamalo, M., Sordo-Ward, A. & Solana-Gutiérrez, J. (2012) Responses of riparian guilds to flow alterations in a Mediterranean stream. *Journal of Vegetation Science*, **23**, 443–458.

Belmar, O., Velasco, J. & Martinez-Capel, F. (2011) Hydrological classification of natural flow regimes to support environmental flow assessments in intensively regulated Mediterranean rivers, Segura River basin (Spain). *Environmental Management*, **47**, 992–1004.

Bonada, N., Prat, N., Resh, V.H., & Statzner, B. (2006) Developments in aquatic insect biomonitoring: A comparative analysis of recent approaches. *Annual Review of Entomology*, **51**, 495–523.

Bonada, N., Dolédec, S. & Statzner, B. (2007) Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implications for future climatic scenarios. *Global Change Biology*, **13**, 1658–1671.

Bonada, N. & Resh, V. (2013) Mediterranean-climate streams and rivers: geographically separated but ecologically comparable freshwater systems. *Hydrobiologia*, **719**, 1–29.

Breitburg, D.L., Baxter, J.W., Hatfield, C.A., Howarth, R.W., Jones, C.G., Lovett, G.M., *et al.* (1998) Understanding effects of multiple stressors: ideas and challenges. *Successes, Limitations, and Frontiers in Ecosystem Science* (eds Pace, M.L. & Groffman, P.M.), pp. 416–431. Springer, New York, USA.

Chapin, F.S.III, Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., *et al*. (2002) Consequences of changing biodiversity. *Nature*, **405**, 234–242.

CHS (2007). *Estudio General sobre la Demarcación Hidrográfica del Segura.* Confederación Hidrográfica del Segura, Murcia, Spain.

Clapcott, J.E., Young, R.G., Goodwin, E.O. & Leathwick, J.R. (2010) Exploring the response of functional indicators of stream health to land-use gradients. *Freshwater Biology*, **55**, 2181–2199.

Cooper, S.D., Lake, P.S., Sabater, S., Melack, J.M. & Sabo, J.L. (2013) The effects of land use changes on streams and rivers in mediterranean climates. *Hydrobiologia*, **719**, 383–425.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Leveque, C., *et al*. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, **81**, 163–182.

Elliott, M. & Quintino, V. (2007) The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Marine Pollution Bulletin*, **54**, 640–645.

Ferreira, M.T., Aguiar, F.C. & Nogueira, C. (2005) Changes in riparian woods over space and time: influence of environment and land use. *Forest Ecology and Management*, **212**, 145–159.

Ferreira, M.T. & Aguiar, F.C. (2006) Riparian and aquatic vegetation in Mediterranean-type streams (western Iberia). *Limnetica*, **25**, 411–424.

Filipe, A.F., Lawrence, J.E. & Bonada, N. (2013) Vulnerability of stream biota to climate change in mediterranean climate regions: a synthesis of ecological responses and conservation challenges. *Hydrobiologia*, **719**, 331–351.

Friberg, N., Bonada, N., Bradley, D.C., Dunbar, M.J., Edwards, F.K., Grey, J., *et al*. (2011) Biomonitoring of human impacts in freshwater ecosystems: the good, the bad and the ugly. *Advances in Ecological Research*, **44**, 1–68.

Garófano-Gómez, V. (2013) *Riparian vegetation patterns according to hydrogeomorphological factors at different spatial and temporal scales in Mediterranean rivers*. PhD dissertation, Polytechnic University of Valencia, Valencia, Spain.

Gil-Olcina, A. (2000) Acondicionamiento hidráulico y desnaturalización del río Segura. *Ería,* **51**, 45–59.

Giorgi, F. & Lionello, P. (2008) Climate change projections for the mediterranean region. *Global and Planetary Change*, **63**, 90–104.

Gregory, S.V., Swanson, F.J., McKee, W.A. & Cummins, K.W. (1991) An ecosystem perspective of riparian zones. *Bioscience*, **41**, 540–551.

Grindlay, A., Zamorano, M., Rodriguez, M.I., Molero, E. & Urrea, M.A. (2009) Territorial transformation and water utilization: hydrological planning scenarios in the Segura river basin. *Fourth International Conference on Sustainable Development and Planning,* **2**, 975-984.

Gutiérrez-Cánovas, C., Sánchez-Fernández, D., Velasco, J., Millán, A. & Bonada, N. (2015) Similarity in the difference: changes in community functional features along natural and anthropogenic stress gradients. *Ecology,* **96**, 2458–2466.

Hooke, J.M. (2006) Human impacts on fluvial systems in the Mediterranean region. *Geomorphology*, **79**, 311–335.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., *et al.* (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, **486**, 105–108.

Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., *et al*. (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters*, **13**, 76–86.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, **21**, 178–185.

Milly, P.C.D., Dunne, K.A. & Vecchia, A.V. (2005) Global pattern of trends in streamflow and water availability in a changing climate. *Nature*, **438**, 347–350.

Ministry for the Evironment (2004) *Water in Spain*. Secretaría de Estado de Aguas y Costas, Madrid, Spain.

Moss, B., Hering, D., Green, A.J., Aidoud, A., Becares, E. & Beklioglu, M. (2009) Climate change and the future of freshwater biodiversity in Europe: A primer for policy-makers. *Freshwater Reviews*, **2**, 103–130.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, **28**, 167–177.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Nilsson, C., Ekblad, A., Gardfjell, M. & Carlberg, B. (1991) Long-term effects of river regulation on river-margin vegetation. *Journal of Applied Ecology*, **28**, 963–987.

Nilsson, C. & Grelsson, G. (1995) The fragility of ecosystems: a review. *Journal of Applied Ecology*, **32**, 677–692.

Resh, V.H. (2008) Which group is best? Attributes of different biological assemblages used in freshwater biomonitoring programs. *Environmental Monitoring and Assessment*, **138**, 131–138.

Ríos, S. (1994) *El Paisaje vegetal de las riberas del Río Segura*. PhD dissertation, University of Murcia, Murcia, Spain.

Sabater, F., Butturini, A., Martí, E., Muñoz, I., Romaní, A., Wray, J. & Sabater, S. (2000) Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. *Journal of the North American Benthological Society*, **19**, 609–620.

Sala, O.E., Chapin, F.S.III, Armesto, J.J., Berlow, R., Bloomfield, J., Dirzo, R., *et al*. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

Saunders, D.L., Meeuwig, J.J. & Vincent, A.C.J. (2002) Freshwater protected areas: Strategies for conservation. *Conservation Biology*, **16**, 30–41.

Stella, J.C., Rodríguez-González, P.M., Dufour, S. & Bendix, J. (2013) Riparian vegetation research in Mediterranean-climate regions: common patterns, ecological processes, and considerations for management. *Hydrobiologia*, **719**, 291–315.

Strayer, D.L. & Dudgeon, D. (2010) Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society,* **29**, 344–358.

Tierno de Figueroa, J.M.T., López-Rodríguez, M.J., Fenoglio, S., Sánchez-Castillo, P. & Fochetti, R. (2012) Freshwater biodiversity in the rivers of the Mediterranean Basin. *Hydrobiologia,* **719**, 137–186.

Velasco, J. (2008) *Manual para la restauración de riberas en la cuenca del río Segura*. Confederación Hidrográfica del Segura, Murcia, Spain.

Villarreal, M.L., Drake, S., Marsh, S.E. & McCoy, A.L. (2012) The influence of wastewater subsidy, flood disturbance and neighbouring land use on current and historical patterns of riparian vegetation in a semi-arid watershed. *River Research and Applications*, **28**, 1230–1245.

Vinebrooke, R.D., Cottingham, K.L., Norberg, J., Scheffer, M., Dodson, S.I., Maberly, S.C., *et al.* (2004) Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. *Oikos*, **104**, 451–457.

Ward, J.V., Tockner, K., Arscott, D.B. & Clarett, C. (2002) Riverine landscape diversity. *Freshwater Biology*, **47**, 517–539.

Chapters

Halophilic riparian vegetation in Rambla Salada (Murcia)

Chapter 1

Environmental determinants of woody and herbaceous riparian vegetation patterns in a semi-arid Mediterranean basin

Mundo river valley near Liétor (Albacete)

Abstract

What environmental variables determine riparian vegetation patterns? Are there differences between woody and herbaceous species? To answer these questions, we first explored the composition and richness patterns of both riparian woody and herbaceous species in a semiarid Mediterranean basin. Then, we assessed the environmental factors (climate, geology, topography, hydromorphology and land use) that best explain these patterns. We used the following methodological approaches: clustering analyses, distance-based linear models, generalised linear models and hierarchical partitioning procedures. Valley shape, drought duration, river habitat heterogeneity, water conductivity and agricultural land use were the most important variables explaining variation in species composition for both groups. Woody riparian richness was mainly influenced by flow conditions and valley shape, whereas herbaceous one was more dependent on substrate features. Thus, although some differences in the importance of individual variables were observed, we found a notable congruence in the composition and species richness of both groups and also in the main types of variables explaining these patterns (hydromorphology and land use, especially agriculture). Our results show that both communities could be treated in a holistic way, since they respond similarly to the strong natural and anthropogenic environmental gradients present in Mediterranean basins.

Introduction

As transitional areas between aquatic and terrestrial ecosystems, riparian zones are a key component of fluvial ecosystems. These areas have interesting and unique characteristics from biological, functional, ecological and landscape perspectives (Wiens, 2002). They present disproportionately high species diversity and ecosystem services in comparison with surrounding terrestrial ecosystems (Nilsson & Svedmark, 2002). Furthermore, riparian vegetation influences the whole river ecosystem function (e.g. aquatic primary production) and structure (e.g. aquatic communities' composition and richness) through different mechanisms such as shading, organic matter supply or providing habitat for aquatic biota (Gregory *et al.,* 1991).

A number of studies have determined relationships among the riparian vegetation patterns and natural and/or anthropogenic factors at multiple scales, such as those related to climate (e.g. Nilsson *et al.,* 1991), topography (e.g. Baker, 1989), geology (e.g. Lyon & Gross, 2005), hydromorphology (e.g. Renöfält *et al.,* 2007) or land use (Allan, 2004). However, most of these previous studies have assessed the influence of just one specific group of variables, which in some cases could result in only a partial interpretation of the results. In addition, the response of riparian vegetation to some of these groups of variables has been scarcely tested in Mediterranean areas and it could be different from that observed in temperate ones.

In Mediterranean basins, riparian zones are the paradigm of biologically interesting yet highly impacted ecosystems. These areas support unique ecological communities, constitute a refuge for many species (Brinson & Verhoeven, 1999) and host a large proportion of the regional species pool in a highly populated, fragmented and agriculturally dominated landscape (Aguiar & Ferreira, 2005; Stella *et al.,* 2013). In natural basins, middle and low river reaches are supposed to support greater riparian species richness than headwaters due to higher riparian habitat availability and physical heterogeneity (River Continuum Concept, Vannote *et al.,* 1980). However, given the strong anthropogenic pressures in most of the Mediterranean basins (flow regulation by dams and intensive agriculture in the valleys), hydrological and land-use variables can be more important explaining riparian vegetation patterns (Tabacchi *et al.,* 1996; Ferreira & Moreira, 1999) than riparian habitat availability, and consequently, the opposite pattern could be observed. In addition, Mediterranean basins usually show a strong climatic gradient from wet and cold headwaters to dry and hot lowlands so we expect that aridity also constrains riparian composition and richness values in lower stream reaches. Thus, although Mediterranean riparian species are naturally adapted to flashfloods, low precipitation and seasonal droughts, they are outstanding limiting factors for the occurrence of many riparian species in semiarid rivers (Lite *et al.,* 2005), especially woody ones (Salinas & Casas, 2007). Moreover, the natural adaptations' effectiveness of riparian species is compromised by the increasing human alterations that make these environmental regimes more unpredictable. In fact, Mediterranean areas could turn even more extreme in the short term, as climatic change is expected to decrease mean annual rainfall, alter precipitation seasonality and increase droughts in these areas (Giorgi & Lionello, 2008; European Commission, 2009). Thus, given the high vulnerability of aquatic and riparian communities to global changes (Sala *et al.,* 2000), it seems urgent to improve the existing knowledge regarding the factors shaping these highly diverse and functionally interesting communities in the Mediterranean biodiversity hotspot.

Riparian diversity patterns vary not only among regions as a consequence of their associated environmental and anthropogenic conditions, but also among plant groups (Tabacchi & Planty-Tabacchi, 2001). Most studies have examined the diversity patterns of herbaceous and woody species together (Tabacchi *et al.,* 1996; Aguiar *et al.,* 2006). Although both groups share the same habitat (i.e. riparian area), according to their different role in plant succession, evolutionary histories, functional traits and ecological requirements, the diversity patterns and the variables influencing them could differ (Sagers & Lyon, 1997; Nichols *et al.,* 1998). Thus, a higher dependence of Mediterranean woody species on water-related variables (e.g. flow or drought period) could be found (Salinas & Casas, 2007), while herbaceous species could be more sensitive to some physical attributes such as substrate characteristics or geomorphic heterogeneity (Sagers & Lyon, 1997). However, studies developed in Mediterranean areas have usually focused on riparian woody species communities, whereas non-woody groups have been traditionally understudied (Aguiar *et al.,* 2009; Stella *et al.,* 2013). Finally, divergences in the responses of both groups to environmental and anthropogenic variables would have implications for the management and conservation of the riparian ecosystem, as management measures should be different for each group of species to be effective.

Here, we aimed (i) to explore the composition and richness patterns of both riparian woody and herbaceous species in a semiarid Mediterranean basin with marked environmental and anthropogenic gradients and (ii) to assess the environmental factors (climate, geology, topography, hydromorphology and land use) that best explain these patterns. Considering the exposed above, we expected these strong environmental and anthropogenic gradients to shape biological communities forming a longitudinal continuum species replacement in terms of composition for both groups of species, following the River Continuum Concept. Regarding the richness distribution pattern, given the aforementioned particularities of Mediterranean basins and contrarily to what is expected in other areas, a continuous longitudinal decreasing richness pattern from humid and undisturbed headwaters to arid and impaired lowlands could be found. Accordingly, hydromorphological, land-use and climatic variables are expected to be the main groups of variables influencing both groups' species composition and richness patterns.

Materials and methods

Data collection

Field data

A total of 81 survey units were selected to represent the wide range of environmental (natural and anthropogenic) conditions in the Segura basin (Fig. 1). Each locality was sampled once between 2010 and 2012 (25–30 localities each year) during late spring and summer (always under low flow conditions) along 500 m length reaches at both riversides, with this period being more suitable when using one-shot surveys (Ferreira & Aguiar, 2006). Within these 500 m length reaches, we recorded the occurrence of riparian species, from water margin up to natural bankfull width, obtaining two lists of species for each survey unit (woody and herbaceous species). Within riparian herbs, given our sampling design (we needed three different years to survey 81 localities once), annual plants were not considered due to their high temporal variation (Naiman *et al.*, 2005; Ferreira & Aguiar, 2006). Thus, the term 'herbaceous' refers here only to perennial, non-strictly aquatic herbaceous species.

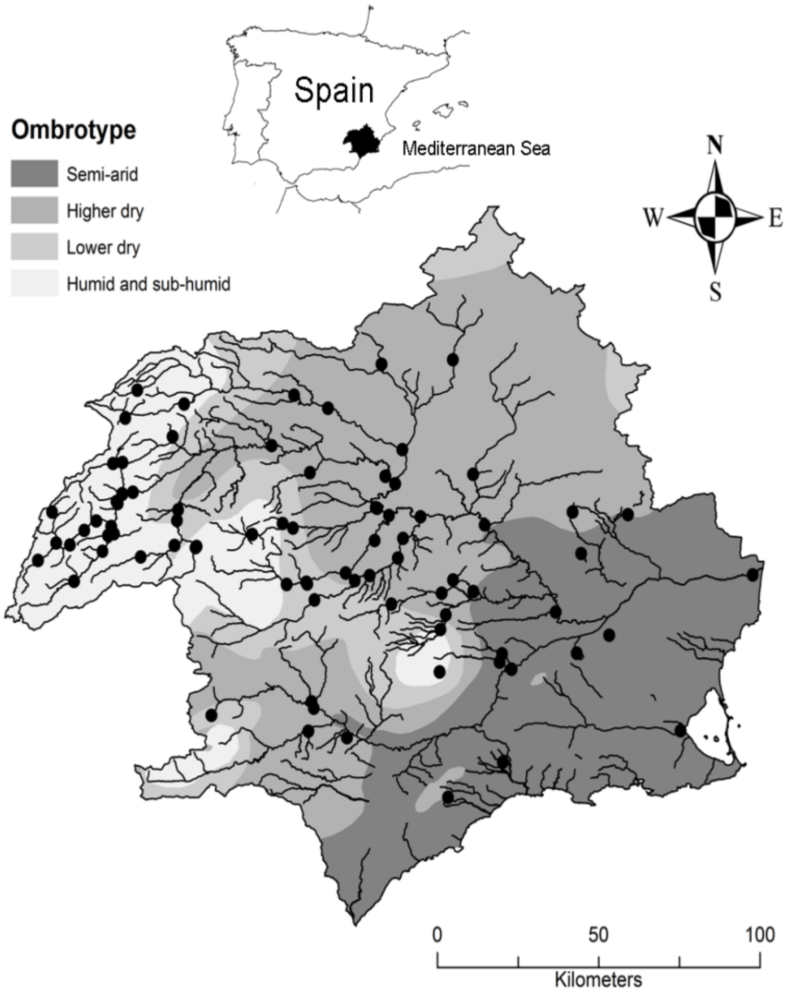


Fig. 1. Geographic location of the Segura river basin in the Iberian Peninsula showing the 81 survey units and the climatic gradient represented by the ombrotype classes; as defined by Rivas-Martínez (1985).

Within each of the 81 survey units, a number of environmental variables at reach scale (see Appendix 1.1) were measured directly in the field: water conductivity, hydromorphological variables (valley shape, riverbed grain size, bank profile, flow, water depth and width and channel artificiality) and the percentage of different land uses beyond the riparian area using two buffers (5 and 50 m width). These variables were measured following the river habitat survey (RHS) protocol (Raven *et al.,* 1997) which was designed to characterise and assess physical structure and habitat variables. The RHS requires ten measurements (one each 50 m) within each survey unit. Thus, average values of each variable were calculated for each one of the survey units (500 m) as well as the final value of the habitat quality assessment (HQA) (Raven *et al.,* 1998). The HQA is a synthetic index derived from RHS data to assess river habitat quality and heterogeneity. It evaluates several important physical attributes including aquatic, channel and bank features and has been widely used to diagnose impacts on biota (Szoszkiewicz *et al.,* 2006).

GIS data

For each survey unit, variables at broader scales were estimated from various sources of available digital cartographical information and using different geographic information systems (GIS). At basin (the entire area draining to the survey unit) and sub-basin scales (surface draining exclusively to each survey unit but excluding the area that drains to the nearest upstream river confluence), variables associated with climate, geology, land use, topography and hydrology were computed for each sampling site (see Appendix 1.1) by combining the ArcGIS software (v 9.2) (ESRI, Redlands, California, USA) and the analysis toolkit NetMap (www.netmaptools.org; Benda *et al.,* 2007). Climate data (1-km resolution) created by the Spanish Ministry for Environment interpolating series from the Spanish weather station network (Estrela *et al.,* 1999) were used. Geology in the sub-basin was characterised through cartography 1:50,000 elaborated by the Geological and Mining Institute of Spain (IGME). Forested area in the sub-basin was estimated from the layers (1:25,000) in the Occupation Information System of Soil in Spain (SIOSE).

Topographical variables were derived using a 25 m digital elevation model developed by the National Geographic Institute (IGN). Finally, one of the hydromorphological variables was the duration of the zero-flow period (number of days with no flow), which gives a valuable measure of temporal intermittency at reach scale. It was estimated in each survey unit using the integrated system for rainfall–runoff modelling (SIMPA) due to a lack of gauged data for all of the survey units. Additionally, a binary variable (hydrological regime) was generated to describe the flow regime ('altered' or 'natural') at each survey unit according to the existence or absence of water regulation infrastructures (reservoirs and dams) and water abstractions upstream.

Statistical analyses

Environmental variables were transformed and standardised. Spearman's correlations were then used to identify highly correlated variables within each group of environmental variables. Accordingly, between those variables showing Spearman correlation coefficients greater than 0.7, those with greater number of significant correlations were discarded for subsequent analysis (variables with an asterisk in Appendix 1.1) to avoid redundant information.

Species composition

Although some studies support the inclusion of rare species in multivariate studies (Prendergast *et al.,* 1993; Marchant, 2002), rare species (those at < 4 survey units) were removed before calculating Bray-Curtis distances among sites on the presence/absence biological matrix to reduce noise, as rare species can be detected as outliers by multivariate analyses in species association studies, obscuring the analysis of the whole data set (Gauch, 1982). Based on the Bray-Curtis distance matrix, hierarchical clustering procedures were conducted independently for woody and herbaceous species to characterise the different species assemblages. The obtained clustered groups were validated through SIMPROF tests, which provide significant objective stopping rules for ever-finer dissection into compositional subgroups (Clarke *et al.,* 2008). Distance-based Linear Models (DistLM) were used to identify those environmental factors that best explained the compositional variation among sites. Additionally, dbRDA ordination plots were used to visualise the influence of the selected environmental variables on clustered assemblages. The analyses were performed using PRIMER-E software (Clarke & Gorley, 2006) with the add-on package PERMANOVA+ (Anderson *et al.,* 2008).

Species richness

Firstly, we tried to identify some relationship between species composition and richness distribution patterns. For this, we tested if there were significant differences among the species richness of the clustered assemblages following a Kruskal–Wallis ANOVA by mean rank tests with Multiple Post hoc comparisons.

The observed richness values of both woody and herbaceous species were regressed against the selected environmental variables using generalised linear models (GLMs; McCullagh & Nelder, 1989) assuming a Poisson distribution for the dependent variable. A stepwise procedure was used to insert environmental variables into the model. Linear and quadratic (as well as cubic, only for flow) relationships were tested. Akaike's Information Criterion (AIC) was used to evaluate alternative models. Correction for data overdispersion was applied. Finally, normality (Shapiro–Wilk test) and spatial independence (Moran's I test) of residuals were assessed (*P*-value <0.05).

Given the coupled environmental and anthropogenic gradients in the study area, the exclusive effect of each set of variables (climate, geology, hydromorphology, land use and topography) on the richness distribution pattern was quantified using a hierarchical partitioning procedure. This process involved computation of the increase in the fit of all models with a group of variables compared with the equivalent model without that group of variables (for more details, see Chevan & Sutherland, 1991). Thus, the independent and joint contributions were expressed as the percentage of the total deviance explained by the corresponding models, which allowed the relative significance of each group of variables in explaining species richness distribution to be tested. The Statistica package 8.0. (StatSoft, 2007) was used for these computations.

Results

A total of 74 woody and 56 herbaceous species were recorded in the 81 survey units (see Appendix 1.2 for details), which represent approximately 72%of the previously recorded woody taxa in the entire basin (Ríos, 1994).

Species composition

Clustering procedures discriminated three different woody riparian assemblages (Fig. 2a) and five for herbaceous ones (Fig. 2b). The DistLM explained 34% of total variance in woody riparian composition and 28% for herbaceous species. Hydromorphological variables (valley shape, zero-flow period duration, habitat quality and hydrological regime), agriculture in the surrounding area and water conductivity were the main variables explaining woody composition (Table 1). Woody riparian species showed a progressive change from headwater streams with V-shaped valleys, permanent flows, heterogeneous river habitats and low water conductivities, characterised mainly by *Salix* spp. and *Fraxinus angustifolia* (assemblage W1 in Fig. 2a) to lowland reaches with wider valleys, intermittent flows, homogeneous river habitats and higher conductivities, characterised by the presence of *Tamarix canariensis, T. boveana* and *Nerium oleander* (assemblage W3). Midland areas had intermediate conditions but were influenced by hydrological disturbance and agricultural land use. They were characterised by the presence of *Populus nigra* and *Populus alba* (assemblage W2).

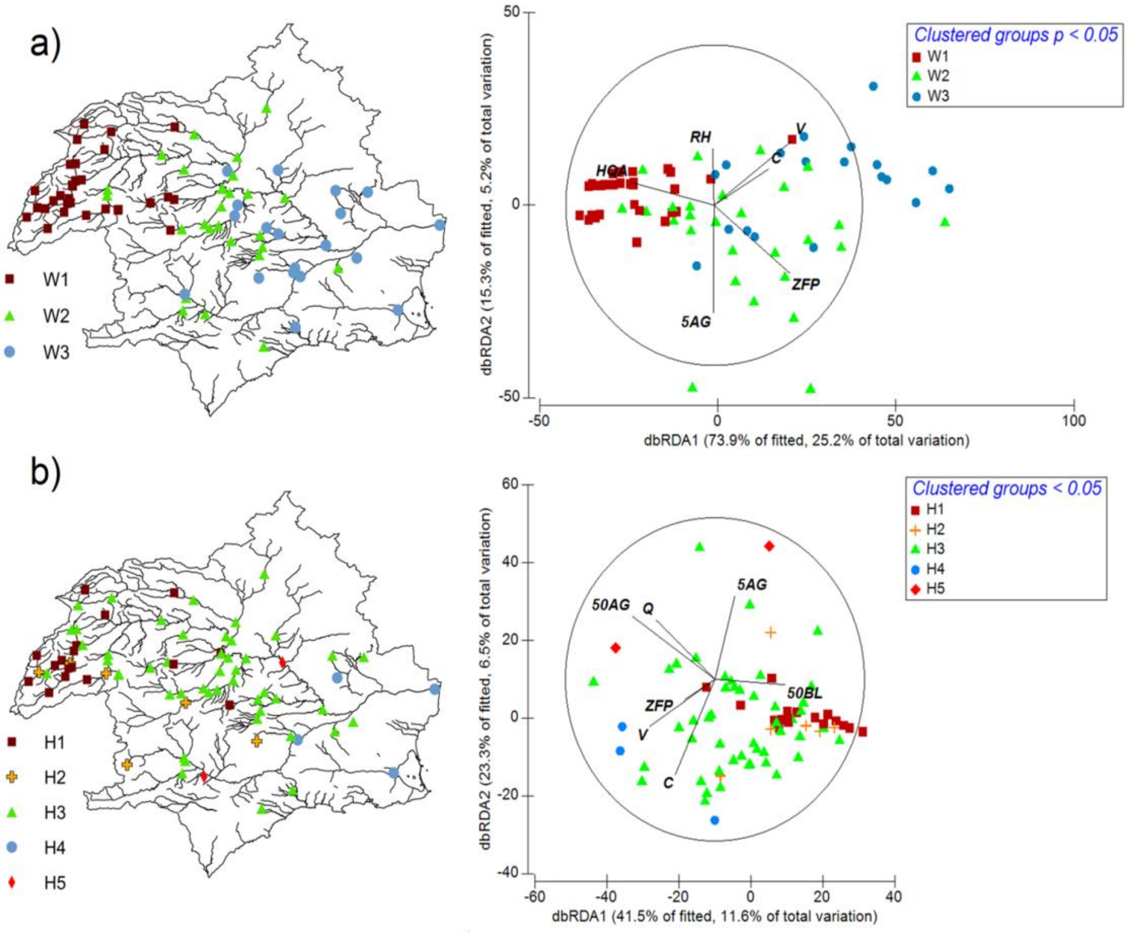


Fig. 2. Spatial distribution of the different clustered assemblages and dbRDA ordination plot relating composition cluster grouping and significant environmental variables for (a) woody species and (b) herbaceous species. HQA= Aquatic habitat quality assessment; RH= Hydrological regime; V=Valley shape; C=Conductivity; ZFP=Zero-flow period duration; Q=Flow; 50BL= Broadleaf/mixed semi-natural forest; 50AG and 5AG= Agriculture in the 50 and 5 m. buffer, respectively.

Five groups of herbaceous assemblages were identified. DistLM revealed that apart from valley shape (V-shaped), land use (agriculture and seminatural forests within the 50 m buffer), hydrological variables (flow discharge and zero-flow period duration) and water conductivity were the main variables explaining herbaceous composition (Table 1; Fig. 2b). In forested freshwater headwater streams, two assemblages were detected (see Fig. 2b): assemblage H1 characterised by species that require permanently humid substrates, shading and moderate temperature, such as horsetails (*Equisetum* spp.) and horsemint, (*Mentha longifolia*) and assemblage H2, mainly characterised by *Scirpoides holoschoenus*. As in the case of woody plants, the midlands were dominated by a widely distributed heterogeneous assemblage (H3) consisting of cattails (*Typha* spp.) rushes (*Juncus* spp.), mints (*Mentha* spp.) and Ravenna grass (*Saccharum ravennae*). In the wide valleys of the southern lowlands, where long drought periods and moderate high salinity values are found, the observed assemblage (H4) was dominated by the common reed (*Phragmites australis*). Finally, the group H5 characterised by the exotic giant reed (*Arundo donax*), appeared in sites with a high proportion of agriculture.

Table 1. Best DistLM results for woody and herbaceous species composition.

Variable	Individual explained variance (%)	Cumulative explained variance (%)	*P*-value	AIC
Woody composition				
Valley shape	15.05	15.05	0.001	608.98
Zero-flow duration	11.07	21.52	0.001	604.89
Habitat quality	11.44	27.24	0.001	601.05
Hydrological regime	3.10	29.75	0.01	600.36
5Agriculture	3.44	32.05	0.016	599.79
Water conductivity	2.19	34.11	0.021	599.42
Herb composition				
Valley shape	7.03	7.03	0.001	603.78
50Agriculture	5.83	12.32	0.001	601.21
5Agriculture	3.66	15.75	0.008	600.1
Flow	3.25	19.21	0.006	599.03
50 Broadleaf/mixed semi-		23.12	0.001	597.08
Water conductivity	4.53	25.56	0.012	596.44
Zero-flow duration	3.93	27.85	0.030	596.01

Species richness

A clear longitudinal woody species richness gradient was identified from the richest headwater streams located mainly in the northwest to the poorest lowland streams in the southeast (Fig. 3a). Accordingly, the Kruskal–Wallis test showed significant differences in the number of species among woody assemblages (W1 > W2 > W3; $P < 0.001$). However, the herbaceous richness distribution did not present such a clear longitudinal pattern (Fig. 3b). H1 and H3 were the richest assemblages [(H1 = H3) > (H2 = H4) > H5; $P < 0.05$].

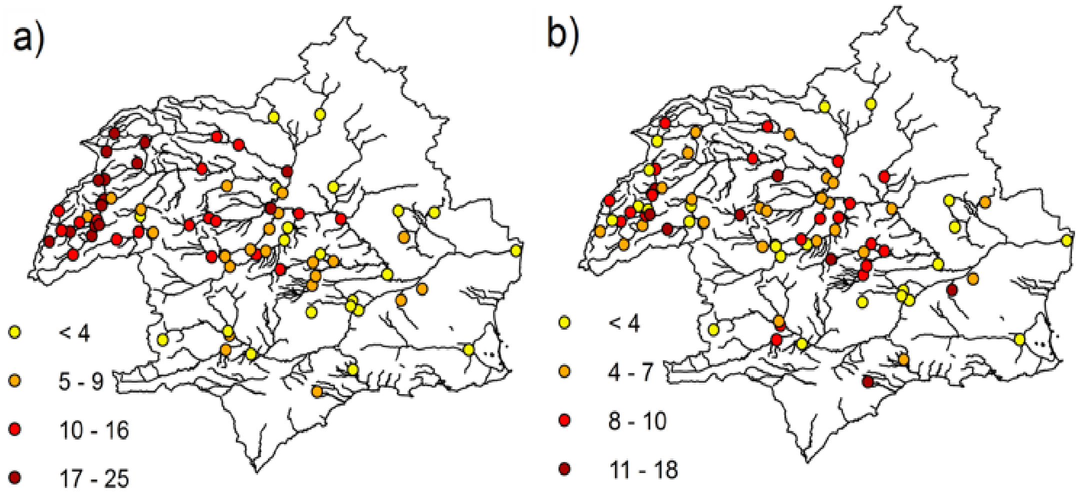


Fig. 3. Observed riparian richness patterns in (a) woody species and (b) herbs.

GLM showed 24 and 14 significant variables ($P < 0.05$) explaining woody and herbaceous species richness, respectively (Appendix 1.3). The best richness model explained 76.27% of total deviance (AIC = 363.84) for woody species and 52.74% (AIC = 366.36) for herbs (Table 2). Flow discharge (39.22% of explained deviance) and valley shape (36.79%) were the most relevant variables for woody species, whereas riverbed grain size (17.22%) and the percentage of conglomerated substrate in the sub-basin (10.74%) were the most important for herbs. Differences in significant individual factors explaining woody and herb richness between both species groups were found, although they belonged to the same groups of variables (mainly regarding hydromorphology and land use). No statistical or spatial autocorrelation was found among GLMs residuals ($P < 0.05$).

Finally, hierarchical partitioning confirmed that hydromorphological and land-use variables accounted for the greatest percentage of exclusive explained deviance for both woody (28.69 and 16.89%, respectively) (Appendix 1.4) and herbaceous (16.23 and 17.94%, respectively) species richness (Appendix 1.5). Geological variables also had a moderate independent effect for both riparian groups (10.17% for woody and 9.09% for herbaceous richness). On the contrary, climate and topography were capable of explaining lower percentages of deviance (< 5%).

Table 2. Best GLM for woody and herbaceous species richness.

Variable	Sign of the relationship	% individual explained deviance	% accumulated explained deviance	*P* - value	AIC
Woody species richness					
Flow	+			<0.0001	590.14
Flow^2	-			<0.001	568.31
Flow^3	+	39.22	39.22	0.001	471.87
Valley shape	-	36.80	61.27	<0.0001	404.09
Habitat quality assessment	+	32.92	64.64	0.002	393.90
50 Broadleaf/mixed semi-natural forest	+	8.38	66.93	0.005	387.61
5Grassland	-			<0.001	385.87
5Grassland^2	+	11.2	71.52	<0.0001	375.01
50Grassland	+			0.002	373.76
50Grassland^2	-	8.42	74.43	0.007	368.51
Conglomerated substrate	-	8.38	76.27	0.018	363.84
Herb species richness					
Riverbed grain size	+	17.22	17.22	0.001	404.68
Conglomerated substrate	-	10.74	25.54	0.022	394.42
5Tilled land	-	9.34	30.63	0.026	388.93
Slope	+	7.63	35.3	0.006	384.05
Forested sub-basin	+	6.61	40.38	0.004	378.56
Artificial channel	+			0.016	375.55
Artificial channel^2	-	6.52	46.9	0.014	372.96
Annual mean real evapotranspiration	-	5.84	52.74	0.003	366.36

Discussion

Composition patterns

As expected, a species replacement occurred in both riparian groups along the strong environmental and anthropogenic longitudinal gradients. Our results revealed similar patterns for woody and herbaceous plants but greater percentage of explained variance was found for woody species. The dominance of European species with high water requirements (e.g. *Salix alba*, *Equisetum* spp. and *Mentha longifolia*) was observed in headwaters, forming well–developed, low-impacted riparian galleries. At the other extreme, southern stream reaches were composed of simpler communities characterised by species adapted to drought, salinity and human disturbances such as *Tamarix canariensis*, *T. boveana*, *Nerium oleander* and *Phragmites australis*

(Salinas *et al.,* 2000; Salinas & Casas, 2007).

The relative congruency on both groups' composition patterns evidences that variables shaping both woody and herb assemblages were similar. The strong environmental continuous gradient influenced both biological communities, which showed continuum synchronised species replacements (River Continuum Concept, Vannote *et al.,* 1980). In general, riparian assemblages seemed to be mainly influenced by valley shape, agriculture, flow permanence and water conductivity. Valley shape determines riparian habitat availability and the geomorphologic and microclimatic features of river banks (e.g. V-shaped valleys, canyons or gorges limit riparian area, but they can create greater shading and lower evaporation making them suitable for determined riparian species; Garófano-Gómez *et al.,* 2011). In addition, it determines the potential extent of agricultural land-use in watercourses' surroundings (other of the main variables modifying riparian patterns). Regarding agriculture, it not only constrains the riparian area, but also alters riparian integrity, nutrient enrichment and the sedimentation process (Allan, 2004). These agricultural alterations limit the presence of certain species and favour the dominance of weeds, exotic and nitrophilous species (Décamps & Tabacchi, 1994; Nilsson *et al.,* 1994) such as the exotic giant reed (*Arundo donax* L.*)*, a species clearly favoured by disturbance (Quinn & Holt, 2008). In addition, as expected in semiarid areas, flow permanence was also an important factor influencing riparian patterns. Thus, it seems that the observed assemblages were more dependent on river runoff and groundwater rather than precipitation (Smith *et al.,* 1998). The alteration of natural flow regime caused by dam regulation and water abstraction for agricultural purposes intensifies the drought duration (Belmar *et al.,* 2013) and the species filtering effect (i.e. losing sensitive species; Poff & Zimmerman, 2010). Thus, water scarcity produces a positive selection of drought traits (e.g. long roots) preventing the occurrence of other features (e.g. broad leaves) (Douma *et al.,* 2012). Finally, the natural saline stress mainly caused by the presence of evaporitic substrates in some areas of the basin is intensified by agricultural practices. It constrained even more the pool of species that were able to establish and grow in certain locations, reducing it to those species with physiological adaptations to face this high salinity (e.g. the halophyte *Tamarix boveana)*.

Finally, compared with other climatic areas, riparian vegetation and other river communities (e.g. macroinvertebrates) seem to be poorly structured in some Mediterranean basins (see Ferreira & Moreira, 1999; Carbonell *et al.,* 2011; Belmar *et al.,* 2012). Thus, the relatively weak relationship between composition patterns and environmental variables (< 40% of explained variance) found in Mediterranean ecosystems in general, and the study area in particular, could be explained by the specific features of these areas (i.e. areas with high natural and anthropogenic stress; Gasith & Resh, 1999), which lead to the ubiquitous occurrence of resilient, opportunistic and relatively persistent species assemblages (Puig *et al.,* 1991). In addition, riparian composition patterns could be also influenced by other variables not considered in our study: historical processes or biological interactions between woody and herbaceous layers, such as, light competition (Villarreal *et al.,* 2012). However, although light competition is one of the main biological interactions between both plant groups and shading (estimated as "woody layer continuity", a semi-continuous variable derived from RHS protocol) resulted significant (DistLM analyses, R^2=0.04, p=0.001) explaining herb composition, it was not able to improve the final model (the same percentage of variance remained unexplained).

Species richness patterns

Similar richness patterns for woody and herbaceous species were found. In general, hydromorphological and land use variables were identified as the most important set of variables in explaining these patterns, but differences in the most important individual variables were detected. The richest woody riparian areas were situated in headwater streams where V-shaped valleys, moderate and perennial flows, heterogeneous river habitats, forests and meadows were present. These are the only areas with reduced anthropogenic pressures, as they are often located in difficult-to-access places that count on some sort of environmental protection status (Casas *et al.,* 2006). In addition, these areas show higher water availability throughout the year, which enables the presence of a greater number of species since flow intermittency and human impacts produce woody richness declines in Mediterranean basins (Salinas & Casas, 2007; Belmar *et al.,* 2013). Moreover, although wide lowland semiarid valleys showing complex and well-developed riparian corridors could hold greater richness than headwaters due to the lack of physical constraints to riparian vegetation development (Gregory *et al.,* 1991; Lite *et al.,* 2005), our results highlight that lowlands mostly contained impaired rivers with simple communities and low species richness. Therefore, although a longitudinal richness gradient has been found, our results revealed the opposite pattern to that expected in natural basins, where greater habitat availability and species richness (more habitat is supposed to host more richness) are usually found in medium and low river reaches (River Continuum Concept, Vannote *et al.,* 1980).

In the case of herbaceous species richness, although we have not obtained such a clear longitudinal pattern, the areas that accounted for the highest richness values also corresponded to upper reaches of natural streams mainly characterised by loose, coarse riverbed substrates located in forested and calcareous basins with a low percentage of crops. Substrate features were especially important explaining herb richness, because they determine the presence and cover of different particles size in the banks that possibility the colonization of species with different root system complexity (Nilsson *et al.,* 1991). The negative influence of crops and artificial channels on herb richness is consistent with life-history theories regarding adaptations to disturbances because disturbed areas usually show a dominance of annual herbaceous species and fewer perennial ones (Grime, 1979; Walker *et al.,* 1986).

Finally, as exposed above, the influence of shading provided by woody layer could be important in explaining herbaceous richness patterns. Similarly, although woody layer continuity (estimated as above) resulted significant (8.7% of explained deviance, p-value=0.0071) it was not selected by the best model. Surprisingly, this relationship was linear and positive. Although we expected a negative linear (the less woody layer, the more herb species) or quadratic (intermediate woody continuity could favour greater richness values as species of different shading tolerance could grow in the same place) relationship, the most favourable areas for woody species were in general also better for herbs. Thus, it seems that hydromorphological and anthropogenic variables influenced herb richness more than the shading effect of the woody layer.

Concluding remarks

Our results support the hypothesis that riparian communities in semiarid Mediterranean basins turn less diverse and experience changes in species composition as anthropogenic (land use, dam regulation) and natural (drought, salinity) disturbances increase and intensify downstream. Despite their lower riparian habitat availability, headwaters were the most favourable areas for both woody and herbaceous species due to the absence of anthropogenic pressures and milder environmental conditions.

Although some differences were observed, a notable congruence in both groups' species composition and richness distribution patterns was found and, consequently, in the variables shaping them: the hydromorphological (particularly those related to irregular water availability) and land-use (mainly agriculture) ones. This outcome evidences the importance of managing buffer areas appropriately in Mediterranean basins (all the models included land-use variables), since anthropogenic land use modified and impoverished species composition (e.g. favouring the dominance of exotic and generalist species) and richness patterns respectively, while natural land use helped to preserve native species and relatively high riparian richness values.

Large-scale, long-term variables such as climate, which determine the broad physical template and catchment characteristics (Naiman *et al.*, 2005), had less significance in explaining riparian patterns, at least at basin scale. Thus, their influence could be masked by the direct action of hydrological and land use reach-scale variables. Therefore, environmental features as valley shape, substrate, flow, drought period and salinity, and anthropogenic alterations as dam regulation, water abstraction and land use, seem necessary to describe

Mediterranean riparian systems adequately. Finally, given the similarity between both groups' responses, an overall approach considering the species of both groups jointly or even selecting only one of them could be suitable when studying Mediterranean riparian communities.

References

Aguiar, F.C. & Ferreira, M.T. (2005) Human-disturbed landscapes: effects on composition and integrity of riparian woody vegetation in the Tagus River basin, Portugal. *Environmental Conservation*, **32**, 30–41.

Aguiar, F.C., Ferreira, M.T. & Albuquerque, A. (2006) Patterns of exotic and native plant species richness and cover along a semi-arid Iberian river and across its floodplain. *Plant Ecology*, **184**, 189–202.

Aguiar, F.C., Ferreira, M.T., Albuquerque, A., Rodríguez-González, P. & Segurado, P. (2009) Structural and functional responses of riparian vegetation to human disturbance: performance and spatial scale-dependence. *Fundamental and Applied Limnology/Archiv für Hydrobiologie*, **175**, 249–267.

Allan, J.D. (2004) Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 257–284.

Anderson, M.J., Gorley, R.N. & Clarke, K.R. (2008) *PERMANOVA + for PRIMER: Guide to Software and Statistical Methods*. PRIMER-E, Plymouth, United Kingdom.

Baker, W.L. (1989) Macro- and micro-scale influences on riparian vegetation in Western Colorado. *Annals of the Association of American Geographers*, **79**, 65–78.

Belmar, O., Velasco, J., Gutiérrez-Cánovas, C., Mellado-Díaz, A., Millán, A. & Wood, P.J. (2012) The influence of natural flow regimes on macroinvertebrate assemblages in a semiarid Mediterranean basin. *Ecohydrology*, **6**, 363–379.

Belmar, O., Bruno, D., Martínez-Capel, F., Barquín, J. & Velasco, J. (2013) Effects of flow regime alteration on fluvial habitats and riparian quality in a semiarid Mediterranean region. *Ecological Indicators*, **30**, 52–64.

Benda, L., Miller, D., Andras, K., Bigelow, P., Reeves, G. & Michael, D. (2007) NetMap: A new tool in support of watershed science and resource management. *Forest Science*, **53**, 206–219.

Brinson, M.M. & Verhoeven, J. (1999) Riparian forests. *Maintaining Biodiversity in Forest Ecosystems* (ed Hunter Jr, M.L.), pp. 265–299. Cambridge University Press, New York, USA.

Carbonell, J.A., Gutiérrez-Cánovas, C., Bruno, D., Abellán, P., Velasco, J. & Millán, A. (2011) Ecological factors determining the distribution and assemblages of the aquatic Hemiptera (Gerromorpha and Nepomorpha) in the Segura river basin (Spain). *Limnetica*, **30**, 59–70.

Casas, J.J., Gessner, M.O., Langton, P.H., Calle, D., Descals, E. & Salinas, M.J. (2006) Diversity of patterns and processes in rivers of eastern Andalusia. *Limnetica*, **25**, 155–170.

Chevan, A. & Sutherland, M. (1991) Hierarchical partitioning. *The American Statistician*, **45**, 90–96.

Clarke, K.R. & Gorley, R.N. (2006) *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth, United Kingdom.

Clarke, K.R., Somerweld, P.J. & Gorley, R.N. (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology*, **366**, 56–69.

Décamps, H. & Tabacchi, E. (1994) Species richness in vegetation along river margins. *Aquatic Ecology, Scale, Pattern and Process* (eds Giller, P.S, Hildrew, A.G. & Raffaelli D.G.), pp. 1–20. Blackwell, Oxford, United Kingdom.

Douma, J.C., Bardin, V., Bartholomeus, R.P. & Bodegom, P.M. (2012) Quantifying the functional responses of vegetation to drought and oxygen stress in temperate ecosystems. *Functional Ecology*, **26**, 1355–1365.

Estrela, T., Cabezas, F. & Estrada, F. (1999) La evaluación de los recursos hídricos en el Libro Blanco del Agua en España. *Ingenieriía del Agua*, **6**, 125–138.

European Commission (2009) *Regions 2020. The climate change challenge for European regions* http://ec.europa.eu/regional_policy/sources/docoffic/working/regions2020/pdf/regions2020_climat.pdf. Accessed 1 June 2013.

Ferreira, M.T. & Aguiar, F.C. (2006) Riparian and aquatic vegetation in Mediterranean-type streams (western Iberia). *Limnetica*, **25**, 411–424.

Ferreira, M.T. & Moreira, I.S. (1999) River plants from an Iberian basin and environmental factors influencing their distribution. *Hydrobiologia*, **415**, 101–107.

Garófano-Gómez, V., Martínez-Capel, F., Peredo-Parada, M., Olaya-Marín, E.J., Muñoz Mas, R., Soares-Costa, R.M. & Pinar-Arenas, J.L. (2011) Assessing hydromorphological and floristic patterns along a regulated Mediterranean river: the Serpis river (Spain). *Limnetica*, **30**, 307–328.

Gasith, A. & Resh, V.H. (1999) Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics*, **30**, 51–81.

Gauch, H.G. (1982) *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge, United Kingdom.

Giorgi, F. & Lionello, P. (2008) Climate change projections for the Mediterranean region. *Global and Planetary Change*, **63**, 90–104.

Gregory, S.V., Swanson, F.J., McKee, W.A. &. Cummins, K.W. (1991) An ecosystem perspective of riparian zones. *BioScience*, **41**, 540–551.

Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. Wiley, New York, USA.

Lite, S.J., Bagstad, K.J. & Stromberg, J.C. (2005) Riparian plant species richness along lateral and longitudinal gradients of water stress and flood disturbance, San Pedro River, Arizona, USA. *Journal of Arid Environments*, **63**, 785–813.

Lyon, J. & Gross, N.M. (2005) Patterns of plant diversity and plant–environmental relationships across three riparian corridors. *Forest Ecology and Management*, **204**, 267–278.

Marchant, R. (2002) Do rare species have any place in multivariate analysis for bioassessment?. *Journal of North American Benthological Society*, **21**, 311–313.

McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models, 2nd ed*. Chapman and Hall, London, United Kingdom.

Naiman, R.J., Décamps, H. & McClain, M.E. (2005) *Riparia: Ecology, Conservation, and Management of Streamside Communities*. Elsevier, Amsterdam, The Netherlands.

Nichols, W.F., Killingbeck, K.T., August, P.V. & Grove, B. (1998) The influence of geomorphological heterogeneity on biodiversity II. A landscape perspective. *Conservation Biology*, **12**, 371–379.

Nilsson, C. & Svedmark, M. (2002) Basic principles and ecological consequences of changing water regimes: riparian plant communities. *Environmental Management*, **30**, 468–480.

Nilsson, C., Grelsson, G., Dynesius, M., Johansson, M.E. & Sperens, U. (1991) Small rivers behave like large rivers, effect of postglacial history on plant species richness along riverbanks. *Journal of Biogeography*, **18**, 533–541.

Nilsson, C., Ekblad, A., Dynesius, M., Backe, S., Gardfjell, M., Hellqviist, S., *et al.* (1994) A comparison of species richness and traits of riparian plants between a main river channel and its tributaries. *Journal of Ecology*, **82**, 281–295.

Poff, N.L. & Zimmerman, J.K.H. (2010) Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology*, **55**, 194–205.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. & Gibbons, D.W. (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, **365**, 335–337.

Puig, M.A., Aboal, M. & Soston, A. (1991) New approaches to Mediterranean fluvial communities. *Oecologia Aquatica*, **10**, 13–20.

Quinn, L.D. & Holt, J.S. (2008) Ecological correlates of invasion by Arundo donax in three southern California riparian habitats. *Biological Invasions*, **10**, 591–601.

Raven, P.J., Fox, P., Everard, M., Holmes N.T.H. & Dawson, F.H. (1997) River habitat survey: a new system for classifying rivers according to their habitat quality. *Freshwater Quality: Defining the Indefinable?* (eds Boon, P.J. & Holwell, D.L.), pp. 215–234. The Stationery Office, Edinburgh, United Kingdom.

Raven, P.J., Holmes, N.T.H., Dawson, F.H. & Everard, M. (1998) Quality assessment using river habitat survey data. Aquatic Conservation: *Marine and Freshwater Ecosystems*, **8**, 477–499.

Renöfält, B.M., Merritt, D.M. & Nilsson, C. (2007) Connecting variation in vegetation and stream flow: the role of geomorphic context in vegetation response to large floods along boreal rivers. *Journal of Applied Ecology*, **44**, 147–157.

Ríos, S. (1994) *El Paisaje vegetal de las riberas del Río Segura*. PhD Dissertation. University of Murcia, Murcia, Spain.

Rivas-Martínez, S. (1985) *Biogeografía y vegetación*. Real Academia de las Ciencias Exactas, Físicas y Naturales, Madrid, Spain.

Sagers, C.L. & Lyon, J. (1997) Gradient analysis in a riparian landscape: contrasts among forest layers. *Forest Ecology and Management*, **96**, 13–26.

Sala, O.E., Chapin, F.S.III, Armesto, J.J., Berlow, R., Bloomfield, J., Dirzo, R., *et al*. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

Salinas, M.J. & Casas, J. (2007) Riparian vegetation of two semiarid Mediterranean rivers: basin-scale responses of woody and herbaceous plants to environmental gradients. *Wetlands*, **27**, 831–845.

Salinas, M.J., Blanca, G & Romero, A.T. (2000) Riparian vegetation and water chemistry in a basin under semiarid Mediterranean climate, Andarax River, Spain. *Environmental Management*, **26**, 539–552.

Smith, S.D., Devitt, D.A., Sala, A., Cleverly, J.R. & Busch, D.E. (1998) Water relations of riparian plants from warm desert regions. *Wetlands*, **18**, 687–696.

StatSoft (2007) STATISTICA (data analysis software system), Version 8. www.statsoft.com. StatSoft, Tulsa, USA.

Stella, J.C., Rodríguez-González, P.M., Dufour, S. & Bendix, J. (2013) Riparian vegetation research in Mediterranean-climate regions: common patterns, ecological processes, and considerations for management. *Hydrobiologia*, **719**, 291–315.

Szoszkiewicz, K., Buffagni, A., Davy-Bowker, J., Lesny, J., Chojnicki, B.H., Zbierska, J., *et al.* (2006) Occurrence and variability of river habitat survey features across Europe and the consequences for data collection and evaluation. *Hydrobiologia*, **566**, 267–280.

Tabacchi, E. & Planty-Tabacchi, A.-M. (2001) Functional significance of species composition in riparian plant communities. *Journal of the American Water Resources Association*, **37**, 1629–1637.

Tabacchi, E., Planty-Tabacchi, A.-M., Salinas, M.J. & Décamps, H. (1996) Landscape structure and diversity in riparian plant communities: a longitudinal comparative study. *Regulated Rivers: Research and Management*, **12**, 367–390.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130–137.

Villarreal, M.L., Drake, S., Marsh, S.E. & McCoy, A.L. (2012) The influence of wastewater subsidy, flood disturbance and neighbouring land use on current and historical patterns of riparian vegetation in a semi-arid watershed. *River Research and Applications*, **28**, 1230–1245.

Walker, L.R., Zasada, J.C. & Chapin III, F.S. (1986) The role of life-history processes in primary succession on an Alaskan floodplain. *Ecology*, **67**, 1243–1253.

Wiens, J.A. (2002) Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology*, **47**, 501–515.

Supporting Information

Appendix 1.1. Explanatory environmental variables considered by factor type.

Appendix 1.2. Riparian taxa recorded in the study area.

Appendix 1.3. Individual explained deviance of each environmental variable on woody and herbaceous species richness.

Appendix 1.4. Hierarchical partitioning procedure applied to woody species richness.

Appendix 1.5. Hierarchical partitioning procedure applied to herbaceous species richness.

Appendix 1.1. Explanatory environmental variables considered by factor type: C=Climate, G=Geology, T= Topography, L=Land Use, H=Hydromorphology. *Variables excluded for subsequent analyses due to high correlation rates (R > 0.7). N, A=Natural, Altered; d/y=Days per year; U=Undercut; V=Vertical; S=Steep; GE=Gentle; CP=Composite; B=Natural berm; D=Deep vee; S=Shallow vee; GO=Gorge; CO=Concave/Bowl; O=No obvious valley side; AS=Asymmetrical.

Var.	Meaning	Group	Source	Spatial scale	Type	Unit
EI	Annual mean real evapotranspiration	C	GIS	basin	Continuous	mm
EP	Annual mean potential evapotranspiration	C	GIS	basin	Continuous	mm
PREC	Annual mean precipitation	C	GIS	basin	Continuous	mm
TEMP*	Annual mean temperature	C	GIS	basin	Continuous	mm
CALC	Calcareous substrate	G	GIS	sub-basin	Semi-continuous	%
CONG	Conglomerated substrate	G	GIS	sub-basin	Semi-continuous	%
SED*	Sedimentary substrate	G	GIS	sub-basin	Semi-continuous	%
PERM	Permeability	G	GIS	sub-basin	Semi-continuous	%
C	Water Conductivity	G	Survey	local	Continuous	µS/cm
SLOPE	Slope	T	GIS	basin	Semi-continuous	%
ORI	Average orientation	T	GIS	local	Continuous	degree
ELEV	Elevation	T	GIS	local	Continuous	m
FOR	Forested	L	GIS	sub-basin	Semi-continuous	%
50BL	Broadleaf/mixed semi-natural forest	L	Survey	50 m buffer	Semi-continuous	%
50AG	Agriculture	L	Survey	50 m buffer	Semi-continuous	%
50TL	Tilled land	L	Survey	50 m buffer	Semi-continuous	%
50TH	Tall herb rank vegetation	L	Survey	50 m buffer	Semi-continuous	%
50GR	Grassland	L	Survey	50 m buffer	Semi-continuous	%
5BL*	Broadleaf/mixed semi-natural forest	L	Survey	5 m buffer	Semi-continuous	%
5AG	Agriculture	L	Survey	5 m buffer	Semi-continuous	%
5TL	Tilled land	L	Survey	5 m buffer	Semi-continuous	%
5TH	Tall herb rank vegetation	L	Survey	5 m buffer	Semi-continuous	%
5GR	Grassland	L	Survey	5 m buffer	Semi-continuous	%
RH	Hydrological regime	H	GIS	basin	Categorical	N, A
ZFP	Zero-flow period duration	H	GIS	local	Continuous	d/y
Q	Flow	H	Survey	local	Continuous	m^3/s
WD*	Water depth	H	Survey	local	Continuous	m
WW*	Water width	H	Survey	Local	Continuous	m
V	Valley shape	H	Survey	Local	Categorical (6 classes)	D, S, GO, CO, O, AS
HQA	Habitat quality assessment	H	Survey	local	Semi-continuous	0-100
BANK*	Bank profile	H	Survey	local	Categorical (6 profiles)	U, V, S, GE, CP,B
BED	Riverbed grain size	H	Survey	local	Categorical (6 size classes)	mm
ART	Artificial channel	H	Survey	local	Semi-continuous	%

Appendix 1.2. Riparian taxa recorded in the study area.

Woody plants	**Perennial herbs**
Acer opalus Miller subsp. *granatensis* (Boiss.) Font Quer & Rothm	*Adiantum capillus-veneris* L.
Agrostis stolonifera L.	*Arundo donax* L.
Ailanthus altissima (Mill.) Swingle	*Carex distans* L.
Anabasis hispanica Pau	*Carex extensa* Good
Arthrocnemum macrostachyum (Moric.) Moris	*Carex flacca* Schreber
Asparagus acutifolius L.	*Carex hispida* Willd.
Atriplex halimus L.	*Carex pendula* Huds.
Bupleurum fruticosum L.	*Cyperus laevigatus* L. subsp. *distachyos* (All.) Maire & Weiller
Celtis australis L.	*Eleocharis palustris* (L.) Roem. et Schult.
Clematis vitalba L.	*Epilobium hirsutum* L.
Coriaria myrtifolia L.	*Epilobium parviflorum* Schreb.
Cornus sanguinea L.	*Equisetum ramosissimum* Desf.
Corylus avellana L.	*Equisetum palustre* L.
Corylus hispanica Mill. ex D. Rivera & al.	*Equisetum telmateia* Ehrh.
Crataegus monogyna Jacq.	*Eupatorium cannabinum* L.
Dorycnium rectum (L.) Ser. In DC.	*Glyceria notata* Chevall.
Ficus carica L.	*Humulus lupulus* L.
Fraxinus angustifolia Vahl.	*Imperata cylindrica* (L.) Raeuschel
Fraxinus excelsior L.	*Iris foetidissima* L.
Fraxinus ornus L.	*Iris pseudacorus* L.
Halocnemum strobilaceum (Pall.) M. Bieb.	*Iris serotina* L.
Hedera helix L.	*Juncus articulatus* L.
Ilex aquifolium L.	*Juncus bufonius* L.
Juglans regia L.	*Juncus inflexus* L.
Laurus nobilis L.	*Juncus maritimus* Lam.
Ligustrum vulgare L.	*Juncus subnodulosus* Schrank
Lonicera biflora Desf.	*Juncus subulatus* Forsk.
Lonicera periclymenum L. subsp. *hispanica* (Boiss. & Reuter) Nyman	*Lysimachia ephemerum* L.
Morus alba L.	*Lysimachia vulgaris* L.
Myrtus communis L.	*Lythrum salicaria* L.
Nerium oleander L.	*Mentha aquatica* L.
Phoenix canariensis Chabaud	*Mentha longifolia* L.
Phoenix dactylifera L.	*Mentha pulegium* L.
Platanus orientalis L.	*Mentha suaveolens* Ehrh.
Platanus x hybrida Brot	*Mentha piperita* L.
Populus alba L. var. *alba*	*Origanum vulgare* L.
Populus alba L. var. *pyramidalis* Bunge	*Oryza sativa* L.
Populus nigra L. var *nigra*	*Peucedanum hispanicum* (Boiss.) Endl.
Populus nigra L. var. *italica*	*Phragmites australis* (Cav)Trin. Ex. Steudel
Populus x canadensis Moench	*Plantago major* L.
Populus × canescens (Aiton) Sm.	*Potentilla reptans* L.
Prunus insititia L.	*Primula vulgaris* Hudson
Prunus mahaleb L.	*Ranunculus repens* L.
Quercus faginea Lam.	*Rumex conglomeratus*
Rosa canina L.	*Saccharum ravennae* (L.) Murray
Rubia peregrina L. subsp. *longifolia* (Poiret) O. Bolòs	*Samolus valerandi* L.
Rubia peregrina L. subsp. *peregrina*	*Schoenus nigricans* L.

Woody plants	**Perennial herbs**
Rubus caesius L.	*Scirpoides holoschoenus* L.
Rubus ulmifolius Schott.	*Scirpus maritimus* L.
Salix alba L.	*Scirpus lacustris* L.
Salix atrocinerea Brot.	*Scrophularia auriculata* L.
Salix babylonica L.	*Sonchus maritimus L.* subsp. *aquatilis* (Pourr.) Nyman
Salix elaeagnos Scop. subsp. *angustifolia* (Cariot) Rech. fil.	*Thalictrum speciosissimum* L.
Salix fragilis L.	*Trifolium repens* L.
Salix neotricha Görz	*Typha angustifolia* L.
Salix pedicellata Desf.	*Viola riviniana* Reichemb.
Salix purpurea L. subsp. *lambertiana* (Sm.) A.Newman ex Rech. fil.	
Salix triandra L. subsp. *discolor* (Koch) Arcangeli	
Sambucus nigra L.	
Sarcocornia fruticosa (L.) A. J. Scott	
Smilax aspera L.	
Sorbus aria (L.) Crantz	
Suaeda vera Forskål ex J.F. Gmelin	
Tamarix africana Poir.	
Tamarix boveana Bunge	
Tamarix canariensis Willd.	
Tamarix gallica L.	
Ulmus glabra Hudson	
Ulmus minor Mill.	
Viburnum lantana L.	
Viburnum tinus L.	
Vinca difformis Pourret	
Vitis vinifera L.	
Washingtonia robusta H.A.Wendl	

Appendix 1.3. Individual explained deviance of each environmental variable on woody and herbaceous species richness. ns= non-significant.

Variable	Acronym	Woody plants explained deviance (%)	Term	Perennial herbs explained deviance (%)	Term
Flow	Q	39.22	3	ns	
Valley shape	V	36.8		ns	
Water Conductivity	C	33.05	2	ns	
Habitat quality assessment	HQA	32.92	1	6.47	1
50 Broadleaf/mixed semi-natural forest	50BL	28.38	1	ns	
Zero-flow period duration	ZFP	22.47	1	ns	
Precipitation	PREC	19.52	2	ns	
5 Agriculture	5AG	13.88	1	7.57	1
River-bed grain size	BED	12.81	1	17.22	1
50 Agriculture	50AG	12.75	1	4.65	1
50 Tilled land	50TL	12.14	1	6.54	2
5 Grassland	5GR	11.2	2	ns	
Forested sub-basin	FOR	10.47	2	6.61	1
Permeability	PERM	8.69	1	8.86	1
50 Grassland	50GR	8.48	2	ns	
Conglomerated substrate	CONG	8.38	1	10.74	1
5 Tilled land	5TL	7.96	1	9.34	1
Elevation	ELEV	7.18	2	ns	
Artificial channel	ART	7.16	2	6.52	2
Calcareous substrate	CALC	4.42	2	7.54	2
Annual mean real evapotranspiration	EI	4.06	1	5.84	1
Hydrological regime	RH	3.42		ns	
Annual mean potential evapotranspiration	EP	2.62	2	ns	
Orientation	ORI	2.52	1	ns	
Slope	SLOPE	1.6	2	7.63	1
50 Tall herb	50TH	ns		5.95	2
5 Tall herb	5TH	ns		ns	

Appendix 1.4. Hierarchical partitioning procedure applied to woody species richness. Percentage of independent and joined explained deviance and AIC (Akaike's Information Criterion) values for the different sets of environmental predictors are shown. H=Hydromorphology, L=Land Use, G=Geology, C=Climate, T= Topography.

	% Explained deviance	**H**	**L**	**G**	**C**	**T**	**AIC**
H	68.48	68.48					382.03
S	55.3		55.3				423.69
G	44.35			44.35			459.32
C	26.47				26.47		522
T	12.65					12.65	609.19
H + S	75.64	20.34	7.16				366.11
H +G	72.64	28.29		4.16			372.97
H + C	70.18	43.72			1.7		376.82
H + T	69.66	57				1.18	379.75
S + G	63.89		19.55	8.59			396.62
S + C	55.3		28.83		0		423.69
S + T	55.3		42.65			0	423.69
G + C	44.35			17.88	0		459.32
G + T	44.35			31.69		0	459.32
C + T	26.47				13.81	0	522
H + S + G	76.27	12.38	3.63	0.63			363.84
H + S + C	75.64	20.34	5.46		0		366.11
H + S + T	75.64	20.34	5.98			0	366.11
H + G + C	72.64	28.29		2.46	0		372.97
H + G + T	73.7	29.35		4.04		1.06	371.15
H + C + T	70.18	43.72			0.52	0	376.82
S + G + C	63.89		19.55	8.59	0		396.62
S + G + T	63.89		19.55	8.59		0	396.62
S + C + T	55.3		28.83		0	0	423.69
G + C + T	44.35			17.88	0	0	459.32
H + S + G + C	76.27	12.38	3.63	0.63	0		363.84
H + S + G + T	76.27	12.38	2.57	0.63		0	363.84
H + G + C + T	73.7	29.35		3.52	0	1.06	364.84
S + G + C + T	63.89		19.55	8.59	0	0	396.62
H + S + C + T	75.64	20.34	5.46		0	0	366.11
H + S + G + C +T	76.27	12.38	2.57	0.63	0	0	363.84
Exclusive explained deviance		28.69	16.89	10.17	2.66	1	

Appendix 1.5. Hierarchical partitioning procedure applied to herbaceous species richness. Percentage of independent and joined explained deviance and AIC (Akaike's Information Criterion) values for the different sets of environmental predictors are shown. H=Hydromorphology, L=Land Use, G=Geology, C=Climate, T= Topography.

	% Explained deviance	**H**	**L**	**G**	**C**	**T**	**AIC**
H	26.19	26.19					395.47
S	27.9		27.9				392.95
G	18.48			18.48			402.83
C	4.43				4.43		415.52
T	7.63					7.63	410.81
H + S	44.85	16.95	18.66				377.99
H +G	33.49	15.01		7.3			386.72
H + C	29.89	25.46			3.7		392.01
H + T	30.78	23.15				4.59	390.70
S + G	37.22		18.74	9.32			383.31
S + C	30.1		25.67		2.2		391.68
S + T	28.87		21.24			0.97	392.08
G + C	25.48			21.05	7		396.46
G + T	18.48			10.85		0	402.83
C + T	13.85				4.22	7.42	403.65
H + S + G	49.95	12.73	16.46	5.1			371.18
H + S + C	46.17	16.07	16.28		1.32		376.04
H + S + T	44.85	15.98	14.07			0	377.99
H + G + C	37.29	11.81		7.4	3.8		383.11
H + G + T	37.15	18.67		6.37		3.66	383.32
H + C + T	35.72	21.87			4.94	5.83	385.43
S + G + C	43.56		18.08	13.46	6.34		379.72
S + G + T	37.22		18.74	8.35		0	383.31
S + C + T	37.95		24.1		9.08	7.85	380.13
G + C + T	25.48			11.63	7	0	396.46
H + S + G + C	50.51	6.95	13.22	4.34	0.56		369.65
H + S + G + T	49.95	12.73	12.8	5.1		0	371.18
H + G + C + T	42.19	16.71		6.47	5.04	4.9	380.70
S + G + C + T	43.56		18.08	5.61	6.34	0	379.72
H + S + C + T	48.11	10.16	12.39		3.26	1.94	372.46
H + S + G + C +T	52.74	9.18	10.55	4.63	2.79	2.23	366.36
Exclusive explained deviance		16.23	17.94	9.09	4.63	3.06	

Chapter 2

Responses of Mediterranean aquatic and riparian communities to human pressures at different spatial scales

Segura river

Abstract

Mediterranean river ecosystems are subjected to intense human pressures and impacts that affect both their aquatic and riparian communities. However, given their stratified position in the river ecosystem and varying ecological requirements, aquatic and riparian communities can respond differently to such pressures. These biological responses could also vary depending on the nature of the disturbances, the spatial scale considered and the indicators used as response variable. Here, we aim to assess the influence of the main human pressures present in Mediterranean rivers (agricultural land use and hydromorphological alteration) on the biodiversity and ecological condition indicators of both riparian and aquatic communities at two spatial scales: reach and basin. For this purpose, a total of 56 sampling sites covering the study area (Segura basin, SE Spain) were surveyed. Water beetles and woody riparian vegetation richness were used respectively as biodiversity surrogates of aquatic and riparian communities, and the Iberian Biomonitoring Working Party (IBMWP) and Riparian Quality Index (RQI) were used to assess the ecological status of both communities. As expected, we found a general decrease in both richness and ecological condition when human pressures increased, regardless of the spatial scale considered. Nonetheless, agricultural land use was the main pressure explaining riparian richness and quality, whereas aquatic communities' responses were highly related to hydromorphological alteration. Contrary to expected, in general, variables at basin scale had a greater effect than those variables operating at local scale. In addition, ecological condition indices responded more clearly to human pressures than biodiversity surrogates. Therefore, land use and hydrological planning at basin scale are essential complements to conservation and restoration efforts, traditionally carried out at reach scale, in order to maintain stream ecosystem integrity and biodiversity.

Introduction

The high human pressures on inland aquatic ecosystems have caused these habitats to become recognised as some of the most threatened in the world (Saunders *et al*., 2002). This is especially evident in the Mediterranean Basin, one of the Earth's biodiversity hotspots (Myers *et al*., 2000), where the long history of substantial human impacts on the landscape and fluvial systems has been well-documented (Hooke, 2006). These areas provide a wide anthropogenic gradient suitable for studying the influence of human pressures on fluvial communities. Thus, understanding the processes and relationships between human pressures, spatial heterogeneity and riverine communities in Mediterranean areas constitutes a major challenge in freshwater ecology and conservation (Bonada & Resh, 2013; Cooper *et al*., 2013), particularly in the current context of global change (Sala *et al*., 2000).

Although frequently overlooked in limnological studies (Ferreira & Aguiar, 2006), riparian areas are an integral part of riverine ecosystems (Ward *et al*., 2002) that influence both the structure and functioning of aquatic communities (Sabater *et al*., 2000). Thus, aquatic and riparian communities are mutually interdependent in terms of ecological processes. These large terrestrial-aquatic linkages occur in both directions, existing important flows of energy and material between these adjacent systems (Naiman & Décamps, 1997). Conservation and management strategies are usually focused on aquatic or riparian community but sparsely on both of them. Despite the existing interconnection between both communities, given their stratified position in the river ecosystem and their varying functional traits and ecological requirements, their responses to human pressures could also differ.

Riparian and aquatic communities' responses could also differ depending upon the nature of these pressures and the spatial scale considered (Richards *et al*., 1996; Ferreira & Aguiar, 2006; Aguiar *et al*., 2009). The hydromorphological alteration of rivers as a result of flow regulation, and land-use changes can be considered among the main human disturbances modifying freshwater biological communities, especially in Mediterranean areas (Belmar *et al*., 2013; Stella *et al*., 2013; Bruno *et al*., 2014;), where they exacerbate the natural stress of river ecosystems (Stromberg *et al*., 2004; Kroll *et al*., 2013). Given the scarcity of water resources and the wide agricultural surfaces in these areas, both pressures are highly interconnected, as water supply for irrigation is the main cause for water demands (Zimmer, 2010). Therefore, although agriculture and hydromorphological alteration cause deep modifications in aquatic and riparian communities (Ward, 1998; Allan, 2004), their responses to these pressures can differ depending on the nature of the human pressure. We consider that agricultural land use could be exerting a greater influence on riparian communities, since they are directly impacted by agricultural processes (e.g. occupation of riparian area, greater amount of sediments, modification of river bank profile), whereas strictly aquatic communities could respond more clearly to in-stream disturbances such as hydromorphological alteration (e.g. low ability to persist after the hydropeaking process caused by dam releases, micro and mesohabitat reduction, homogenisation, or bed substrate modification).

Regarding the spatial scale, most previous studies have reported that land-use and hydrological alteration acting at local scale are important for shaping river communities (e.g. Nilsson *et al*., 1991; Nerbonne & Vondracek, 2001; Sponseller *et al*., 2001; Fernandes *et al*., 2011), and some of them have also documented the importance of these pressures at wider scales (Yates & Bailey, 2011; Wahl *et al*., 2013). Thus, although alteration processes at both scales seem to be important (Stewart *et al*., 2001; Johnson *et al*., 2007; Marzin *et al*., 2013), a greater influence of those operating at reach scale can be detected, as both aquatic and riparian communities are directly exposed to these local impacts, especially in semiarid rivers (Boyero, 2003; Aguiar & Ferreira, 2005; Monteagudo *et al*., 2012).

Finally, as results can also vary depending on the indicator used to estimate the biological communities' responses, we decided to use both biodiversity and ecological condition indicators. Firstly, biodiversity indicators are well-surveyed and taxonomically stable groups of organisms whose species richness patterns or rarity can be considered as similar to those of unsurveyed taxa in the same region (Pearson, 1994). Secondly, indicators of ecological condition are widely used to assess river health (Karr, 1999; Bonada *et al*., 2006). They are complementary integrative and holistic indices that involve a wide range of metrics in order to obtain a measure of quality (Feest *et al*., 2010). Although it seems evident that ecological condition indices should clearly respond to human pressures, as they are ultimately designed to assess their effects, this assumption has been scarcely tested. Furthermore, many ecological studies regarding the influence of human pressures on biological communities continue using richness as a response variable (Birk *et al*., 2012).

Many studies have separately tested the influence of diverse human pressures on river communities, the varying biological responses depending on the spatial scale considered, the convergence on the sensitivity of several ecological indicators or the contrasting response of aquatic and riparian communities facing these anthropogenic disturbances. Nevertheless, as far as we know, no holistic studies considering all of these different aspects together (kind of pressure, scale, response variable and target community) have been conducted. Therefore, in this study, we aim to assess the influence of agricultural land use and hydromorphological alteration at basin and reach scales on the biodiversity and ecological condition of both Mediterranean riparian and aquatic communities. Based on the information above, we predict the following: 1) although both types of human pressures are expected to modify riparian and aquatic communities, agricultural land use could have a greater influence on riparian communities, whereas hydromorphological alteration could have a clearer relationship with strictly aquatic communities; 2) human pressures acting at reach and basin scales will modify riparian and aquatic communities, although a greater effect from those operating at reach scale may be found; 3) ecological condition indicators will be more sensitive to human pressures in both communities than biodiversity indicators.

Materials and methods

Data collection

Biological data

A total of 56 sampling sites were selected to represent the wide range of human pressures present in the basin (Fig. 1), that simultaneously minimise the confounding effect of the main natural stressors (i.e. water salinity and flow temporality). For this reason, we selected permanent flow rivers (excluding temporary streams sensu Belmar *et al*., 2013) with electrical conductivity < 5,000 μS cm-1. Finally, urban areas were excluded because they represent very particular conditions that present an isolated distribution and cover only 2.1% of the entire study area (estimated from Corine Land Cover 2000).

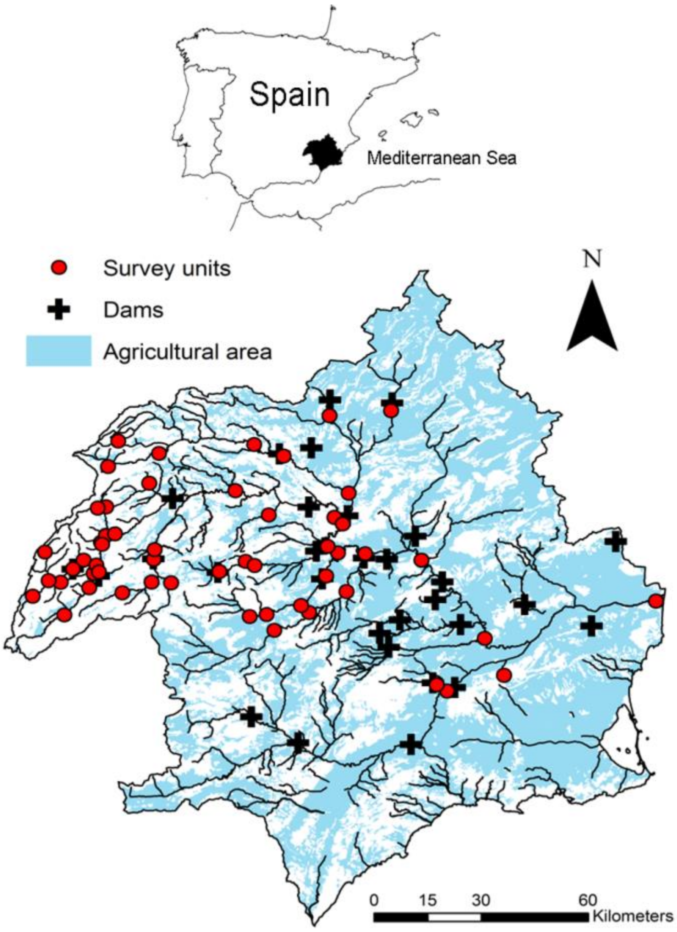


Fig. 1. Geographic location of the study area showing the 56 sampling sites, agricultural area and the main dams.

Woody riparian vegetation richness and the Riparian Quality Index (RQI, González del Tánago *et al*., 2006) were used as surrogates of biodiversity and to assess the ecological status of the riparian communities, respectively. RQI is a widely used index in the Iberian Peninsula because it has been proven to detect human impacts on riparian ecosystems (Navarro-Llácer *et al*., 2010; Barquín *et al*., 2011; Belmar *et al*., 2013). RQI is composed of several sub-indices characterising lateral, longitudinal and vertical continuity, composition, structure, regeneration and bank condition. Although the effect of anthropogenic alteration on vegetation could vary depending upon the function and features of the type of vegetation considered (Bunn & Arthington, 2002), woody riparian species are long-lived, stable and sensitive to human pressures, and can therefore be used as suitable indicators of hydromorphological and land-use disturbances (Nilsson *et al*., 1991; Bejarano *et al*., 2012; Villarreal *et al*., 2012).

Coleoptera richness and the Iberian Biomonitoring Working Party (IBMWP, Alba-Tercedor *et al*., 2002) were used as a surrogate of biodiversity and an indicator of the ecological status for the aquatic communities, respectively. Water beetles richness was used as a surrogate of biodiversity for strictly aquatic communities, as it has proven showed to be a good biodiversity indicator in aquatic ecosystems (Guareschi *et al*., 2012), especially in the study area (Sánchez-Fernández *et al*., 2006). Their high diversity makes them potential candidates for assessing the effects of land use, even at larger spatial scales (Minaya *et al*., 2013). The IBMWP is a quality index largely used in the Iberian Peninsula (Munné & Prat, 2009), based on differential tolerance to the organic pollution of aquatic macroinvertebrate families. Although both biological indicators can be positively correlated, the use of a higher taxonomic resolution (water beetle species richness) could provide additional and complementary information to family-based indices such as IBMWP in terms of ecological response to disturbances (Kroll *et al*., 2013).

Riparian data were obtained for each sampling site along 500 m length reaches, whereas macroinvertebrates were only collected in the last 100 m (downstream). Riparian and macroinvertebrate surveys were conducted between 2010 and 2011 during late spring and early summer, corresponding to the maximum species activity season (invertebrates) and also the most suitable period for riparian vegetation, particularly when using one-shot surveys (Ferreira & Aguiar, 2006). Furthermore, it has been observed that this seasonal sample taken from Mediterranean streams is representative of the pooled annual macroinvertebrate community (Bonada *et al*., 2007).

Within each survey unit, we recorded the occurrence of woody riparian species, through ten transects from the water margin up to the natural bankfull width, obtaining a unique list of species by site. Additionally, the RQI index was also calculated for each sampling site. Macroinvertebrates were sampled with a kick-net of 500 µm mesh, following a multihabitat standardised protocol, covering all mesohabitat types present in the reach (Jáimez-Cuéllar *et al*., 2002). Each kick-sample was examined in the field and sampling sites were consistently surveyed until no further families or water beetle species (morphotypes) were found in each mesohabitat. The kick-sample contents were pooled into a unique site-sample, preserved in 96% ethanol and identified to family level, except for Coleoptera, which were identified in the laboratory to species level in order to obtain the water beetle richness and IBMWP score for each locality.

Human pressures at reach and basin scale

At basin scale, a hydromorphological alteration score was derived using the number of dams (count), their regulatory capacity (hm^3) and the area of irrigated land (%) (as a surrogate of water extraction) draining to each sampling site, as these variables are associated with the main hydromorphological alterations in the study area (see Belmar *et al*., 2013). At reach scale, hydromorphological alteration was assessed using the Habitat Modification Score (HMS) derived from the River Habitat Survey protocol (Raven *et al*., 1997; Environment Agency, 2003), which assesses the hydromorphological modification of the river channel in the 500 m reach, considering weirs, dams, outfalls, realignments, reinforcement and resectioning among other variables. It has been widely used as a surrogate of hydromorphological alteration (e.g. Erba *et al*., 2006; Bona *et al*., 2008).

The percentage of agriculture (both irrigated and non-irrigated crops) at reach (200 m buffer at both sides of the sampling site; i.e. an area of 200,000 m^2) and basin (entire area draining to the sampling site) scales were computed for each locality by combining the ArcGIS software 9.2 (ESRI, Redlands, California, USA) and the analysis toolkit *NetMap* (Benda *et al*., 2007), based on the available digital information (1:25,000) provided by the Occupation Information System of Soil in Spain (SIOSE).

Statistical analyses

Spearman's rank correlation coefficients were used to discard highly ($R > 0.7$) correlated human pressures at the different spatial scales considered to reduce collinearity among predictors. Although the anthropogenic variables were moderately correlated, none of them showed a Spearman correlation coefficient higher than 0.7, and all of them were used in the analyses. Generalised Linear Models (GLMs) (McCullagh & Nelder, 1989) with different combinations of variables (a total of 36 models) were performed to test the influence of human pressures on riparian and aquatic ecological condition (RQI and IBMWP) and species richness (riparian and water beetle richness). Thus we studied the effect of:

1) individual anthropogenic variables [a: Reach agriculture (200 m buffer), b: Basin agriculture, c: Reach hydromorphological alteration (HMS), d: Basin hydromorphological alteration],

2) type of pressure (agriculture: a + b; hydromorphological alteration: c + d)

3) spatial scale (reach: a + c; basin: b + d)

4) the combination of all types of pressures and scales considered (a + b + c + d) (see Appendix 2.1 in Supporting Information).

GLMs were carried out assuming a Poisson distribution for the dependent variables. A stepwise procedure was used to insert environmental variables into the model (Nicholls, 1989) and linear and quadratic relationships were tested. The percentage of explained deviance was used to evaluate the models' performance. Outliers were identified and removed in each model (if applicable). Finally, normality (Shapiro-Wilk test) and spatial independence (Moran's I test, ArcGIS 9.2) of residuals were assessed. Prior to the analyses, hydromorphological variables (c and d) were log-transformed and agricultural percentages at both scales (a and b) were arcsine-square-root transformed to improve linearity. All explanatory variables were z-standardised (mean=0, SD=1) to allow model coefficient comparison. These statistical analyses were carried out using the 'corrgram', 'car' and 'MASS' packages of the statistical computing software R (R Development Core Team, 2012).

Results

Strong decreasing patterns from rich, well-conserved headwaters to poor, impaired lowlands were found for both riparian and macroinvertebrate communities (Fig. 2). The values of agricultural area ranged from 0 to 67.8% at reach scale and from 0 to 94.6% at basin scale. The hydromorphological alteration at reach scale (HMS) ranged from 0 to 3480, whereas the basin hydromorphological index at basin scale ranged from 0 (minimum flow alteration) to 14 (maximum flow alteration) among the different localities.

In general, GLMs showed a clear decrease in richness and ecological condition for both riparian (Fig. 3) and aquatic macroinvertebrate communities (Fig. 4) when human pressure increased, independently of the type of pressure or the spatial scale considered (Table 1). It is worth noting that, with some exceptions (e.g. linear response to basin agriculture) most of the relationships were humped. This general decrease takes place with the exception of the first phases of alteration, in which species richness and ecological condition seem to remain constant or even in some cases, increase slightly.

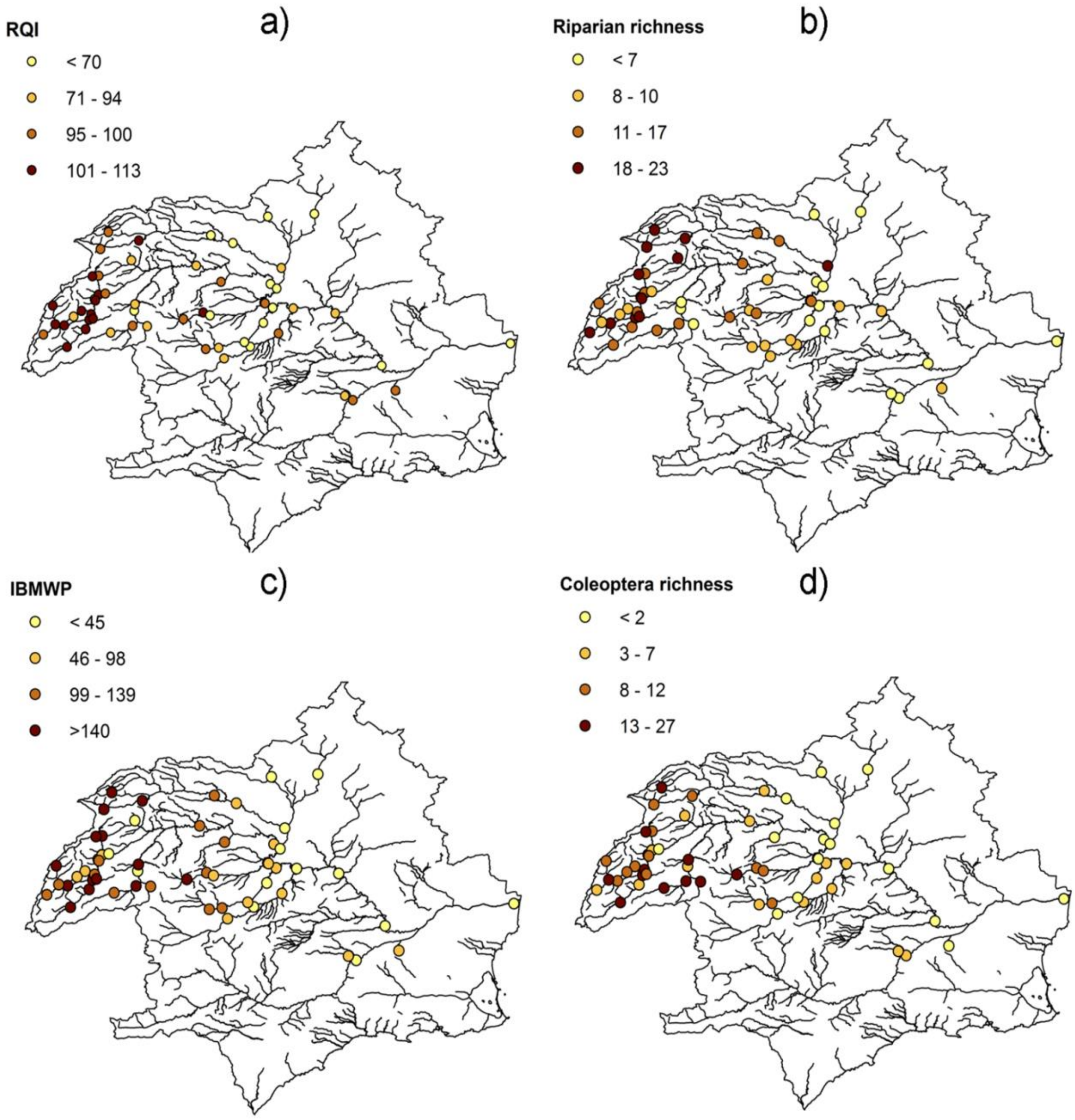


Fig. 2. Distribution of riparian and macroinvertebrate quality and richness values in the study area: a) RQI, b) Riparian woody species richness, c) IBMWP and d) Coleoptera species richness.

Although the patterns were similar for riparian vegetation and aquatic macroinvertebrates, differences in the percentage of explained deviance were detected (Table 1). For example, in general, the greater percentages of explained deviance corresponded to agricultural land use for riparian communities and hydromorphological disturbances for macroinvertebrates. The basin scale pressures were able to explain a higher percentage of deviance than those at local scale. Moreover, it seems that ecological condition indicators responded more clearly than biodiversity indices to human pressures. Lastly, models combining all of the pressures displayed a relatively high percentage of explained deviance, especially for riparian and macroinvertebrate-based condition indices.

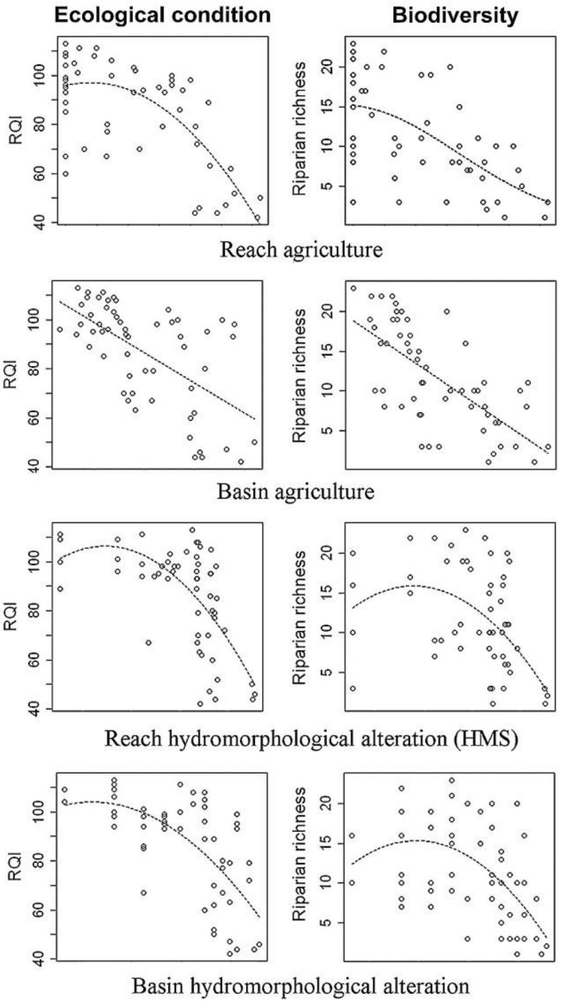


Fig. 3. Response of riparian condition (RQI) and riparian richness to agriculture and hydromorphological disturbances at reach and basin scales according to GLM results.

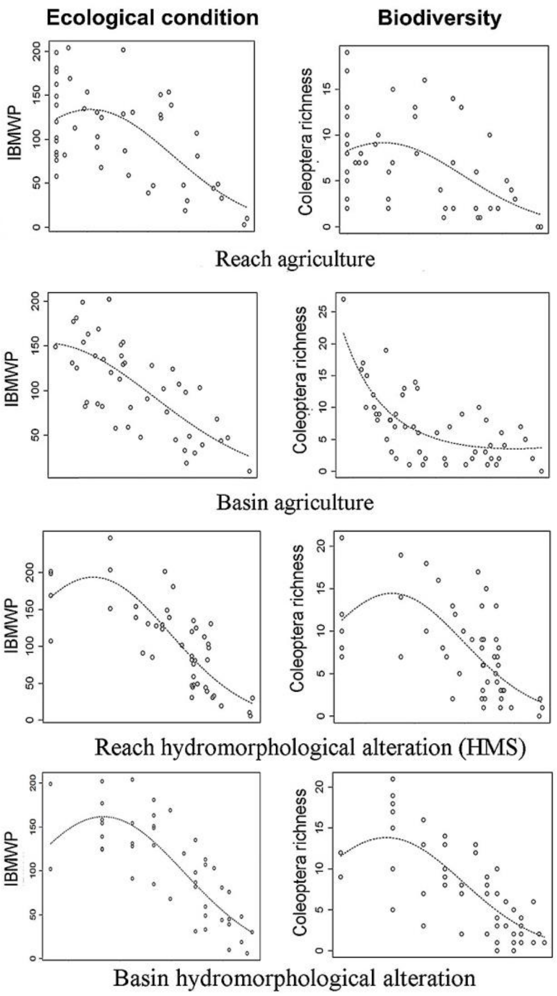


Fig. 4. Response of macroinvertebrate-based quality index (IBMWP) and water beetle richness to agriculture and hydromorphological disturbances at reach and basin scales according to GLM results.

All of the models' residuals showed spatial independence, whereas some exceptions were found in the normal distribution assumption (6 of 36 models showed *p*-values between 0.01 and 0.05). However, the risk of false significant relationships in GLM results is minimal given the high number of samples and the high significance of the variables and terms entered into the models ($P < 0.01$) (see Appendix 2.2 in Supporting Information).

Table 1. GLM analyses showing the percentages of explained deviance for significant (*p*-value < 0.01) individual variables, type of impact, scale and the combination of all considered pressures.

Anthropogenic disturbance	RQI	Riparian richness	IBMWP	Coleoptera richness
Reach agriculture (a)	51.4	40.0	41.1	26.1
Basin agriculture (b)	34.3	45.6	51.4	45.4
Reach hydromorphological alteration (c)	39.8	22.6	60.9	39.2
Basin hydromorphological alteration (d)	41.4	29.1	64.5	54.2
Agriculture (a+b)	54.6	51.1	60.2	45.4
Hydromorphological alteration (c+d)	48.0	29.1	70.0	54.2
Reach scale (a+c)	63.7	45.0	74.6	44.8
Basin scale (b+d)	50.1	50.6	78.5	53.4
Whole (a+b+c+d)	67.4	55.0	82.9	57.9

Discussion

We found a general decrease in species richness and the ecological quality of both riparian and aquatic communities from the headwaters to the lowlands. This clear negative relationship was found for both agricultural land use and hydromorphological alteration regardless of the spatial scale considered, thereby confirming the importance of human pressures shaping biological communities in fluvial ecosystems, and particularly in Mediterranean rivers. The similarity in the responses displayed by both communities agrees with results obtained in other climatic areas (Rios & Bailey, 2006), evidencing that both communities are intensively interconnected through physical processes and fluxes of energy and nutrients, and respond similarly to multi-scaled abiotic drivers (Gregory *et al*., 1991).

Although a general decline in richness and ecological condition was observed in both communities as human pressures intensified, at low rates of alteration the values of both types of biological indicators remained constant or even increased slightly, particularly regarding hydromorphological alteration. Opposite to the detrimental and impoverishing effect of medium or high intensity disturbances on target communities, low-intensity stream modification could promote certain habitat heterogeneity (Bertrand *et al*., 2004), leading to a slight increase in macroinvertebrate and riparian-based values. Another possible explanation is the high variability (data dispersion) of index values found in survey units at low alteration rates. As several human activities can be simultaneously altering riverine communities, this dispersion could be due to the effects of other human pressures or natural stressors. Taking into account that we are only using anthropogenic variables, models combining all the pressures displayed a relatively high percentage of explained deviance.

Type of impact: agriculture vs. hydromorphological alteration

Although riparian and aquatic communities were negatively influenced by both types of human pressures, in general, agricultural land use seemed to be the most important disturbance for riparian communities, whereas hydromorphological alteration showed a clearer relationship to aquatic communities. Therefore, despite the dramatic ecological implications that stream modification has on the structure and function of river ecosystems as a whole (Elosegi & Sabater, 2013), agriculture seems to exert a more intense effect on riparian vegetation, since it is more directly and physically impacted by some of these agricultural practices. Agriculture constitutes an impact that not only constrains the riparian area by causing the loss of riparian forests, it also alters river and riparian integrity, habitat quality, bank stability nutrient enrichment and the sedimentation process (Roth *et al.*, 1996; Allan, 2004). Finally, both types of disturbance favour the invasion of weeds and exotic, opportunistic species and a decline in woody species (Ferreira & Moreira, 1995; Greet *et al.*, 2012). This species substitution usually involves a modification of the functional trait combination of the riparian community, which can lead to a reduction of the ecosystem services it provides (e.g. soil fixation, organic matter supply).

The more direct relationship between hydromorphological alteration and strictly aquatic communities reflects the lower ability of freshwater biota to withstand this disturbance that impoverishes fluvial communities. Previous analyses in the study area have shown the important role of natural flow variability in determining the composition and richness of macroinvertebrates (Belmar *et al.*, 2012). Although aquatic Mediterranean communities have evolutionary mechanisms and adaptations to face the extreme natural events and predictable flow variability typical of these semiarid areas (e.g. flash floods and droughts), they cannot cope with those caused by the anthropogenic alteration of flow regimes, given their different timing, frequency, predictability and magnitude (Kroll *et al*., 2013). Its negative effects can be even worse if such altered flow discharge occurs during sensitive life stages, as is the case with large-scale, unpredictable and frequent dam releases during summer to meet agricultural demands. Only resistant and rapidly dispersive species are able to avoid their effects (Allan, 2004). Rivers and streams in the study area have experienced significant changes in flow regimes by dam regulation similar to those described in other arid and semiarid Mediterranean areas: the dams have reduced the flow magnitude, changed their frequency and inverted seasonal flow patterns downstream (Grantham *et al*., 2013). These changes have resulted in increased channel dimensions, homogeneous aquatic habitats, altered sedimentation and channel-bed grain size, as well as the absence of in-channel debris and submerged vegetation (Ligon *et al*., 1995; Bunn & Arthington, 2002). This reduces the diversity of resources and refuges for fauna and has negative effects on banks and riparian vegetation too (Navarro-Llácer *et al*., 2010; Belmar *et al*., 2013). Hydromorphological alteration can also produce an increase in the duration of droughts in the most arid areas, leading to the "terrestrialisation" of fluvial ecosystems and loss of freshwater biota (Sabater & Tockner, 2010).

The weaker relationship between aquatic community and agriculture in comparison with hydromorphological alteration could be due to the buffering effect of riparian areas mitigating the effect of agricultural land-use in the basin, avoiding a deeper impact on aquatic communities, particularly in areas hosting well-conserved riparian galleries (Naiman & Décamps, 1997; Riseng *et al*., 2011). Thus, further research will be necessary to unravel the potential role of riparian vegetation in mitigating the impact produced by human pressures on aquatic communities (i.e. not as a variable response, but as a predictor).

Spatial scale dependence

Our results showed that human pressures negatively influenced aquatic and riparian communities, regardless of the scale considered, as pointed out by previous studies (Gregory *et al*., 1991; Allan, 2004; Burcher *et al*., 2007). We expected a clearer relationship between riverine communities and human pressures acting at reach scale than those at basin scale, as other authors had previously found (Sponseller *et al*., 2001; Strayer *et al*., 2003; Moerke & Lamberti, 2006). In fact, several studies did not find relationships between catchment disturbances (land cover) and river communities (Heino *et al*., 2002; Rios & Bailey, 2006). However, our results did not meet our predictions. We found that variables at basin scale had an effect at least comparable or even greater to those operating at the local scale. These findings agree with other studies stating that human pressures acting at basin scale seem to also play a major role in riparian vegetation (Salinas & Casas, 2007; Aguiar *et al*., 2009) and macroinvertebrate communities (Dolédec *et al*., 2011; Magierowski *et al*., 2012). Therefore, a non-locally impacted reach does not necessarily result in good ecological condition or biodiversity values, as catchment disturbances could exert a strong influence through erosion, sediment load, chemistry (Törnblom *et al*., 2011), organic matter input, in-stream primary production (Dolédec *et al*., 2011), the invasion of exotic species (Poff *et al*., 2007; Greet *et al*., 2012) or habitat homogenisation (Belmar *et al*., 2013). Furthermore, large-scale and chronic disturbances in a watershed can limit river diversity over the long term (Harding *et al*., 1998). However, the majority of restoration efforts are focussed on reducing local alteration, which is insufficient in order to guarantee acceptable ecological condition values in freshwater ecosystems (Bernhardt & Palmer 2011; Kail & Wolter, 2013). Thus, this restoration effort should focus on measures at the river basin scale in a greater extent in order to develop more effective management strategies.

Type of indicator: biodiversity vs. ecological condition

Although we found a high congruence in the indicators' response to human disturbances, as expected, the sensitiveness of ecological condition indicators (RQI and IBMWP) were generally higher than that of those for biodiversity (richness of woody riparian and water beetles), given their holistic and integrative nature. Despite the methodological differences between the ecological condition indicators used here, they have been identified as sensitive to different types of disturbances including land use change and stream modification (Munné a Prat, 2009; Sánchez-Montoya *et al*., 2010; Belmar *et al*., 2013; Garófano-Gómez *et al*., 2013). In particular, among all the indicators used here, IBMWP was the most sensitive one. It seems that its scoring system based on the different tolerance to pollution of aquatic macroinvertebrate families could be sensitive even for no pollutant human pressures (i.e. hydromorphological alteration).

However, the lower sensitivity of richness measures can be due to the fact that human pressures produced an impoverishment or simplification in the communities, modifying not only the number of species, but also the quality and composition of the aquatic and riparian communities. Thus, richness measurements do not weigh the importance of losing a particular species and fail to consider its sensitivity or importance in ecosystem functioning (i.e. all species have the same weight). For example, the loss of stenoic sensitive taxa (Gutiérrez-Cánovas *et al*., 2013) or their substitution by generalist or opportunistic species is a common occurrence as a response to human disturbances (Devictor *et al*., 2008), which can result in communities with similar richness but different composition. Therefore, the use of holistic and integrative indicators considering as many river ecosystem components as possible (e.g. composition, structure, functioning, diversity) or scoring the occurrence of species depending on its sensitiveness is preferable to partial and/or simple parameters as richness measures.

Management implications

The combined use of ecological condition indicators of both macroinvertebrate and riparian vegetation provides a more realistic and complete picture of the status of river ecosystems leading to improved planning, monitoring and evaluation of management strategies, restoration and conservation measures. Holistic and integrative management seems the best option to reach the prior objective of optimising river conservation as a whole (European Commission, 2000/60/EC).

Although both communities' responses were similar, different management measures could be proposed for each community (e.g. for strictly aquatic communities, a greater effort on mitigating hydromorphological alteration should be done). Our results suggest scale-dependent sensitivity of aquatic and riparian communities to human pressures, which has general management implications. Land use and hydrological planning at basin scale are essential complements to traditional, local and disconnected restoration measures in order to successfully preserve and restore stream ecosystem integrity, biodiversity as well as longitudinal and lateral connectivity. Furthermore, reverting the human transformation of land use and limiting the current expansion of agriculture in the study area would help to minimise detriment to the river ecosystems because it is simultaneously one of the main causes of high water demands and stream modification.

References

Aguiar, F.C. & Ferreira, M.T. (2005) Human-disturbed landscapes: effects on composition and integrity of riparian woody vegetation in the Tagus River basin, Portugal. *Environmental Conservation*, **32**, 30–41.

Aguiar, F.C., Ferreira, M.T., Albuquerque, A., Rodríguez-González, P & Segurado, P. (2009) Structural and functional responses of riparian vegetation to human disturbance: performance and spatial scale-dependence. *Fundamental and Applied Limnology*, **175**, 249–267.

Alba-Tercedor, J., Jáimez-Cuéllar, P., Álvarez, M., Avilés, J., Bonada, N., Casas, J., *et al.* (2002) Caracterización del estado ecológico de ríos mediterráneos ibéricos mediante el índice IBMWP (antes BMWP'). *Limnetica*, **21**, 175–185.

Allan, J.D. (2004) Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 257–284.

Barquín, J., Fernández, D., Álvarez-Cabria, M. & Peñas, F.J. (2011) Riparian quality and habitat heterogeneity assessment in Cantabrian rivers. *Limnetica*, **30**, 329–346.

Bejarano, M.D., González del Tánago, M., Garcia de Jalón, D., Marchamalo, M., Sordo-Ward, A. & Solana-Gutiérrez, J. (2012) Responses of riparian guilds to flow alterations in a Mediterranean stream. *Journal of Vegetation Science*, **23**, 443–458.

Belmar, O., Velasco, J., Martínez-Capel, F. & Marin, A.A. (2010) Natural flow regime, degree of alteration and environmental flows in the Mula stream (Segura River basin, SE Spain). *Limnetica*, **29**, 353–368.

Belmar, O., Velasco, J., Gutiérrez-Cánovas, C., Mellado-Díaz, A., Millán, A. & Wood, P.J. (2012) The influence of natural flow regimes on macroinvertebrate assemblages in a semiarid Mediterranean basin. *Ecohydrology*, **6**, 363–379.

Belmar, O., Bruno, D., Martínez-Capel, F., Barquín, J. & Velasco J. (2013) Effects of flow regime alteration on fluvial habitats and riparian quality in a semiarid Mediterranean region. *Ecological Indicators*, **30**, 52–64.

Benda, L., Miller, D., Andras, K., Bigelow, P., Reeves, G. & Michael, D. (2007) NetMap: a new tool in support of watershed science and resource management. *Forest Science*, **53**, 220–238.

Bernhardt, E.S. & Palmer, M.A. (2011) River restoration: the fuzzy logic of repairing reaches to reverse catchment scale degradation. *Ecological Applications*, **21**, 1926–1931.

Bertrand, C., Franquet, E., Chomerat, N. & Cazaubon, A. (2004) An approach to the intermediate disturbance hypothesis at the landscape scale: the effects of hydro-dynamic disturbance on phytoplankton communities. *Fundamental and Applied Limnology/Archiv für Hydrobiologie*, **161**, 351–369.

Birk, S., Bonne, W., Borja, A., Brucet, S., Courrat, A., Poikane, S., *et al.* (2012) Three hundred ways to assess Europe's surface waters: an almost complete overview of biological methods to implement the Water Framework Directive. *Ecological Indicators*, **18**, 31–41.

Bona, F., Falasco, E., Fenoglio, S., Iorio, L. & Badino, G. (2008) Response of macroinvertebrate and diatom communities to human-induced physical alteration in mountain streams. *River Research and Applications*, **24**, 1068–1081.

Bonada, N. & Resh, V.H. (2013) Mediterranean-climate streams and rivers: geographically separated but ecologically comparable freshwater systems. *Hydrobiologia*, **719**, 1–29.

Bonada, N., Prat, N., Resh, V.H. & Statzner, B. (2006) Developments in aquatic insect biomonitoring: a comparative analysis of recent approaches. *Annual Review of Entomology*, **51**, 495–523.

Bonada, N., Dolédec, S. & Statzner, B. (2007) Taxonomic and biological trait differences of stream macroinvertebrate communities between Mediterranean and temperate regions: implications for future climatic scenarios. *Global Change Biology*, **13**, 1658–1671.

Boyero, L. (2003) Multiscale patterns of spatial variation in stream macroinvertebrate communities. *Ecological Research*, **18**, 365–379.

Bruno, D., Belmar, O., Sánchez-Fernández, D. & Velasco, J. (2014) Environmental determinants of woody and herbaceous riparian vegetation patterns in a semi-arid Mediterranean basin. *Hydrobiologia*, **730**, 45–57.

Bunn, S.E. & Arthington, A.H. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, **30**, 492–507.

Burcher, C.L., Valett, H.M. & Benfield, E.F. (2007) The land-cover cascade: relationships coupling land and water. *Ecology,* **88**, 228–242.

Cooper, S.D., Lake, P.S., Sabater, S., Melack, J.M. & Sabo, J.L. (2013) The effects of land use changes on streams and rivers in Mediterranean climates. *Hydrobiologia*, **719**, 383–425.

Devictor, V., Julliard, R. & Jiguet, F. (2008) Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, **117**, 507–514.

Dolédec, S., Phillips, N. & Townsend, C. (2011) Invertebrate community responses to land use at a broad spatial scale: trait and taxonomic measures compared in New Zealand rivers. *Freshwater Biology*, **56**, 1670–1688.

Elosegi, A. & Sabater, S.(2013) Effects of hydromorphological impacts on river ecosystem functioning: a review and suggestions for assessing ecological impacts. *Hydrobiologia*, **712**, 129–143.

Environment Agency (2003) *River Habitat Survey in Britain and Ireland. Field Survey Guidance Manual.* Environment Agency, Bristol, United Kingdom.

Erba, S., Buffagni, A., Holmes, N., O’Hare, M., Scarlett, P. & Stenico, A. (2006) Preliminary testing of River Habitat Survey features for the aims of the WFD hydro-morphological assessment: an overview from the STAR Project. *Hydrobiologia*, **566**, 281–296.

European Commission (2000) Directive 2000/60/EC of the European Parliament and of the Council. *Official Journal of the European Union,* **327**, 1–72.

Feest, A., Aldred, T.D. & Jedamzik, K. (2010) Biodiversity quality: a paradigm for biodiversity. *Ecological Indicators*, **10**, 1077–1082.

Fernandes, M.R., Aguiar, F.C. & Ferreira, M.T. (2011) Assessing riparian vegetation structure and the influence of land use using landscape metrics and geostatistical tools. *Landscape and Urban Planning*, **99**, 166–177.

Ferreira, M.T. & Moreira, I.S. (1995) The invasive component of the macroflora from river systems within agricultural Mediterranean areas. *Plant Invasions – General Aspects and Special Problems* (eds Pysek, P., Prach, K., Rejmanek, M. & Wade, P.M.), pp. 117–127. SPB Academic Publishing, Amsterdam, The Netherlands.

Ferreira, M.T. & Aguiar, F.C. (2006) Riparian and aquatic vegetation in Mediterranean type streams (Western Iberia). *Limnetica*, **25**, 411–424.

Garófano-Gómez, V., Martínez-Capel, F., Bertoldi, W., Gurnell, A., Estornell, J. & Segura-Beltrán, F. (2013) Six decades of changes in the riparian corridor of a Mediterranean river: a synthetic analysis based on historical data sources. *Ecohydrology*, **6**, 536–553.

González del Tánago, M., García de Jalón, D., Lara, F. & Garilleti, R. (2006) Índice RQI para la valoración de las riberas fluviales en el contexto de la directiva marcodel agua. *Ingeniería Civil*, **143**, 97–108.

Grantham, T.E., Figueroa, R. & Prat, N. (2013) Water management in Mediterranean river basins: a comparison of management frameworks, physical impacts, and ecological responses. *Hydrobiologia*, **719**, 451–482.

Greet, J., Cousens, R. & Webb, A. (2012) More exotic and fewer native plant species: riverine vegetation patterns associated with altered seasonal flow patterns. *River Research and Applications*, **29**, 686–706.

Gregory, S.V., Swanson, F.J., McKee, W.A. & Cummins, K.W. (1991) An ecosystem perspective of riparian zones. *Bioscience*, **41**, 540–551.

Guareschi, S., Gutiérrez-Cánovas, C., Picazo, F., Sánchez-Fernández, D., Abellán, P.,Velasco, J. & Millán, A. (2012) Aquatic macroinvertebrate biodiversity: patterns and surrogates in mountainous Spanish national parks. *Aquatic Conservation*, **22**, 598–615.

Gutiérrez-Cánovas, C., Millán, A., Velasco, J., Vaughan, I.P. & Ormerod, S.J. (2013) Contrasting effects of natural and anthropogenic stressors on beta diversity in river organisms. *Global Ecology and Biogeography*, **22**, 796–805.

Harding, J.S., Benfield, E.F., Bolstad, P.V., Helfman, G.S. & Jones, E.B.D. (1998) Stream biodiversity: the ghost of land use past. *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 14843–14847.

Heino, J., Muotka, T., Paavola, R., Hämäläinen, H. & Koskenniemi, E. (2002) Correspondence between regional delineations and spatial patterns in macroinvertebrate assemblages of boreal headwater streams. *Journal of the North American Benthological Society,* **21**, 397–413.

Hooke, J.M. (2006) Human impacts on fluvial systems in the Mediterranean region. *Geomorphology*, **79**, 311–335.

Jáimez-Cuéllar, P., Vivas, S., Bonada, N., Robles, S., Mellado, A., Álvarez, M., *et al.* (2002) Protocolo Guadalmed (PRECE). *Limnetica*, **21**,187–204.

Johnson, R.K., Furse, M.T., Hering, D. & Sandin, L. (2007) Ecological relationships between stream communities and spatial scale: implications for designing catchment-level monitoring programmes. *Freshwater Biology*, **52**, 939–958.

Kail, J. & Wolter, C. (2013) Pressures at larger spatial scales strongly influence the ecological status of heavily modified river water bodies in Germany. *Science of the Total Environment*, **454**, 40–50.

Karr, J.R. (1999) Defining and measuring river health. *Freshwater Biology*, **41**, 221–234.

Kroll, S.A., Ringler, N.H., De las Heras, J., Goméz-Alday, J.J., Moratalla, A. & Briggs, R.D. (2013) Analysis of anthropogenic pressures in the Segura Watershed (SE Spain), with a focus on inter-basin transfer. *Ecohydrology*, **6**, 878–888.

Ligon, F.K., Dietrich, W.E. & Trush, W.J. (1995) Downstream ecological effects of dams. *Bioscience*, **45**, 183–192.

Magierowski, R.H., Davies, P.E., Read, S.M. & Horrigan, N. (2012) Impacts of land use on the structure of river macroinvertebrate communities across Tasmania, Australia: spatial scales and thresholds. *Marine and Freshwater Research,* **63**, 762–776.

Marzin, A., Verdonschot, P.F. & Pont, D. (2013) The relative influence of catchment, riparian corridor, and reach-scale anthropogenic pressures on fish and macroinvertebrate assemblages in French rivers. *Hydrobiologia*, **704**, 375–388.

McCullagh, P. & Nelder, J.A. (1989) *Generalized Lineal Models.* Chapman and Hall, London, United Kingdom.

Minaya, V., McClain, M.E., Moog, O. & Singer, G. (2013) Scale-dependent effects of rural activities on benthic macroinvertebrates and physico-chemical characteristics in headwater streams of the Mara River, Kenya. *Ecological Indicators*, **32**, 116–122.

Moerke, A.H. & Lamberti, G.A. (2006) Scale-dependent influences on water quality, habitat, and fish communities in streams of the Kalamazoo River basin, Michigan (USA). *Aquatic Sciences*, **68**, 193–205.

Monteagudo, L., Moreno, J.L. & Picazo, F. (2012) River eutrophication: irrigated vs. non-irrigated agriculture through different spatial scales. *Water Research*, **46**, 2759–2771.

Munné, A. & Prat, N. (2009) Use of macroinvertebrate-based multimetric indices for water quality evaluation in Spanish Mediterranean rivers: an intercalibartion approach with the IBMWP index. *Hydrobiologia*, **628**, 203–225.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Naiman, R.J. & Décamps, H. (1997) The ecology of interfaces: riparian zones. *Annual Review of Ecology, Evolution, and Systematics*, **28**, 621–658.

Navarro-Llácer, C., Baeza, D. & De las Heras, J. (2010) Assessment of regulated rivers with indices based on macroinvertebrates, fish and riparian forest in the south-east of Spain. *Ecological Indicators*, **10**, 935–942.

Nerbonne, B.A. & Vondracek, B. (2001) Effects of local land use on physical habitat, benthic macroinvertebrates, and fish in the White water River, Minnesota, USA. *Environmental Management,* **28**, 87–99.

Nicholls, A.O. (1989) How to make biological surveys go further with generalised linear models. *Biological Conservation*, **50**, 51–75.

Nilsson, C., Ekblad, A., Gardfjell, M. & Carlberg, B. (1991) Long-term effects of river regulation on river-margin vegetation. *Journal of Applied Ecology*, **28**, 963–987.

Pearson, D.L. (1994) Selecting indicator taxa for the quantitative assessment of biodiversity. *Philosophical Transactions of the Royal Society B*, **345**, 75–79.

Poff, N., Olden, J.D., Merritt, D.M. & Pepin, D.M. (2007) Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 5732–5737.

R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Raven, P.J., Fox, P., Everard, M., Holmes N.T.H. & Dawson, F.H. (1997) River habitat survey: a new system for classifying rivers according to their habitat quality. *Freshwater Quality: Defining the Indefinable?* (eds Boon, P.J. & Holwell, D.L.), pp. 215–234. The Stationery Office, Edinburgh, United Kingdom.

Richards, C., Johnson, L.B. & Host, G.E. (1996) Landscape-scale influences on stream habitats and biota. *Canadian Journal of Fisheries and Aquatic Sciences,* **53**, 295–311.

Rios, S.L. & Bailey, R.C. (2006) Relationship between riparian vegetation and stream benthic communities at three spatial scales. *Hydrobiologia*, **553**,153–160.

Riseng, C.M., Wiley, M.J., Black, R.W. & Munn, M.D. (2011) Impacts of agricultural land use on biological integrity: a causal analysis. *Ecological Applications*, **21**, 3128–3146.

Roth, N.E., Allan, J.D. & Erickson, D.L. (1996) Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology*, **11**, 141–156.

Sabater, S. & Tockner, K. (2010) Effects of hydrologic alterations on the ecological quality of river ecosystems. *Water Scarcity in the Mediterranean* (eds Sabater, S. & Barceló, D.), pp. 15–39. Springer Berlin Heidelberg, Berlin, Germany.

Sabater, F., Butturini, A., Martí, E., Muñoz, I., Romaní, A., Wray, J. & Sabater, S. (2000) Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. *Journal of the North American Benthological Society*, **19**, 609–620.

Sala, O.E., Chapin, F.S.III, Armesto, J.J., Berlow, R., Bloomfield, J., Dirzo, R., *et al*. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

Salinas, M.J. & Casas, J.J. (2007) Riparian vegetation of two semi-arid Mediterranean rivers: basin-scale responses of woody and herbaceous plants to environmental gradients. *Wetlands*, **27**, 831–845.

Sánchez-Fernández, D., Abellán, P., Mellado, A., Velasco, J. & Millán, A. (2006) Are water beetles good indicators of biodiversity in Mediterranean aquatic ecosystems? The case of the Segura river basin (SE Spain). *Biodiversity and Conservation*, **15**, 4507–4520.

Sánchez-Montoya, M.M., Vidal-Abarca, M.R. & Suárez, M.L. (2010) Comparing the sensitivity of diverse macroinvertebrate metrics to a multiple stressor gradient in Mediterranean streams and its influence on the assessment of ecological status. *Ecological Indicators*, **10**, 896–904.

Saunders, D.L., Meeuwig, J.J. & Vincent, A.C.J. (2002) Freshwater protected areas: strategies for conservation. *Conservation Biology*, **16**, 30–41.

Sponseller, R.A., Benfield, E.F. & Valett, H.M. (2001) Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biology*, **46**,1409–1424.

Stella, J.C., Rodríguez-González, P.M., Dufour, S. & Bendix, J. (2013) Riparian vegetation research in Mediterranean-climate regions: common patterns, ecological processes, and considerations for management. *Hydrobiologia*, **719**, 291–315.

Stewart, J.S., Wang, L., Lyons, J., Horwatich, J.A. & Bannerman, R. (2001) Influence of watershed, riparian-corridor, and reach-scale characteristics on aquatic biota in agricultural watersheds. *Journal of the American Water Resources Association*, **37**, 1475–1487.

Strayer, D.L., Power, M.E., Fagan, W.F., Pickett, S.T.A. & Belnap, J. (2003) A classification of ecological boundaries. *Bioscience*, **53**, 723–729.

Stromberg, J., Briggs, M., Gourley, C., Scott, M., Shafroth, P. & Stevens, L. (2004) Human alterations of riparian ecosystems. *Riparian Areas of the Southwestern United States: Hydrology, Ecology, and Management* (eds Baker Jr, M., Ffolliott, P., DeBano, L. & Neary, D.G.), pp. 101–126. Lewis Publishers, FLorida, USA.

Törnblom, J., Angelstam, P., Degerman, E., Henrikson, L., Edman, T. & Temnerud, J. (2011) Catchment land cover as a proxy for macroinvertebrate assemblage structure in Carpathian Mountain streams. *Hydrobiologia*, **673**, 153–168.

Villarreal, M.L., Drake, S., Marsh, S.E. & McCoy, A.L. (2012) The influence of wastewater subsidy, flood disturbance and neighbouring land use on current and historical patterns of riparian vegetation in a semi-arid watershed. *River Research and Applications*, **28**, 1230–1245.

Wahl, C.M., Neils, A. & Hooper, D. (2013) Impacts of land use at the catchment scale constrain the habitat benefits of stream riparian buffers. *Freshwater Biology*, **58**, 2310–2324.

Ward, J.V. (1998) Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation*, **83**, 269–278.

Ward, J.V., Tockner, K., Arscott, D.B. & Clarett, C. (2002) Riverine landscape diversity. *Freshwater Biology*, **47**, 517–539.

Yates, A.G. & Bailey, R.C. (2011) Effects of taxonomic group, spatial scale and descriptor on the relationship between human activity and stream biota. *Ecological Indicators*, **11**, 759–771.

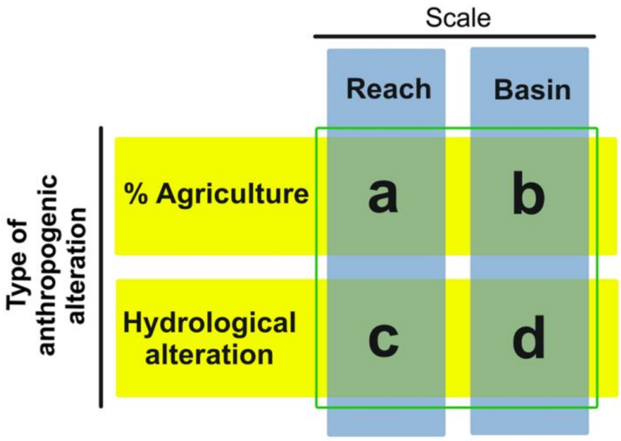
Zimmer, A. (2010) New water uses in the Segura basin: conflicts around gated communities in Murcia. *Water International*, **35**, 34–48.

Supporting Information

Appendix 2.1. Diagram showing the anthropogenic pressures considered in the study and the different combination of models run.

Appendix 2.2. GLM analyses showing the number of samples, percentages of explained deviance, AIC values and model equations for the different combination of pressures affecting riparian and macroinvertebrate richness and ecological condition indicators.

Appendix 2.1. Diagram showing the anthropogenic pressures considered (a, b, c, d) in the study and the different combination of models run. Blue: spatial scale; Yellow: type of pressure; Green square: the combination of all considered pressures.



Appendix 2.2. GLM analyses showing the number of samples (n), percentages of explained deviance, AIC values and model equations for the different combination of pressures affecting riparian and macroinvertebrate richness and ecological condition indicators (*P*-value < 0.01).

RQI	n	% explained deviance	AIC	Model
Reach agriculture* (a)	56	51.43	498	$-0.12a^2 -0.11a + 4.56$
Basin agriculture (b)	56	34.3	546	$-0.15b +4.45$
Reach hydromorphological alteration (HMS) (c)	56	39.8	532	$-0.08c^2 -0.23c +4.53$
Basin hydromorphological alteration (d)	56	41.43	527	$-0.06d^2 -0.17d +4.5$
Agriculture* (a+b)	56	54.57	491	$-0.11a^2 -0.08a -0.06b +4.55$
Hydromorphological alteration (c+d)	56	47.94	510	$-0.05c^2 -0.15c -0.08d + 4.5$
Reach scale (a+c)	56	63.74	466	$-0.09a^2 -0.09a -0.04c^2 -0.13c +4.57$
Basin scale (b+d)	56	50.15	503	$-0.03d^2 -0.13d -0.09b +4.48$
Whole (a+b+c+d)	56	67.38	456	$-0.07a^2 -0.11a -0.07d - 0.05c+ 4.54$

Riparian richness	n	% explained deviance	AIC	Model
Reach agriculture (a)	56	39.99	362	$-0.15a^2 -0.35a +2.53$
Basin agriculture (b)	56	45.57	348	$-0.41b +2.37$
Reach hydromorphological alteration (HMS) (c)	56	22.6	398	$-0.16c^2 -0.38c +2.58$
Basin hydromorphological alteration (d)	56	29.15	384	$-0.18d^2 -0.37d +2.57$
Agriculture (a+b)	56	51.07	338	$-0.30b -0.19a +2.36$
Hydromorphological alteration (c+d)	56	29.15	384	$-0.18d^2 -0.37d +2.57$
Reach scale (a+c)	56	45.03	353	$-0.13c^2 -0.28c -0.32a +2.49$
Basin scale (b+d)	56	50.57	342	$-0.09d^2 -0.18d -0.33b +2.46$
Whole (a+b+c+d)	56	55.03	334	$-0.10d^2 -0.16d -0.18a -0.22b +2.45$

IBMWP	n	% explained deviance	AIC	Model
Reach agriculture* (a)	47	41.07	1044	$-0.27a^2 -0.24a +4.84$
Basin agriculture (b)	47	51.42	899	$-0.14b^2 -0.41b +4.68$
Reach hydromorphological alteration (HMS) (c)	47	60.91	691	$-0.17c^2 -0.48c +4.74$
Basin hydromorphological alteration (d)	47	64.47	440	$-0.16d^2 -0.46d +4.72$
Agriculture (a+b)	47	60.22	692	$-0.08b^2 -0.33b -0.19a^2 -0.05a +4.77$
Hydromorphological alteration (c+d)	47	70.03	323	$-0.20d^2 -0.49d -0.04c^2 -0.08c +4.71$
Reach scale (a+c)	47	74.64	291	$-0.15c^2 -0.55c -0.22a^2 -0.21a +4.82$
Basin scale (b+d)	47	78.52	262	$-0.14d^2 -0.41d -0.15b^2 -0.28b +4.74$
Whole (a+b+c+d)	47	82.88	192	$-0.12d^2 -0.33d -0.13c -0.13b^2 -0.29b +4.7$

Coleoptera richness	n	% explained deviance	AIC	Model
Reach agriculture* (a)	49	26.11	303	$-0.24a^2 -0.21a +2.21$
Basin agriculture* (b)	52	45.44	231	$-0.07b^2 -0.55b +1.81$
Reach hydromorphological alteration (HMS) (c)	51	39.16	232	$-0.23c^2 -0.54c +2.16$
Basin hydromorphological alteration (d)	52	54.2	195	$-0.23d^2 -0.56d +2.13$
Agriculture* (a+b)	52	45.44	231	$-0.07b^2 -0.55b +1.81$
Hydromorphological alteration (c+d)	52	54.2	195	$-0.23d^2 -0.56d +2.13$
Reach scale* (a+c)	52	44.78	238	$-0.24c^2 -0.70c -0.14a +2.10$
Basin scale (b+d)	55	53.38	289	$-0.15d^2 -0.39d -0.37b +2.00$
Whole (a+b+c+d)	55	57.9	281	$-0.14d^2 -0.28d -0.39b -0.18c +1.97$

*Models whose residuals do not completely fulfill ($0.01 < p\text{-value} < 0.05$) normal distribution

Chapter 3

Impacts of environmental filters on functional redundancy in riparian vegetation

Abstract

Understanding ecosystem responses to multiple environmental pressures is a long-standing interest in ecology. 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. Besides, 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, i.e. drought, flow regulation and agricultural intensity. We explored the relationships between functional measures and environmental stressors, thus considering the potential effect of natural environmental variability. We also assessed the predictability of FR and calculated it for the entire river network. 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.

In summary, we found non-random detrimental effects along environmental filters for riparian functional redundancy, meaning that increased stress could jeopardise stability, resistance and resilience of these systems. FR could provide additional and complementary information to taxonomic richness on how communities respond to stress. All these findings along with the basin-wide variation of FR can assist environmental managers in improving biomonitoring and ecosystem management.

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 jeopardise the goods and services provided to humanity (Chapin *et al.,* 2002; 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 (BEF; Duffy, 2008; 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 species can overcome environmental filters (Kraft *et al.,* 2015), a non-random species sorting along environmental gradients is expected (Shipley *et al.,* 2006; 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 *et al.,* 2013) and if they can act synergistically to affect ecosystem resilience and stability (Sasaki *et al.,* 2015).

We used a database of woody riparian plants from a semiarid 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 *et al.,* 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 functional indices, and that FR response should be predictable from large-scale geographic 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

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, i.e. three abundance classes according to species dominance (dominant, frequent, present).

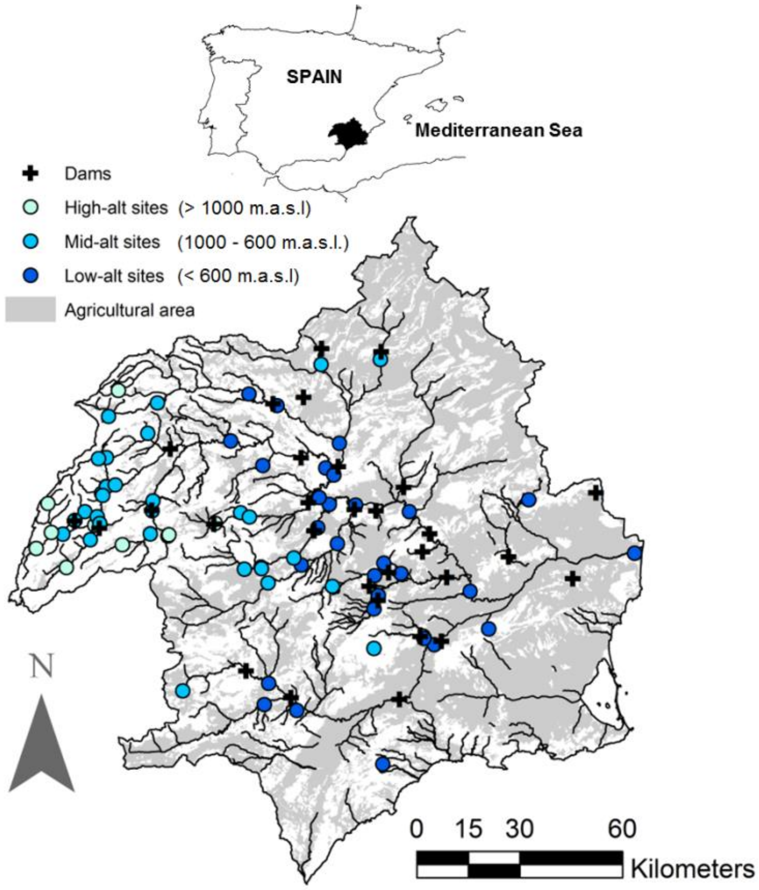


Fig. 1. Geographic location of the study area showing the 71 sampling sites classified by elevation (alt), the agricultural area and the main dams.

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 characterise the functional features of the species recorded (Lavorel & Garnier, 2002; Cornelissen *et al.,* 2003; Appendix 3.1 in 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, disturbance regime; Díaz & Cabido, 2001). Species-specific mean trait values were compiled from 59 online trait databases and scientific publications (Appendix 3.2 in Supporting Information). The final trait dataset is found in Appendix 3.3 in Supporting Information.

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 functional redundancy and a lack of consensus about them. Thus, FR was obtained for each sampling site from two different approaches: i) considering functional redundancy 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 functional diversity (using Rao's quadratic entropy) (Pillar *et al.,* 2013; data comparing both methods are available in Appendix 3.4). 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 functional groups must represent different life strategies with a clear ecological significance (Naiman, *et al.,* 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 eigen-vectors 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. Second, 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 functional redundancy 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 3.4 for further details).

We calculated the three primary components of functional diversity (richness, evenness and divergence *sensu* Mason *et al.,* 2005) to compare their response with those obtained using functional redundancy. 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 *et al.,* 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 standardised 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 *et al.,* 2008). Functional divergence (FDis) 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 recognised as the most important anthropogenic stressors impacting aquatic and riparian ecosystems (Nilsson & Berggren, 2000; Allan, 2004), and particularly in Mediterranean and semiarid areas as the study area (Kroll *et al.,* 2013; 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, California, USA) and the analysis toolkit NetMap (www.netmaptools.org; 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 *et al.* (2010) and adapted from Belmar *et al.* (2013). This method uses the number of dams and their regulatory capacity (hm^3) 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 semiarid rivers are normally subjected. This filter sorts the regional species pool, leaving species that have developed adaptations to drought (Peñuelas *et al.,* 2001). Drought duration was estimated at reach scale using the data from the Integrated System for Rainfall–Runoff Modelling (SIMPA) (Belmar *et al.,* 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 *et al.,* 2011). The site-specific values of the environmental filters are shown in Appendix 3.3.

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 summarises well the natural environmental gradients occurring in the study area (Díaz *et al.,* 2008). We tested the significance of simple and quadratic coefficients for each z-standardised (mean=0, SD=1) filter as well as the pairwise-filter interaction terms to look for potential combined effects. Before their standardisation, 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 minimises 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 functional groups) 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 *et al.,* 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 randomisations, 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 (a = 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 if the relationship between FR and species richness was different from what is expected by chance.

Finally, using the best model obtained for FR, we forecasted their values for the entire river network. Thus, rivers were divided in homogeneous reaches characterised 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', 'nmle' and 'vegan'; R Development Core Team, 2013). See R code and FR functions used in Appendix 3.3.

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. 2 and Appendix 3.5 in Supporting Information for details).

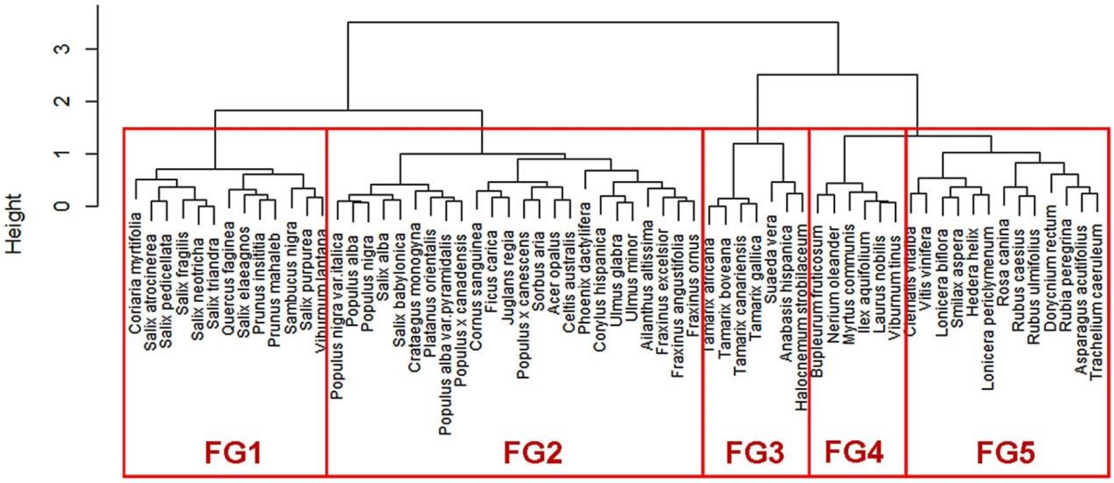


Fig. 2. Dendrogram resulting from classifying riparian species according to their similarity in the functional effect traits (those that influence the role of each plant on ecosystem services). FG=Functional Group.

Generally, we found that community functional measures significantly decreased with increasing environmental filters (Fig. 3). 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 3.6).

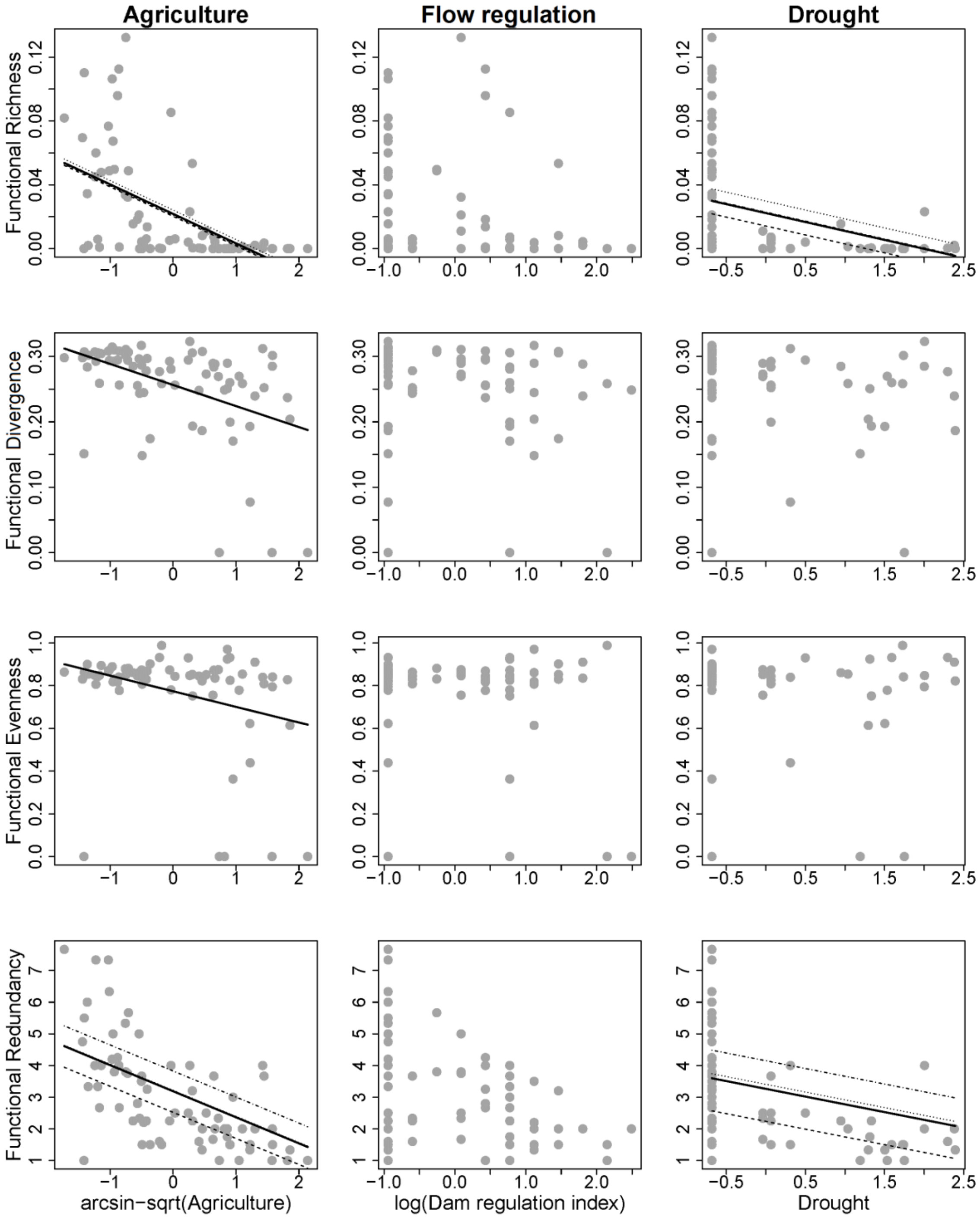


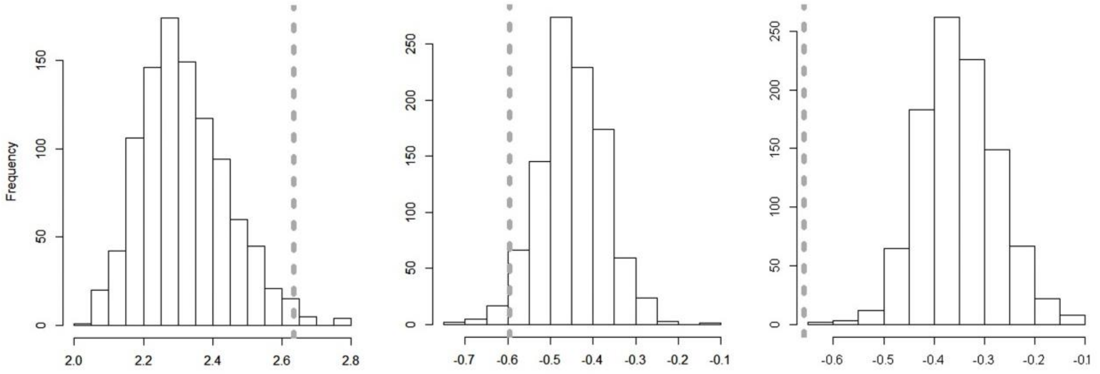
Fig. 3. Plots showing the response of functional redundancy and three measures of functional diversity to single environmental filters estimated through mixed-effect models. The solid line represents the fitted models for each single stressor, dashed lines represent the fitted model for the lowland rivers, dotted lines show the fitted model for the mid altitude rivers and dashed-dotted lines display the fitted model for the high altitude rivers.

Table 1. Results of mixed-effect models showing the best-fitting model equation, *p*-values, marginal (R^2m) and conditional goodness-of-fit i.e. R^2 (R^2c) for the different functional diversity indices. A: Agriculture, F: Flow regulation, and D: Drought. Pairwise interactions are noted with an asterisk. ns: non-significant coefficient.

Response variable	Model equation	(A)	(F)	(D)	A*F	A*D	F*D	R^2m	R^2c
FRic	y=0.017-0.016A-0.009D+0.01A*D	< 0.001	ns	0.03	ns	0.018	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	0.004	ns	ns	0.002	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	0.002	0.002	ns	0.59	0.59

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. 4). 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 3.7 in Supporting Information for details about the null models).

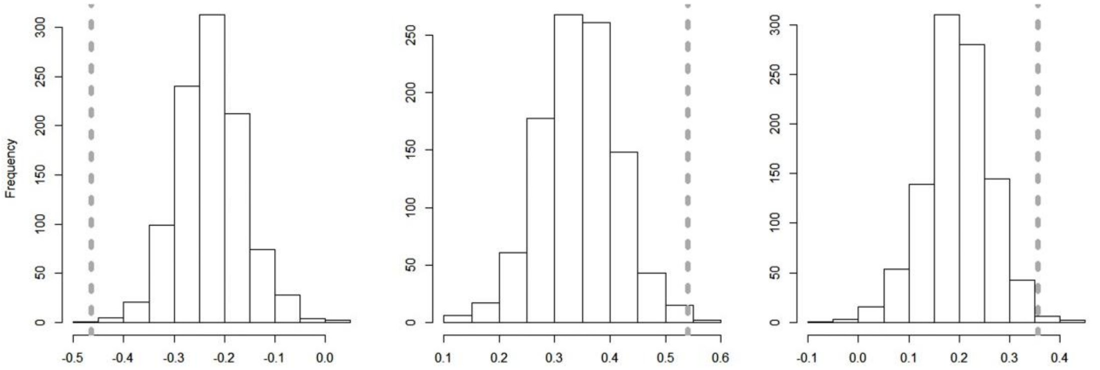
Species richness was positively related to FR and the richness of the different FGs, except for FG3 and FG4 that showed a weak, flat response (Fig. 5). Nevertheless, null model results (Fig. 4) showed that FR increased more than expected by chance as taxonomic richness rose. More concretely, empirical 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. 5). FGR peaked at medium-high values of species richness and FR and consequently at low-moderate anthropogenic stress intensity (Appendix 3.8 in Supporting Information).



Intercept
Z - score = 2.64
p - value = 0.027

Agriculture
Z - score = - 2.07
p - value = 0.047

Drought
Z - score = - 3.77
p - value = 0.001



Flow regulation
Z - score = - 3.66
p - value = 0.003

Agriculture * Drought
Z- score = 2.53
p - value = 0.023

Agriculture * Flow regulation
Z-score = 2.27
p - value = 0.021

Fig. 4. Results of null models showing the simulated distributions for each model parameter of functional redundancy's best fitting-model. Empirical model parameters are showed as vertical dashed grey lines. *z*-scores and *p*-values are shown for each parameter.

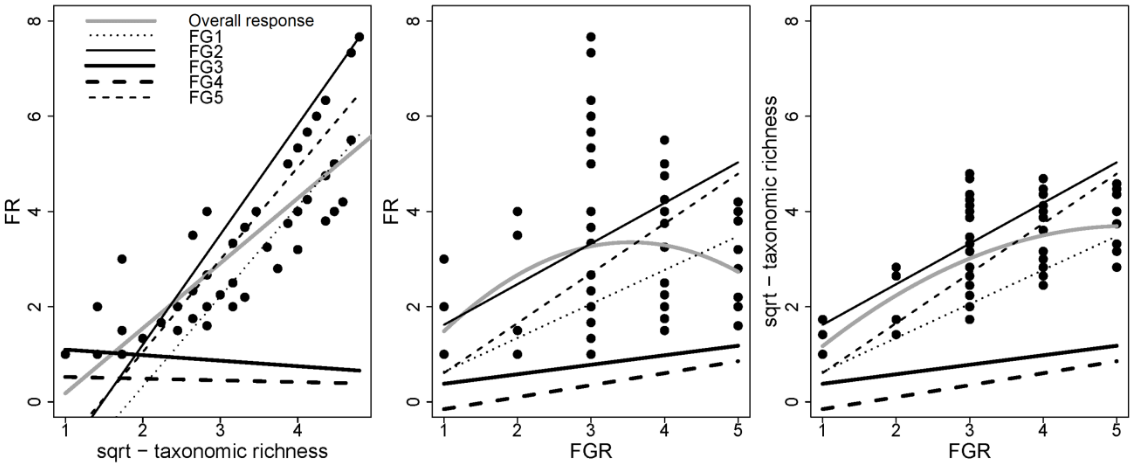


Fig. 5. Plots relating functional redundancy (FR), taxonomic richness and number of functional groups (FGR). Single results for each functional group (FG) are also shown.

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. 6). The model showed a mean error percentage of 36.3 % without any geographic concentration of high residuals.

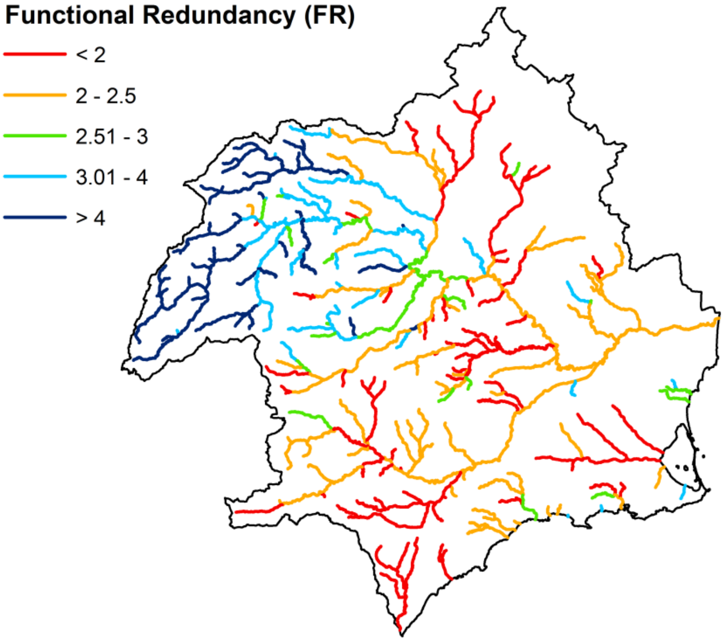


Fig. 6. Predicted FR values for riparian communities in the entire river network of the Segura basin.

Discussion

All environmental filters led to reductions in FR, thereby reducing 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 *et al.,* 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. 5). The reduction in FR could be associated with a loss of richness within some functional groups (mainly FG1, FG2 and FG5), likely as a consequence of different response diversity or trait-combinations of the species within each functional group. 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 *et al.,* 2013).

It is worth noting that functional redundancy 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 functional (intrinsic) redundancy and FD measures decreased as stressors intensified, functional diversity 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; see Appendix 3.9 in Supporting information to check the spatial pattern of FD and FR indices as well as their pairwise relationships). 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 *et al.,* 2012), and water abstraction for irrigation (Belmar *et al.,* 2013). The traits 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 homogenises habitat conditions (Belmar *et al.,* 2013), affecting reproduction, recruitment, dispersal opportunities, succession and fragmentation of the riparian community (Jansson *et al.,* 2000; Nilsson & Berggren, 2000). Drought sorted out woody riparian communities, favouring sclerophyllous and evergreen shrubs (Aguiar & 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 terrestrialisation 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*, 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 *et al.,* 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 inter-taxon and inter-region comparability (McGill *et al.,* 2006). Accordingly, we feel that this kind of measures should be incorporated in conservation prioritisation 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 (Naeem & Wright, 2003; Loreau & Mazancourt, 2013). 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 *et al.,* 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 functional diversity measures to impacts of the most important stressors in Mediterranean rivers as well as the interactions among 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, the 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 condition through restoration measures, as well as to conserve the reaches with better functional conditions.

References

Aguiar, F.C. & Ferreira, M.T. (2005) Human-disturbed landscapes: effects on composition and integrity of riparian woody vegetation in the Tagus River basin, Portugal. *Environmental Conservation*, **32**, 30–41.

Aguiar, F.C., Ferreira, M.T., Albuquerque, A., Rodríguez-González, P & Segurado, P. (2009) Structural and functional responses of riparian vegetation to human disturbance: performance and spatial scale-dependence. *Fundamental and Applied Limnology*, **175**, 249–267.

Allan, J.D. & Flecker, A.S. (1993) Biodiversity conservation in running waters. *BioScience*, **43**, 32–43.

Allan, J.D. (2004) Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 257–284.

Bejarano, M.D., Marchamalo, M., García de Jalón, D. & González del Tánago, M. (2010) Flow regime patterns and their controlling factors in the Ebro basin (Spain). *Journal of Hydrology*, **385**, 323–335.

Belmar, O., Velasco, J. & Martinez-Capel, F. (2011) Hydrological classification of natural flow regimes to support environmental flow assessments in intensively regulated Mediterranean rivers, Segura River basin (Spain). *Environmental Management*, **47**, 992–1004.

Belmar, O., Bruno, D., Martínez-Capel, F., Barquín, J. & Velasco J. (2013) Effects of flow regime alteration on fluvial habitats and riparian quality in a semiarid Mediterranean region. *Ecological Indicators*, **30**, 52–64.

Benda, L., Miller, D., Andras, K., Bigelow, P., Reeves, G. & Michael, D. (2007) NetMap: a new tool in support of watershed science and resource management. *Forest Science*, **53**, 220–238.

Biggs, R., Schlüter, M., Biggs, D., Bohensky, E.L., BurnSilver, S., Cundill, G., *et al*. (2012) Toward principles for enhancing the resilience of ecosystem services. *Annual Review of Environment and Resources*, **37**, 421–448.

Bruno, D., Belmar, O., Sánchez-Fernández, D. & Velasco, J. (2014a) Environmental determinants of woody and herbaceous riparian vegetation patterns in a semi-arid Mediterranean basin. *Hydrobiologia*, **730**, 45–57.

Bruno, D., Belmar, O., Sánchez-Fernández, D., Guareschi, S., Millán, A. & Velasco, J. (2014b) Responses of Mediterranean aquatic and riparian communities to human pressures at different spatial scales. *Ecological Indicators*, **45**, 456–464.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., *et al.* (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.

Catford, J.A., Morris, W.K., Vesk, P.A., Gippel, C.J. & Downes, B.J. (2014) Species and environmental characteristics point to flow regulation and drought as drivers of riparian plant invasion. *Diversity and Distributions,* **20**, 1084–1096.

Chapin, F.S.III, Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., *et al*. (2002) Consequences of changing biodiversity. *Nature*, **405**, 234–242.

Clapcott, J.E., Young, R.G., Goodwin, E.O. & Leathwick, J.R. (2010) Exploring the response of functional indicators of stream health to land-use gradients. *Freshwater Biology*, **55**, 2181–2199.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., *et al*. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.

Cornwell, W.K. & Ackerly, D.D. (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, **79**, 109–126.

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W. & Mouquet, N. (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecology Letters*, **13**, 1030–1040.

Díaz, S. & Cabido, M. (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, **16**, 646–655.

Díaz, A.M., Alonso, M.L.S, and Gutiérrez, M.R.V-A. 2008. Biological traits of stream macroinvertebrates from a semi-arid catchment: patterns along complex environmental gradients. *Freshwater Biology*, **53**, 1–21.

Douma, J.C., Bardin, V., Bartholomeus, R.P. & Bodegom, P.M. (2012) Quantifying the functional responses of vegetation to drought and oxygen stress in temperate ecosystems. *Functional Ecology*, **26**, 1355–1365.

Duffy, J.E. (2008) Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment*, **7**, 437–444.

Elmqvist, T., Folke, C., Nystrom, M., Peterson, G., Bengtsson, J., Walker, B. & Norberg, J. (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, **1**, 488–494.

Falcone, J.A., Carlisle, D.M. & Weber, L.C. (2010) Quantifying human disturbance in watersheds: Variable selection and performance of a GIS-based disturbance index for predicting the biological condition of perennial streams. *Ecological Indicators*, **10**, 264–273.

Ferreira, M.T. & Aguiar, F.C. (2006) Riparian and aquatic vegetation in Mediterranean-type streams (western Iberia). *Limnetica*, **25**, 411–424.

Fonseca, C.R. & Ganade, G. (2001) Species functional redundancy, random extinctions and the stability of ecosystems. *Journal of Ecology*, **89**, 118–125.

Guillemot, N., Kulbicki, M., Chabanet, P. & Vigliola, L. (2011) Functional redundancy patterns reveal non-random assembly rules in a species-rich marine assemblage. *PloS One*, **6**, e26735.

Gutiérrez-Cánovas, C., Sánchez-Fernández, D., Velasco, J., Millán, A. & Bonada, N. (2015) Similarity in the difference: changes in community functional features along natural and anthropogenic stress gradients. *Ecology,* ***96****, 2458–2466.*

Hladyz, S., Åbjörnsson, K., Chauvet, E., Dobson, M., Elosegi, A., Ferreira, V., *et al*. (2011) Stream ecosystem functioning in an agricultural landscape: the importance of terrestrial-aquatic linkages. *Advances in Ecological Research*, **44**, 211–276.

Hooper, D.U., Chapin, F.S.III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Huijbers, C.M., Schlacher, T.A., Schoeman, D.S., Olds, A.D., Weston, M.A. & Connolly, R.M. (2015) Limited functional redundancy in vertebrate scavenger guilds fails to compensate for the loss of raptors from urbanized sandy beaches. *Diversity and Distributions*, **21**, 55–63.

Jansson, R., Nilsson, C. & Renöfält, B. (2000) Fragmentation of riparian floras in rivers with multiple dams. *Ecology*, **81**, 899–903.

Kleyer, M. (1999) Distribution of plant functional types along gradients of disturbance intensity and resource supply in an agricultural landscape. *Journal of Vegetation Science*, **10**, 697–708.

Kraft, N.J., Godoy, O. & Levine, J.M. (2015) Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 797–802.

Kroll, S.A., Ringler, N.H., De las Heras, J., Goméz-Alday, J.J., Moratalla, A. & Briggs, R.D. (2013) Analysis of anthropogenic pressures in the Segura Watershed (SE Spain), with a focus on inter-basin transfer. *Ecohydrology*, **6**, 878–888.

Laliberté, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299–305.

Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., *et al*. (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters*, **13**, 76–86.

Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.

Lawton, J.H. & Brown, V.K. (1993) Redundancy in ecosystems. *Biodiversity and ecosystem function* (eds Schulze, E.-D & Mooney, H.A.), pp. 255–270. Springer-Verlag, Berlin, Germany.

Loreau, M. & Mazancourt, C. (2013) Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters*, **16**, 106–115.

Maire, E., Grenouillet, G., Brosse, S., & Villéger, S. (2015) How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. *Global Ecology and Biogeography*, **24**, 728–740.

Mason, N.W.H., Mouillot, D., Lee, W.G. & Wilson, J.B. (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, **111**, 112–118.

Matsuzaki, S.S., Sasaki, T. & Akasaka, M. (2013) Consequences of the introduction of exotic and translocated species and future extirpations on the functional diversity of freshwater fish assemblages. *Global Ecology and Biogeography*, **22**, 1071–1082.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, **21**, 178–185.

Ministry for the Environment (2004) *Water in Spain*. Secretaría de Estado de Aguas y Costas, Madrid, Spain.

Monteagudo, L., Moreno, J.L. & Picazo, F. (2012). River eutrophication: irrigated vs. non-irrigated agriculture through different spatial scales. *Water Research,* **46**, 2759–2771.

Mori, A.S., Furukawa, T. & Sasaki, T. (2013) Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews*, **88**, 349–364.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, **28**, 167–177.

Naeem, S. & Wright, J.P. (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters*, **6**, 567–579.

Naiman, R.J., Décamps, H. & McClain, M.E. (2005) *Riparia: ecology, conservation, and management of stream side communities*. Elsevier Science, Amsterdam, The Netherlands.

Nilsson, C. & Berggren, K. (2000) Alterations of riparian ecosystems caused by river regulation. *BioScience*, **50**, 783–792.

Nilsson, C. & Svedmark, M. (2002) Basic principles and ecological consequences of changing water regimes: riparian plant communities. *Environmental Management*, **30**, 468–480.

Peñuelas, J., Lloret, F. & Montoya, R. (2001) Severe drought effects on Mediterranean woody flora in Spain. *Forest Science*, **47**, 214–218.

Petchey, O.L., Evans, K.L., Fishburn, I.S. & Gaston, K.J. (2007) Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology*, **76**, 977–985.

Pillar, V.D., Blanco, C.C., Müller, S.C., Sosinski, E.E., Joner, F. & Duarte, L.D. (2013) Functional redundancy and stability in plant communities. *Journal of Vegetation Science*, **24**, 963–974.

Quinn, L.D. & Holt, J.S. (2008) Ecological correlates of invasion by Arundo donax in three southern California riparian habitats. *Biological Invasions*, **10**, 591–601.

R Development Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rosenfeld, J.S. (2002) Functional redundancy in ecology and conservation. *Oikos*, **98**,156–62.

Sabo, J.L. & Power, M.E. (2002) River-watershed exchange: Effects of riverine subsidies on riparian lizards and their terrestrial prey. *Ecology*, **83**, 1860–1869.

Salminen, J., van Gestel, C.A.M. & Oksanen, J. (2001) Pollution-induced community tolerance and functional redundancy in a decomposer food web in metal-stressed soil. *Environmental Toxicology and Chemistry*, **20**, 2287–2295.

Sasaki, T., Katabuchi, M., Kamiyama, C., Shimazaki, M., Nakashizuka, T. & Hikosaka, K. (2014) Vulnerability of moorland plant communities to environmental change: consequences of realistic species loss on functional diversity. *Journal of Applied Ecology*, **51**, 299–308.

Sasaki, T., Furukawa, T., Iwasaki, Y., Seto, M. & Mori, A.S. (2015) Perspectives for ecosystem management based on ecosystem resilience and ecological thresholds against multiple and stochastic disturbances. *Ecological Indicators*, **57**, 395–408.

Shipley, B., Vile, D. & Garnier, E. (2006) From plant traits to plant communities: A statistical mechanistic approach to biodiversity. *Science*, **314**, 812–814.

Tabacchi, E., Lambs, L., Guilloy, H., Planty-Tabacchi, A.M., Muller, E. & Decamps, H. (2000) Impacts of riparian vegetation on hydrological processes. *Hydrological Processes*, **14**, 2959–2976.

Villéger, S., Mason, N.W. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**, 2290–2301.

Walker, B.H. (1992) Biodiversity and ecological redundancy. *Conservation Biology*, **6**, 18–23.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T. & Bentivenga, S. (2011) Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **366**, 2403–2413.

Woodward, G., Gessner, M.O., Giller, P.S., Gulis, V., Hladyz, S., Lecerf, A., *et al*. (2012) Continental-scale effects of nutrient pollution on stream ecosystem functioning. *Science*, **336**, 1438–1440.

Supporting Information

Appendix 3.1. Effect and response traits considered to characterise the functional features of the woody riparian species.

Appendix 3.2. Data sources used to obtain the functional trait values.

Appendix 3.3. R code and data files. Available at:
https://www.dropbox.com/s/21kdu458k5j9a6r/Appendix3.3.rar?dl=0

Appendix 3.4 Details about Functional Redundancy estimations.

Appendix 3.5. Functional group description based on distinctive functional effect traits.

Appendix 3.6. Results of mixed-effects models for single environmental stressors.

Appendix 3.7. Null model results for the individual significant stressors and the best-fitting model for each functional index.

Appendix 3.8. Best-fitting model for the number of functional groups in response to environmental filters.

Appendix 3.9. Spatial pattern of the functional diversity and redundancy indices and their pairwise relationships.

Appendix 3.1. Effect and response traits considered to characterise the functional features of the woody riparian species. Type of traits: C=continuous, SC=semi-continuous, CAT=categorical. Functions and responses involved: B= Biodiversity, CL= Climate, CP= Competence, CU=Cultural, D= Disturbance regime, N= Nutrient cycling, P= Productivity, S= Soil formation and sediment fixation, W= Water availability, MP= Macrophanerophytes, MEP= Mesophanerophytes, NP= Nanophanerophytes, CH= Chamaephytes, E= Epiphytes.

Trait	Effect/ Response	Type	Units/Categories	Response	Function
Max plant height	E	C	M		B, CL, CP, D, N, W
Growth rate	E	SC	Fast / Moderate / Slow		CP, D, N, P, W
Specific leaf area	E	C	$cm^2 g^{-1}$		B, N, P, S, W
Leaf size	E	SC	Large / Moderate / Small		B, N, P
Leaf thickness	E	SC	Gross / Medium / Thin		B, N, P, W
Leaf type	E	CAT	Broadleaf / Needle / Scaly / Palm		B, D, N, S
Leaf compoundness	E	CAT	Simple / Compound		D, N
Leaf deciduousness	E	CAT	Evergreen/Deciduous/ Marcescent		D, N, P, W
Flower colour	E	CAT	Coloured / Not coloured		B, CU
Lateral spread	E	SC	High / Medium / Low		B, CL, P
Ramification	E	SC	High / Medium / Low		B, CL, N, P, S, W
Raunkiaer form	E/R	CAT	MP/MEP/NP/CH/E	CL, D	B, CL, D, N, P, S, W
Plant size	E/R	CAT	Trees / Large shrubs / Small shrubs / Lianas	CL, D	B, CL, D, N, P, S, W
P leaf content	E/R	SC	%	D, N	N
N leaf content	E/R	SC	%	D, N	N, P
C : N ratio	E/R	SC	High / Medium / Low	D, N	N, P
Nitrogen fixation	E/R	CAT	Nitrogen fixer / Non fixer	D, N, W	N, S
Photosynthesis pathway	E/R	CAT	C3 / C4	CL, W	B, N, P, W
Rooting depth	E/R	SC	Deep / Moderate / Shallow	CL, N, W,	B, CL, D, P, S, W
Lifespan	R	SC	Long / Moderate / Short	CL, D	
Shade tolerance	R	SC	High / Medium / Low	CL	
Stem density	R	C	$mg\ mm^{-3}$	D	
Flexibility	R	SC	High / Medium / Low	CL, W	
Fruit type	R	N	Fleshy / Not fleshy	CL, D, W	
Plant thorniness	R	B	Yes / No	CL, W	
Seed mass	R	C	mg	D	
Seed number/fruit	R	C	n	CL, D	
Seed dispersión	R	N	Anemochory / Zoochory / Hydrochory	D	
Pollination	R	N	Wind / Biotic / Accidental / Self	CL, D, W	
Reproduction type	R	N	Sexual / Vegetative / Both	CL, D	

Appendix 3.2. Data sources used to obtain the functional trait values.

Aguinagalde, I., Hampe, A., Mohanty, A., Martín, J.P., Duminil, J. & Petit, R.J. (2005) Effects of life-history traits and species distribution on genetic structure at maternally inherited markers in European trees and shrubs. *Journal of Biogeography*, **32**, 329-339.

Antúnez, I., Retamosa, E.C. & Villar, R. (2001) Relative growth rate in phylogenetically related deciduous and evergreen woody species. *Oecologia*,**128**, 172-180.

Aranda, I., Pardo, F., Gil, L. & Pardos, J.A. (2004) Anatomical basis of the change in leaf mass per area and nitrogen investment with relative irradiance within the canopy of eight temperate tree species. *Acta Oecologica*, **25**, 187-195.

Bejarano, M.D., González del Tánago, M., de Jalón, D.G., Marchamalo, M., Sordo-Ward, Á. & Solana-Gutiérrez, J. (2012) Responses of riparian guilds to flow alterations in a Mediterranean stream. *Journal of Vegetation Science*, **23**, 443-458.

Bell, L.W. (2005) Relative growth rate, resource allocation and root morphology in the perennial legumes, Medicago sativa, Dorycnium rectum and D. hirsutum grown under controlled conditions. *Plant and soil*, **270**, 199-211.

Borghi, M., Tognetti, R., Monteforti, G. & Sebastiani, L. (2008) Responses of two poplar species (Populus alba and Populus x canadensis) to high copper concentrations. *Environmental and Experimental Botany*, **62**, 290–299.

Castro-Diez, P., Villar-Salvador, P., Pérez-Rontomé, C., Maestro-Martínez, M. & Montserrat-Martí, G. (1997) Leaf morphology and leaf chemical composition in three Quercus (Fagaceae) species along a rainfall gradient in NE Spain. *Trees*, **11**, 127-134.

Castro-Díez, P., Montserrat-Martí, G. & Cornelissen, J.H.C. (2003) Trade-offs between phenology, relative growth rate, life form and seed mass among 22 Mediterranean woody species. *Plant Ecology*, **166**, 117-129.

Castro-Díez, P., González-Muñoz, N., Alonso, A., Gallardo, A. & Poorter, L. (2009) Effects of exotic invasive trees on nitrogen cycling: a case study in Central Spain. *Biological Invasions*, **11**, 1973-1986.

Castroviejo, S. (coord). 1986-2012. *Flora iberica* 1-8, 10-15, 17-18, 21. Real Jardín Botánico, CSIC, Madrid, Spain. Available at: http://www.floraiberica.org/.

Ceballos, L. & Ruíz-de-la-Torre, J. (1971) *Árboles y arbustos de la España peninsular*. E.T.S.I. Montes, Madrid, Spain.

Cornelissen, J.H.C., Diez, P.C. & Hunt, R. (1996) Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology*, **84**, 755-765.

Domínguez, M.T., Marañón, T., Carpio, M., Manuel, J., Hidalgo, J.M. & Madejón, P. (2004) Crecimiento y morfología foliar de especies leñosas en las reforestaciones del Corredor Verde del Guadiamar (Sevilla). *Cuaderno de la Sociedad Española de Ciencias Forestales,* **20**, 173-179.

Domínguez, M.T., Aponte, C., Pérez-Ramos, I.M., García, L.V., Villar, R. & Marañón, T. (2012) Relationships between leaf morphological traits, nutrient concentrations and isotopic signatures for Mediterranean woody plant species and communities. *Plant and soil*, **357**, 407-424.

Escudero, A., Del Arco, J.M., Sanz, I.C. & Ayala, J. (1992) Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. *Oecologia*, **90**, 80-87.

Escudero, A. & Mediavilla, S. (2003). Decline in photosynthetic nitrogen use efficiency with leaf age and nitrogen resorption as determinants of leaf life span. *Journal of Ecology*, **91**, 880-889.

Fitter, A.H. & Peat, H.J. (1994) The Ecological Flora Database. *Journal of Ecology*, **82**, 415-425. Available at http://www.ecoflora.co.uk.

González, E., Muller, E., Comín, F.A. & González-Sanchis, M. (2010) Leaf nutrient concentration as an indicator of Populus and Tamarix response to flooding. *Perspectives in Plant Ecology, Evolution and Systematics*, **12**, 257–266.

Gracia, C., Burriel, J.A., Ibáñez, J.J., Mata, T. & Vaydera, J. (2000-2004) *Inventari Ecològic i Forestal de Catalunya. Obra completa*. CREAF, Bellaterra, Spain. http://www.creaf.uab.es/iefc.

Gulías, J., Flexas, J., Mus, M., Cifre, J., Lefi, E. & Medrano, H. (2003) Relationship between Maximum Leaf Photosynthesis, Nitrogen Content and Specific Leaf Area in Balearic Endemic and Non-endemic Mediterranean Species. *Annals of Botany*, **92**, 215-222.

Han, W., Fang, J., Guo, D. & Zhang, Y. (2005) Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. *New Phytologist*, **168**, 377-385.

Herrera, C.M. (1987) Vertebrate-dispersed plants of the Iberian Peninsula: a study of fruit characteristics. *Ecological monographs*, **57**, 305-331.

Herrera, J. (1991) The reproductive biology of a riparian Mediterranean shrub, Nerium oleander L. (Apocynaceae). *Botanical journal of the Linnean Society*, **106**, 147-172.

Hill, M.O., Preston, C.D. & Roy, D.B. (2004) *PLANTATT-Attributes of British and Irish Plants: status, size, life history, geography and habitats*. Centre for Ecology & Hydrology, Monks Wood, United Kingdom.

Hladyz, S., Gessner, M.O., Giller, P.S., Pozo, J. & Woodward, G. (2009) Resource quality and stoichiometric constraints on stream ecosystem functioning. *Freshwater Biology*, **54**, 957–970.

Karrenberg, S. & Suter, M. (2003) Phenotypic trade-offs in the sexual reproduction of Salicaceae from flood plains. *American Journal of Botany*, **90**, 749-754.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., *et al*. (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology*, **96**, 1266–1274.

Lefèvre, F., Barsoum, N., Heinze, B., Kajba, D., Rotach, P., De Vries, S.M.G. & Turok, J. (2001) *EUFORGEN Technical Bulletin: In situ conservation of Populus nigra*. International Plant Genetic Resources Institute, Rome, Italy.

Martínez-Sánchez, J.J., Franco-Leemhuis, J.A. & Vicente-Colomer, M.J. (2008) *Especies silvestres mediterráneas con valor ornamental: selección, producción, viverística y utilización en jardinería*. Dirección General de Medio Natural, Consejería de Agricultura y Agua, Murcia, Spain.

Martínez-Vilalta, J., Mencuccini, M., Vayreda, J. & Retana, J. (2010) Interspecific variation in functional traits, not climatic differences among species ranges, determines demographic rates across 44 temperate and Mediterranean tree species. *Journal of Ecology*, **98**, 1462–1475.

Mediavilla, S., Santiago, H. & Escudero, A. (2002) Stomatal and mesophyll limitations to photosynthesis in one evergreen and one deciduous Mediterranean oak species. *Photosynthetica*, **40**, 553-559.

Mediavilla, S. & Escudero, A. (2003) Relative growth rate of leaf biomass and leaf nitrogen content in several Mediterranean woody species. *Plant Ecology*, **168**, 321-332.

Mediavilla, S., Garcia-Ciudad, A., Garcia-Criado, B. & Escudero, A. (2008) Testing the correlations between leaf life span and leaf structural reinforcement in 13 species of European Mediterranean woody plants. *Functional Ecology*, **22**, 787-793.

Milla, R., Reich, P.B., Niinemets, Ü. & Castro-Díez, P. (2008) Environmental and developmental controls on specific leaf area are little modified by leaf allometry. *Functional Ecology*, **22**, 565-576.

Ministerio de Medio Ambiente (1997-2007) *Tercer Inventario Forestal Nacional*. Dirección General de Conservación de la Naturaleza, Madrid, Spain.

Navarro, R. & Galvez, C. (2002) *Manual para la identificación y reproducción de semillas de especies vegetales autóctonas*. Junta de Andalucía, Cordoba, Spain.

Navarro, T., Nieto-Caldera, J.M., Pérez-Latorre, A.V. & Cabezudo, B. (1993) Estudios fenomorfológicos en la vegetación del sur de España. III: Comportamiento estacional de una comunidad de badlands (Tabernas, Almería. España). *Acta Botánica Malacitana*, **18**, 189-198.

Navas, M.L., Roumet, C., Bellmann, A., Laurent, G. & Garnier, E. (2010) Suites of plant traits in species from different stages of a Mediterranean secondary succession. *Plant Biology*, **12**, 183-196.

Niinemets, Ü. & Valladares, F. (2006)Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs,* **76**, 521–547.

Paula, S., Arianoutsou, M., Kazanis, D., Tavsanoglu, Ç., Lloret, F., Buhk, C., *et al.* (2009) Fire-related traits for plant species of the Mediterranean Basin. *Ecology,* **90**, 1420.

Paula, S. & Pausas, J.G. (2013) *BROT: a plant trait database for Mediterranean Basin species*. Version 2013.06. http://www.uv.es/jgpausas/brot.htm

Petisco, C., García-Criado, B., de Aldana, B.V., Zabalgogeazcoa, I. & Mediavilla, S. (2005) Use of near-infrared reflectance spectroscopy in predicting nitrogen, phosphorus and calcium contents in heterogeneous woody plant species. *Analytical and Bioanalytical Chemistry*, **382**, 458-465.

Prada, M.A. & Arizpe, D. (2008) *Manual de propagación de árboles y arbustos de ribera, Una ayuda para la restauración de riberas en la región mediterránea*. Generalitat Valenciana, Valencia, Spain.

Pujol, J.A., Calvo, J.F. & Ramírez-Díaz, L. (2001) Seed germination, growth, and osmotic adjustment in response to NaCl in a rare succulent halophyte from southeastern Spain. *Wetlands*, **21**, 256-264.

Qu, X.-X., Huang, Z.-Y., Baskin, J.M. & Baskin, C.C. (2008) Effect of temperature, light and salinity on seed germination and radicle growth of the geographically widespread halophyte shrub Halocnemum strobilaceum. *Annals of Botany,* **101**, 293–299.

Reich, P.B. & Oleksyn, J. (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 11001-11006.

Reich, P.B., Wright, I.J. & Lusk, C.H. (2007) Predicting leaf physiology from simple plant and climate attributes: a global GLOPNET analysis. *Ecological Applications*, **17**, 1982-1988.

Rodriguez-Perez, J., Riera, N. & Traveset, A. (2005) Effect of seed passage through birds and lizards on emergence rate of Mediterranean species: differences between natural and controlled conditions. *Functional Ecology*, **19**, 699-706.

Royal Botanic Gardens Kew (2014) *Seed Information Database (SID)*. Version 7.1. Available from: http://data.kew.org/sid/

Ruíz-de-la-Torre, J. (1984). *Árboles y arbustos de España*. Salvat Editores, Barcelona, Spain.

Ruíz-de-la-Torre, J. (2006) *Flora mayor*. Dirección general para la biodiversidad. Ministerio de Medio Ambiente, Madrid, Spain.

Sack, L. (2004) Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation?. *Oikos*, **107**, 110-127.

Sack, L., Grubb, P.J. & Marañón, T. (2003) The functional morphology of juvenile plants tolerant of strong summer drought in shaded forest understories in southern Spain. *Plant Ecology*, **168**, 139-163.

Schweitzer, J.A., Martinsen, G.D. & Whitham, T.G. (2002) Cottonwood hybrids gain fitness traits of both parents: a mechanism for their long-term persistence?. *American Journal of Botany*, **89**, 981-990.

Silva, J.S. & Rego, F.C. (2004) Root to shoot relationships in Mediterranean woody plants from Central Portugal. *Biologia*, **59**, 1-7.

Silva, J.S., Rego, F.C. & Martins-Loução, M.A. (2003) Root distribution of Mediterranean woody plants. Introducing a new empirical model. *Plant Biosystems*, **137**, 63-72.

Stock, W.D. & Verboom, G.A. (2012) Phylogenetic ecology of foliar N and P concentrations and N:P ratios across mediterranean-type ecosystems. *Global Ecology and Biogeography,* **21**, 1147–1156.

USDA, NRCS. (2015) *The PLANTS Database* (http://plants.usda.gov). National Plant Data Team, Greensboro, North Carolina, USA.

Villar, R., Ruiz-Robleto, J., Quero, J.L., Poorter, H., Valladares, F. & Marañón, T. (2004) Tasas de crecimiento en especies leñosas: aspectos funcionales e implicaciones ecológicas. *Ecología del bosque mediterráneo en un mundo cambiante* (ed Valladares, F.), pp. 191-227. Ministerio de Medio Ambiente, EGRAF, S.A., Madrid, Spain.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., *et al*. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821-827.

Appendix 3.4 Details about Functional Redundancy estimations.

There are different ways to estimate FR, which may consist on the average number of species per functional group (i.e. ratio between the species richness and the number of functional groups, e.g. Laliberté *et al.*, 2010; FRa), the difference between taxonomic and functional diversity (e.g. Pillar *et al.,* 2013; FRb) and the sum of the overall species pairwise overlap in the functional space (e.g. Gutiérrez-Cánovas *et al.*, 2015). We discard the latter approach because it requires intraspecific trait information. In this appendix, we show the performance of FRa and FRb estimations from multiple traits.

Eq. 1 *FRa= (Species Richness)/(Number of Functional Groups)*

Details about how to estimate FRa are available in the Materials and Methods section.

Eq. 2 *FRb= (Taxonomic Diversity)-(Functional Diversity)*

We used the Gini-Simpson diversity to quantify *Taxonomic Diversity* (range of values within 0-1) and the Rao's quadratic entropy (Rao, 1982) to estimate *Functional Diversity* (the latter index was standardised by the maximum value to constrain the values within the range of 0-1). Rao index was estimated using the abundance data and the Euclidean transformed version of the effect-traits-based Gower dissimilarity matrix.

We applied eq. 1 and eq. 2 to each of the riparian communities in our dataset to quantify FR. FRb was highly correlated with FRa (Spearman R=0.76; $p<0.001$), as can be also seen in their spatial patterns (Fig. S3.4.1).

For the individual models, both FRa and FRb decreased significantly to agriculture and drought (Fig. S3.4.2, Table S3.4.1). However, only the empirical responses of FRa were significantly distinct from the null models (Table S3.4.2).

The best-fitting model relating FRb with multiple stressors showed a lower explained variance compared to the FRa's optimal model ($R^2=0.40$ vs $R^2=0.59$, respectively; see Table S3.4.3 for further details). Again, only the model coefficients of the FRa were distinguishable from those produced by the null model (Table S3.4.4). For all these reasons, we believe that FRa may provide a better assessment of the anthropogenic impacts on biodiversity.

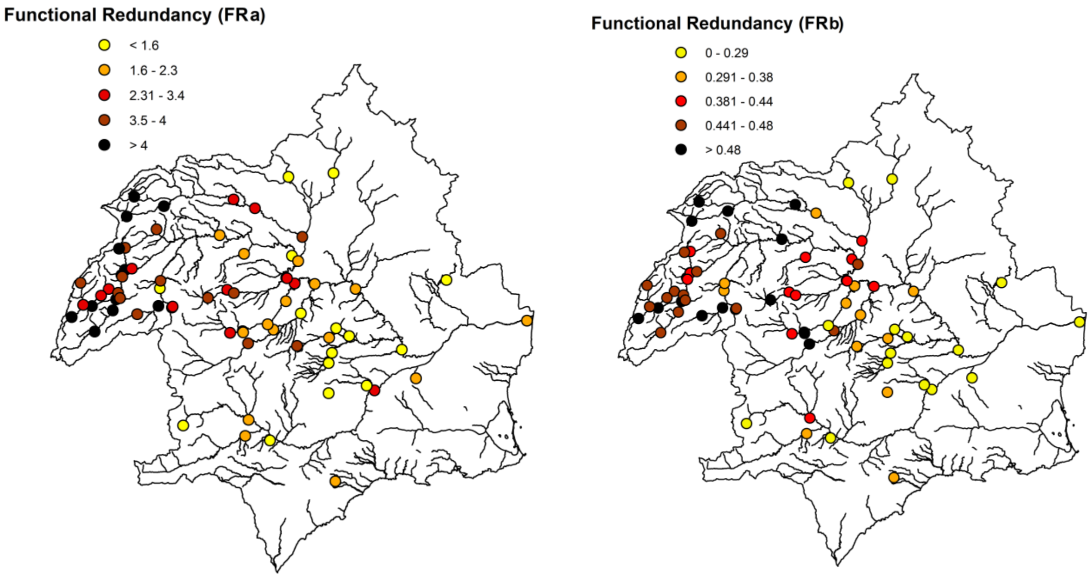


Fig. S3.4.1. Values of FRa and FRb values across the study area classified in five classes (quantiles).

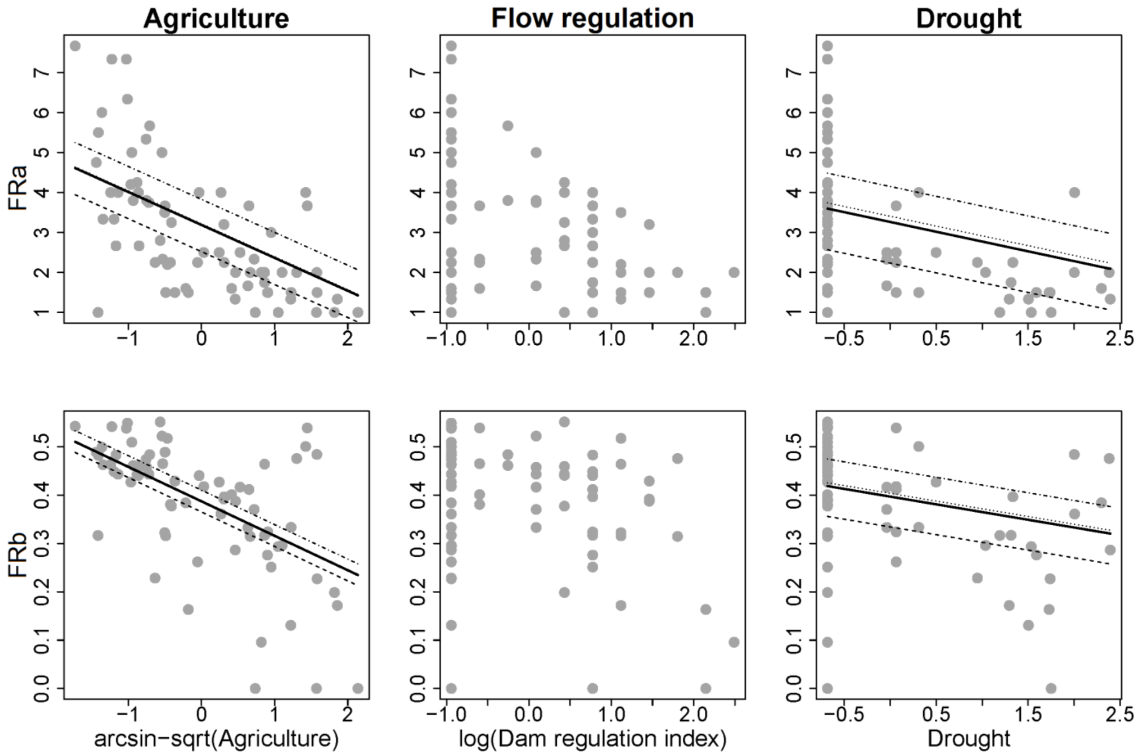


Fig. S3.4.2. Plots showing the response of FRa and FRb single environmental filters. Solid line represents the fitted models for each single stressor, dashed lines represents the fitted model for the lowland rivers, dotted lines show the fitted model for the mid altitude rivers and dashed-dotted lines display the fitted model for the high altitude rivers.

Table S3.4.1. Results of the Linear Mixed-Effect Models relating the divisive and additive estimations of FR (FRa, FRb, respectively) with individual stressors. Intercepts, slopes and goodness of fit for the fixed terms (R^2m) and full model (R^2c). ns: *p*>0.05; *: *p*<0.05; **: *p*<0.01; ***: *p*<0.001.

	stressor	intercept	slope	R^2m	R^2c
FRa	Agriculture	3.189***	-0.824***	0.264	0.459
	Flow regulation	3.298***	-0.183	0.011	0.423
	Drought	3.264***	-0.490**	0.082	0.433
FRb	Agriculture	0.387***	-0.071***	0.292	0.344
	Flow regulation	0.398***	-0.017	0.015	0.269
	Drought	0.397***	-0.032*	0.054	0.277

Table S3.4.2. Results of the null models for the models relating the divisive and additive estimations of FR (FRa, FRb, respectively) with individual stressors. (see Materials and Methods for further details). Red represents significant results.

		Agriculture		Drought	
		intercept	slope	intercept	slope
FRa	z-value	4.98	-2.07	5.13	-2.12
	p-value	0.003	0.047	0.03	0.029
FRb	z-value	-10.1	0.04	-10.2	-1.25
	p-value	0.001	0.971	0.001	0.199

Table S3.4.3. Results of the Linear Mixed Models for the best-fitting models relating the divisive and additive estimations of FR (FRa, FRb, respectively) with multiple stressors. Intercepts, slopes and goodness of fit for the fixed terms (R^2m) and full model (R^2c). A= percentage of agriculture in each basin; Drought: days of drought; F: Flow regulation index (see Materials and Methods for further details about flow regulation). *: *p*<0.05; **: *p*<0.01; ***: *p*<0.001.

	intercept	A	D	F	A:D	A:F	F:D	R^2m	R^2c
FRa	2.660***	-0.624***	-0.642***	-0.475**	0.506**	0.354*		0.59	0.59
FRb	0.397***	-0.075***				-0.033*	0.029*	0.37	0.40

Table S3.4.4. Results of the null models for the best-fitting models relating the divisive and additive estimations of FR (FRa, FRb, respectively) with multiple stressors. A= percentage of agriculture in each basin; Drought: days of drought; F: Flow regulation index (see Materials and Methods for further details about flow regulation). Red represents significant results.

		intercept	A	D	F	A:D	A:F	F:D
FRa	z-value	2.640	-0.070	-3.770	-3.650	2.530	2.260	
	p-value	0.027	0.047	0.001	0.003	0.023	0.021	
FRb	z-value	-9.980	-0.420				-0.080	-1.270
	p-value	0.001	0.681				0.929	0.223

Literature cited

Gutiérrez-Cánovas, C., Sánchez-Fernández, D., Velasco, J., Millán, A. & Bonada, N. (2015) Similarity in the difference: changes in community functional features along natural and anthropogenic stress gradients. *Ecology*, **96**, 2458–2466.

Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., *et al*. (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters*, **13**, 76–86.

Pillar, V.D., Blanco, C.C., Müller, S.C., Sosinski, E.E., Joner, F. & Duarte, L.D. (2013) Functional redundancy and stability in plant communities. *Journal of Vegetation Science*, **24**, 963–974.

Rao, C.R. (1982) Diversity and dissimilarity coefficients - a unified approach. *Theoretical Population Biology*, **21**, 24-43.

Appendix 3.5. Functional group description based on distinctive functional effect traits.

Functional group	**Main effect traits shared by the species within each functional group**
FG1 (shrubby phreatophytes)	Large shrubs, deep roots, fast-medium growth, non-coloured flowers, high-medium C : N ratio, high P, broad, deciduous and simple leaves
FG2 (arboreal phreatophytes)	Trees, deep roots, fast growth, low-medium lateral spread, high-medium C : N ratio, broad, large and deciduous leaves
FG3 (drought-adapted)	Shrubs, deep roots, high ramification and lateral spread, low C : N ratio, low P, squamated, crass and little leaves
FG4 (evergreen shrubs)	Large shrubs, slow growth, low lateral spread, high ramification shallow roots, medium N, low P, large, broad, simple and evergreen leaves
FG5 (Lianas and climbers)	Lianas, medium-fast growth, low ramification, high-medium lateral spread, shallow roots, low P, medium N, evergreen and broad leaves.

FG1 (e.g. *Salix eleagnos*)

FG2 (e.g. *Populus alba*)

FG3 (e.g. *Tamarix canariensis*)

FG4 (e.g. *Nerium oleander*)

FG5 (e.g. *Lonicera biflora*)

Appendix 3.6. Results of mixed-effects models for single environmental stressors showing the models equations, *p*-values, marginal R^2 (R^2m) and conditional R^2 (R^2c). Red represents significant results.

Functional variable	**Model**		**P-value**	**R^2m**	**R^2c**
Functional Richness	Agriculture	$y=0.022-0.018x$	< 0.001	0.296	0.31
Functional Richness	Flow regulation	$y=0.023-0.004x$	0.393	0.011	0.141
Functional Richness	Drought	$y=0.022-0.011x$	0.005	0.109	0.192
Functional Divergence	Agriculture	$y=0.253-0.032x$	< 0.001	0.212	0.212
Functional Divergence	Flow regulation	$y=0.256-0.01x$	0.258	0.02	0.094
Functional Divergence	Drought	$y=0.257-0.008x$	0.351	0.013	0.104
Functional Evenness	Agriculture	$y=0.774-0.073x$	0.008	0.096	0.096
Functional Evenness	Flow regulation	$y=0.774-0.039x$	0.161	0.028	0.028
Functional Evenness	Drought	$y=0.774-0.012x$	0.678	0.002	0.002
Functional Redundancy	Agriculture	$y=3.189-0.824x$	< 0.001	0.264	0.459
Functional Redundancy	Flow regulation	$y=3.298-0.183x$	0.322	0.011	0.423
Functional Redundancy	Drought	$y=3.264-0.49x$	0.004	0.082	0.433

Appendix 3.7. Null model results for the individual significant stressors and the best-fitting model for each functional index.

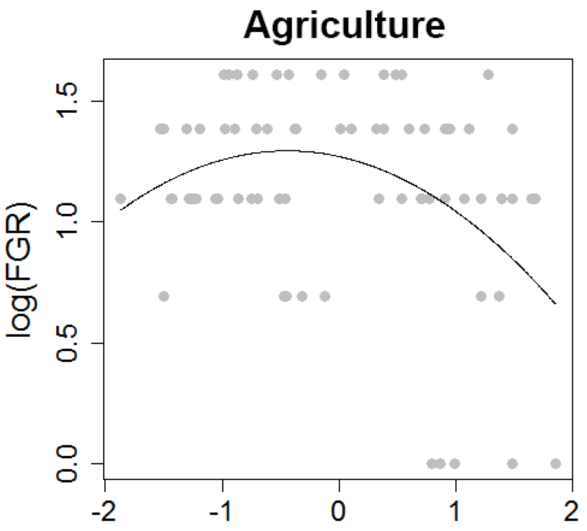
Table S3.7.1. Null model results for the individual significant stressors for each functional index. FRic = Functional richness, FDis = Functional divergence, FEve = Functional evenness, FR = Functional redundancy. Red represents significant results.

Functional variable	**Model**	**Intercept p-value**	**Slope p-value**	**Intercept Z score**	**Slope Z score**
FRic	Agriculture	0.175	0.141	-1.276	1.365
FRic	Flow regulation	-	-	-	-
FRic	Drought	0.145	0.183	-1.345	1.248
FDis	Agriculture	0.013	0.485	-2.799	-0.699
FDis	Flow regulation	-	-	-	-
FDis	Drought	-	-	-	-
FEve	Agriculture	0.001	0.001	109.465	-7.092
FEve	Flow regulation	-	-	-	-
FEve	Drought	-	-	-	-
FR	Agriculture	0.003	0.047	4.982	-2.07
FR	Flow regulation	-	-	-	-
FR	Drought	0.003	0.029	5.13	-2.126

Table S3.7.2. Null model results for the best-fitting models of each functional index. A = Agriculture, D = Drought, F = Flow regulation. Red represents significant results.

Stressors/ Func. indices	**FR**	**FRic**	**FDis**	**FEve**
Model equation	y=2.66-0.624A-0.642D-0.475DR+0.506A:D+0.354A:F	y=0.017-0.016A-0.009D+0.01A:D	y=0.253 -0.032A	y=0.809-0.074A-0.097A:F+0.091D:F
p-value				
Intercept	0.027	0.221	0.013	0.001
A	0.047	0.165	0.485	0.001
D	0.001	0.139	-	-
F	0.003	-	-	-
A:D	0.023	0.123	-	-
A:F	0.021	-	-	0.001
F:D	-	-	-	0.001
Z - score				
Intercept	2.644	-1.185	-2.799	164.522
A	-2.07	1.308	-0.699	8.605
D	-3.774	1.36	-	-
F	-3.659	-	-	-
A:D	2.53	-1.449	-	-
A:F	2.267	-	-	-26.093
F:D	-	-	-	18.406

Appendix 3.8. Best-fitting model for the number of functional groups (FGR) in response to environmental filters.



The best-fitting model for the number of functional groups (FGR) only included a single and quadratic term of agriculture (Fig S4.2., FGR = -0.12Agriculture^2 -0.1Agriculture +1.27; R^{2}c= R^{2}m= 0.13).

Appendix 3.9. Spatial pattern of the functional diversity and redundancy indices and their pairwise relationships.

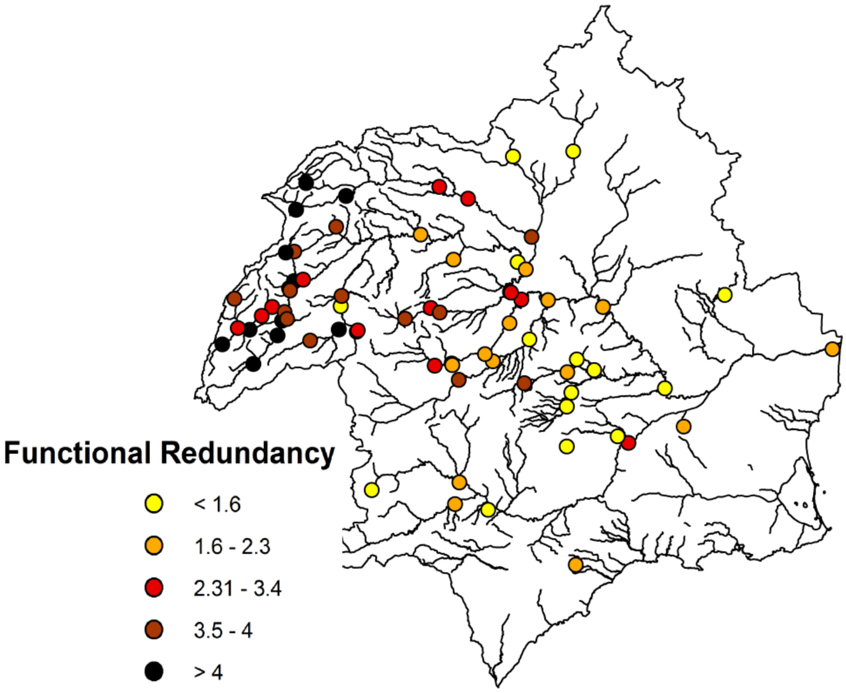


Fig. S3.9.1 Spatial pattern of Functional Redundancy classified in five classes (quantiles).

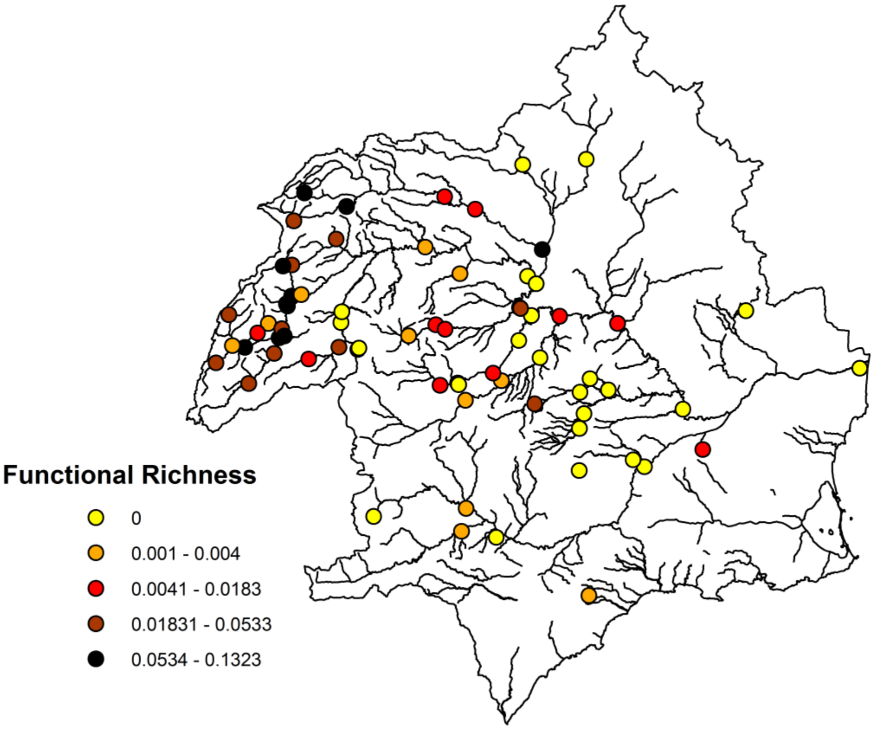


Fig. S3.9.2. Spatial pattern of Functional Richness classified in five classes (quantiles).

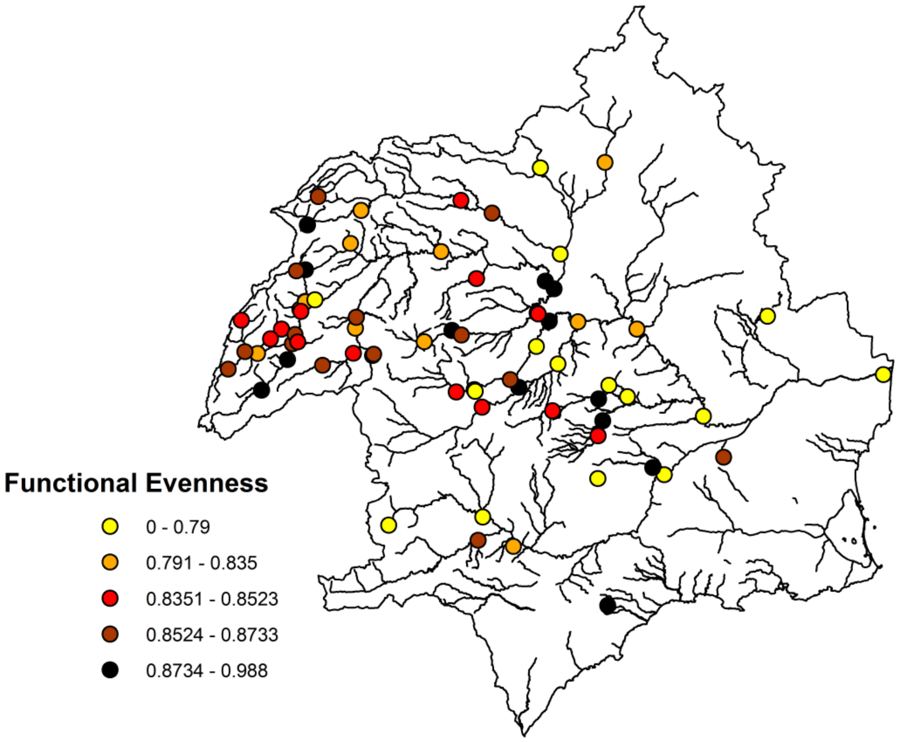


Fig. S3.9.3. Spatial pattern of Functional Evenness classified in five classes (quantiles).

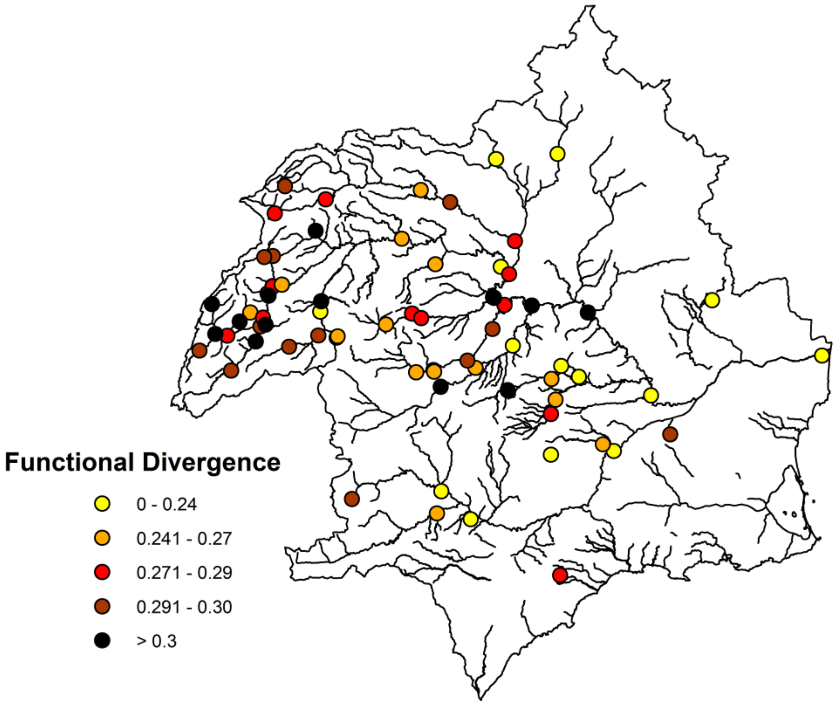


Fig. S3.9.4. Spatial pattern Functional Divergence classified in five classes (quantiles).

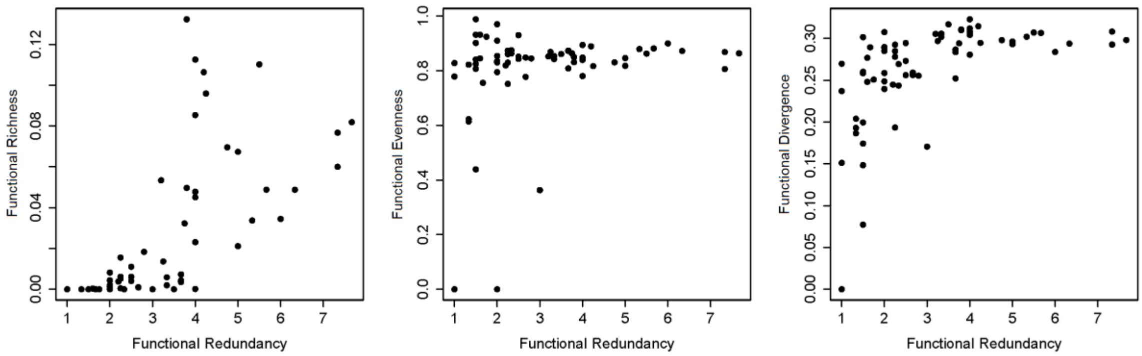


Fig. S3.9.5. Relationships between the different functional measures.

Table S3.9.1. Spearman correlations between functional measures. Red represents significant results (*p*-value< 0.01). FR= Functional Redundancy, FRic= Functional Richness, FEve= Functional Evenness, FDis= Functional Divergence.

	FR	FRic	FEve	FDis
FR	-	0.844	0.322	0.654
FRic		-	0.256	0.662
FEve			-	0.398
FDis				-

Chapter 4

Functional redundancy as a tool for bioassessment: a test using riparian vegetation

Abstract

There is an urgent need to track how natural systems are responding to global change in order to guide management efforts. Traditionally, taxonomically-based metrics have been used as indicators of ecosystem health and conservation status. However, functional approaches offer promising advantages that can improve bioassessment and biomonitoring performance. In this study, we aim to test the applicability of functional redundancy (FR), a functional feature related to the stability, resistance and resilience of ecosystems, as a tool for bioassessment, using woody riparian communities as example. We investigated the response of FR and other traditional taxonomic (species richness) and ecological status (Riparian Quality Index) biomonitoring indices to natural (drought duration) and anthropogenic stressors (flow regulation and agriculture) in a Mediterranean basin. Then, we explored the ability of FR and the other indices to discriminate between different categories of human alteration. Although we found significant negative relationships between all biological indices (taxonomic, functional and ecological quality) and stress gradients, FR was the most explicative indicator to natural and anthropogenic stressors, when considered together. In addition, FR was the most accurate index to discriminate between different categories of human alteration in both perennial and intermittent river reaches, which allowed us to set threshold values to identify undisturbed (reference condition), moderately disturbed and highly disturbed reaches in both types of rivers. Using these thresholds and the best-fitting model, we generated a map of human impact on functional redundancy of riparian communities for all the stretches of the river network. Our results demonstrate that FR shows clear advantages over traditional methods, suggesting that functional approaches should be considered in order to get a better assessment and prediction of the ecosystem responses to environmental changes.

Introduction

Given the increasing intensity of global change drivers (Sala *et al.,* 2000), there is an urgent need to understand how biological communities are responding to multiple environmental disturbances and their consequences on the relationship biodiversity – ecosystem functioning (Hooper *et al.,* 2012). For this task, it is essential to use reliable and versatile bioassessment tools allowing an early, precise and mechanistic evaluation of the effect of anthropogenic impacts on ecosystems.

These bioassessment tools need to be supported by the best scientific knowledge to ensure that they are both adaptive and credible (Friberg *et al.,* 2011). During the last decade, theoretical and empirical studies have demonstrated the utility of functional measures to explore the effects of human activity on biodiversity (e.g. Clapcott *et al.,* 2010; Laliberté *et al.,* 2010; Mouillot *et al.,* 2013). However, this new knowledge has rarely been translated to biomonitoring or environmental management practices (Cadotte *et al.,* 2011; Mouillot *et al.,* 2013), which are mainly focused on taxonomically based indicators (Menezes *et al.,* 2010).

Functional approaches present several advantages over taxonomic-based metrics, such as a better inter-taxon and inter-region comparability (McGill *et al.,* 2006) and predictable mechanistic links between environmental changes and ecosystem functions (Hooper et al. 2005; Mori *et al.,* 2013). Accordingly, recent studies have encouraged the use of functional traits and functional diversity for biomonitoring (e.g. Dolédec & Statzner, 2008; Vandewalle *et al.,* 2010; Chillo *et al.,* 2011). Although a number of functional diversity (e.g. functional richness, evenness, divergence; see Mason *et al*., 2005 for a review) and functional redundancy (FR, Fonseca & Ganade, 2001; Rosenfeld, 2002; Laliberté & Legendre, 2010) measures have been described, FR could be a good candidate to be tested as a bioassessment tool since it has recently been proved to be more sensitive than other functional diversity measures in detecting environmental change (see Chapter 3). In addition, there is evidence that the reduction in FR is caused by non-random habitat filtering along stress gradients (e.g. Laliberté *et al.,* 2010; Gutiérrez-Cánovas *et* *al.,* 2015; Chapter 3). FR can be defined as the number of species contributing similarly to an ecosystem function (Walker, 1992; Lawton & Brown, 1993), being positively related to the stability, resistance and resilience of ecosystems (Hooper *et al.,* 2005; Guillemot *et al.,* 2011). Thus, functionally redundant communities might allow functionally similar species to partly or fully compensate for the loss or failure of others (Rosenfeld, 2002; Guillemot *et al.,* 2011; Biggs *et al.,* 2012). However, although it has lately been used for conservation purposes (e.g. Matsuzaki *et al.,* 2013; Sasaki *et al.,* 2014), its potential as a bioassessment tool has not been explicitly tested yet, especially in the multi stressor context (e.g. Sasaki *et al.,* 2015).

Here, we assessed the applicability of FR as a tool for bioassessment using riparian plants as model organisms and rivers as focal ecosystems. Riparian vegetation is a well-defined key component in the functioning of freshwater ecosystems (Hladyz *et al.,* 2011), providing essential functions (e.g. soil fixation, organic matter supply), goods and services (e.g. clean water, fibre, timber, food and energy). These communities, which are diverse but taxonomically well-known, have been recognised as good indicators of human disturbances (Bejarano *et al.,* 2012; Villarreal *et al.,* 2012; Bruno *et al.,* 2014b) and their use has a long tradition in biomonitoring (e.g. Bunn *et al*., 1999; Werren & Arthington, 2002; Bailey et al., 2004). Besides, there are a number of available databases from which trait information can be gathered.

Changes in land use and flow regulation are globally recognised as the most important anthropogenic stressors impacting aquatic and riparian ecosystems (Nilsson & Berggren, 2000), and particularly in Mediterranean and semiarid areas (Kroll *et al.,* 2013; Bruno *et al.,* 2014b). Concretely, the runoff from agricultural lands carry nitrates and other major ions and nutrients, which alters stream water chemistry (Navarro-Llácer, 2006; Monteagudo *et al.,* 2012) while flow regulation affects the timing, magnitude and seasonality of the flow regime as well as the physical habitat of the rivers (Belmar *et al.,* 2013; Kroll *et al.,* 2013). Both anthropogenic pressures alter sediment cycling, habitat quality, river connectivity, riparian regeneration and integrity (Nilsson & Berggren, 2000; Allan, 2004; Aguiar & Ferreira, 2005), which favour the invasion of weeds and exotic, opportunistic species, accompanied with a decline in woody species (Radosevich *et al.,* 2007; Greet *et al.,* 2012). This species replacement may involve a modification of the functional trait composition of riparian communities, leading to changes in the ecosystem services provided. Besides anthropogenic disturbances, drought is a capital chronic stressor in Mediterranean-climate areas, acting as a perennial filter for the regional species pool (Peñuelas *et al.,* 2001). Drought intensification affects species and trait composition, promoting a replacement of phreatophyte species, which have the lowest tolerance to dry conditions (e.g. *Salix alba* in Mediterranean rivers, González *et al.,* 2012), by drought-adapted species (e.g. *Tamarix* species, Nippert *et al.,* 2010). Thus, bioassessment tools are starting to consider the underlying natural filters that could interact with anthropogenic stressors. Otherwise, we could produce misleading values for bioassessment under natural drought conditions.

To test the usefulness of FR in river bioassessment, we compare the responses of riparian FR and other traditional taxonomic (species richness) and ecological quality (Riparian Quality Index, RQI) indices, along the main gradients of natural (i.e. drought) and anthropogenic stress (i.e. flow regulation and agriculture) in a Mediterranean basin. Then, we also check the capacity of the different indices to discriminate between several previously defined categories of human disturbance. Subsequently, we determine the thresholds in the FR values that better separate the different classes of human disturbance both for perennial and intermittent rivers. Finally, using these thresholds and the predicted values of FR for each one of the stretches of the entire basin, we assign them a class of human impact based on the functional response of the riparian communities. This approach could assist in reaching a cost-effective ecosystem management.

Materials and methods

Data collection

A total of 71 freshwater river reaches were selected to represent the environmental variability along natural flow persistence, land use and hydrological alteration gradients in the study area. In addition, we also account for the remaining environmental variability through altitude since this variable is able to summarise well the natural gradients occurring in the study area (Díaz *et al.,* 2008). 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 identified the presence of woody riparian species, from the low-water margin up to the natural bankfull limit through ten transects, obtaining a unique list of species for each locality.

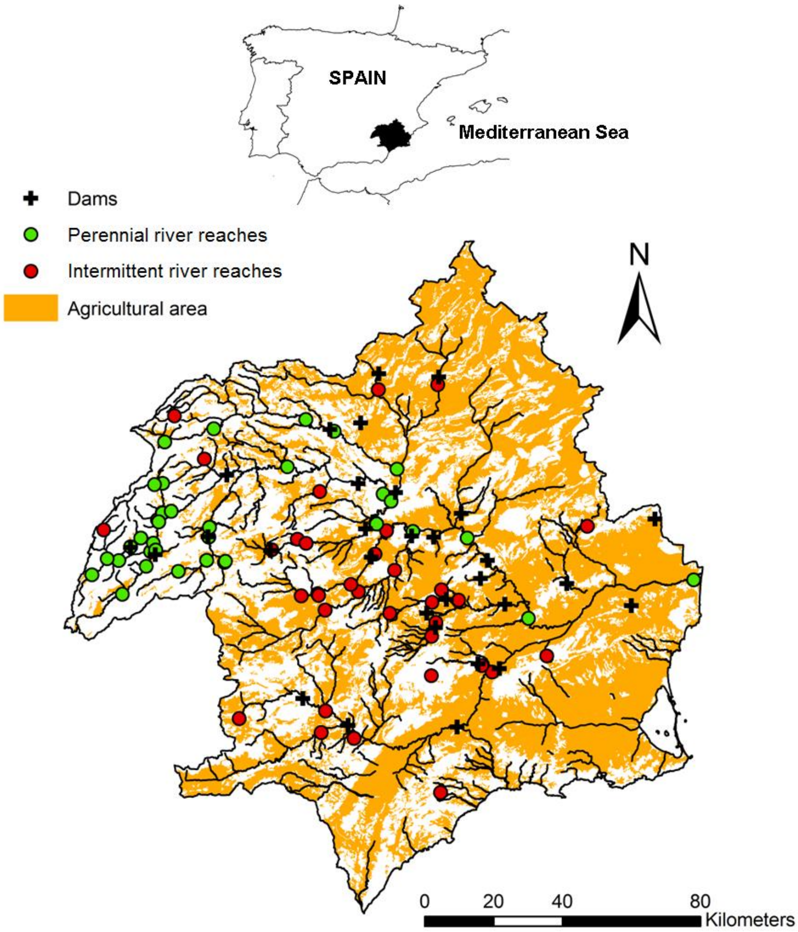


Fig. 1. Geographic location of the study area showing the 71 sampling sites (sorted by perennial and intermittent river reaches), agricultural area and the main dams.

Biological indices

FR was calculated for each sampling site as the ratio between species richness and the number of functional groups (i.e. the average number of species per functional group, Laliberté *et al.,* 2010) because it showed a better performance than other FR estimations, (such as the difference between the taxonomic and functional diversities, Pillar *et al.* 2013) in response to stressors. We used the definition of plant functional groups which considers sets of plants that have traits with similar effects on the dominant ecosystem processes (i.e. with similar effect traits; Díaz & Cabido, 2001). To define functional groups, we gathered a total of 19 continuous, semi-continuous and categorical biological effect traits (i.e. those that directly influence a specific function of the ecosystem (e.g. primary productivity, nutrient cycling, see Díaz & Cabido, 2001) from 59 online trait databases and scientific publications (Appendix 4.1). Extensive and specific Mediterranean databases were prioritised in order to minimise the effect of intraspecific variability. We constructed an effect-trait dissimilarity matrix using the Gower index, which can handle mixed variable types (continuous, semi-continuous and categorical), as well as missing values. Ward's clustering was the method used to classify species in functional groups based on this matrix. We defined 5 functional groups with a suite of coadapted characteristics to environmental conditions of channel and riparian zones that at the same times guarantee a minimum number of species (6 species) to allow further statistical analyses (see further methodological details in Chapter 3).

Besides FR, we calculated two usual biological indices for bioassessment, a taxonomic index, species richness (SR), and another one related with the ecological quality, Riparian Quality Index (RQI). SR was calculated as the number of woody riparian species observed in each sampled reach. RQI is a widely used field index in the Iberian Peninsula to assess the ecological quality of riparian zones (González del Tánago *et al.,* 2006). It is composed of several sub-indices characterising lateral, longitudinal and vertical continuity, composition, structure, regeneration and bank condition. RQI index has been proven to be effective detecting human impacts on riparian ecosystems

(Barquín *et al.,* 2011) and also in our study area (Belmar *et al.,* 2013; Bruno *et al.,* 2014b).

Environmental stressors

Drought duration (days without water flow per year) was used as a surrogate for the natural hydrological stress to which Mediterranean semiarid rivers are normally subjected. It was estimated at reach scale in each fluvial node using the estimates of the Integrated System for Rainfall–Runoff Modelling (SIMPA) (see for details Belmar *et al.,* 2011 and Chapter 3). After delineating the catchment for each sampling site, we used the percentage of agricultural area in each one of these catchments as a surrogate for land use intensity. As proxy of hydromorphological alteration we used the flow regulation index. This index was estimated using the methodology described in Falcone *et al.* (2010) and adapted by Belmar *et al.* (2013). This method uses the number of dams and their regulatory capacity (hm^3) in the drainage area associated with each sampling site. Sites were assigned between 0 to 8 points for each variable based on their percentile value within the data range. Then, those points were added providing an index that potentially ranged from 0 (minimum flow alteration) to 16 (maximum flow alteration).

Data analysis

The relationships between FR, SR and RQI with stressors were tested using linear mixed-effect models (LMEs). We tested the significance of simple and quadratic coefficients for each standardised stressor as well as the between-stressors interaction terms. Before their standardisation, drought duration was log-transformed and agriculture was arcsine-square-root transformed to improve linearity against response variables. In the same way, SR and RQI were squared-root-transformed before the analysis. The models included a fixed part with an intercept and the stressor slopes, along with a random intercept to account for environmental variability. There are two measures of goodness-of-fit for LMEs: conditional R^2 provides the full model goodness-of-fit whilst marginal R^2 only provides this measure for the fixed terms. We are interested in the latter one, which is associated with the effects produced by environmental filters (fixed effects) and excludes the effect of environmental variability (random effects). The environmental variability was included as a three level factor representing elevation typology (high altitude: elevation > 1000 m a.s.l., mid altitude: $1000 \geq$ elevation > 600 m a.s.l., lowlands: elevation $\leq$ 600 m a.s.l.). LMEs were performed using a backward-stepwise procedure retaining the model that minimises the Bayesian Information Criteria (BIC). We checked model assumptions visually (residual normality and homoscedasticity) and using Moran's I test (spatial autocorrelation of residuals, ArcGIS 9.2).

We then explored the sensitivity of FR, SR and RQI to human disturbance intensity, which was estimated using the Mediterranean Reference Criteria index (MRC; Sánchez-Montoya *et al.,* 2009). This index ranges from 0 (high disturbance) to 20 (undisturbed sites), according to the number of criteria met. Sites were classified into three alteration classes: Highly Disturbed (MRC<14 criteria), Moderately Disturbed (MRC within 14-19 criteria) and Undisturbed (MRC=20 criteria; see Fig. S4.2.1 in Appendix 4.2). We performed one-way ANOVA tests to look for differences in the values of FR, SR and RQI among the three categories of human disturbance intensity. To avoid the confounding effect of drought intensity (i.e. human impact can vary depending on the underlying natural stress), ANOVA tests were carried out separately for the two main river typologies in the study area: perennial (main stem and stable rivers) and intermittent rivers (seasonal and temporary), classified following Belmar *et al.* (2011; 2013). Main test model residuals were also checked for normality and homoscedasticity assumptions. Homoscedasticity was not met in most models, thus alpha was set to 0.01 to avoid false positives when applicable. Post-hoc analyses were conducted using a modified version of the Tukey test, more robust against the non-normal or heteroscedastic residuals, and unbalanced data (Herberich *et al.*, 2010).

We established FR reference values separately for perennial and intermittent rivers. For both types of rivers, the FR 75th and 25th percentiles were estimated using the FR value distribution at the Undisturbed sites. The EPA (United States Environmental Protection Agency) considers 75th percentile of reference sites as upper threshold because it is associated with minimally impacted conditions (Herlihy & Sifneos, 2008), while the 25th percentile can be used as the lower boundary of undisturbed classes (e.g. Sánchez-Montoya *et al.*, 2010). Similarly, the 25th percentile of FR values in Moderately Disturbed rivers was used to set the threshold with the Highly Disturbed class. Finally, taking into account the predicted FR values, previously estimated for the entire network using the best-fitting model (Chapter 3), and the thresholds obtained separately for perennial and intermittent rivers, we generated a map of human impact for the whole study area.

All statistical analyses were performed in the R statistical software (libraries: 'ade4', 'car', 'FD', 'multcomp', 'MASS', 'MuMIn', 'nmle', 'party' and 'vegan'; R-Development-Core-Team, 2014). We provide R code and FR functions in Appendix 4.3.

Results

Generally, the three indices declined with increased stress in the individual models (Fig. 2 and Table 1). These relationships showed varying marginal deviances (R^2m), which were higher for SR. All indices showed a significant negative relationship with agriculture, which is probably behind the partial convergence of their spatial patterns (Fig. S4.2.2 in Appendix 4.2). Other negative significant relationships were found for RQI with flow regulation and for FR and SR with drought.

The best-fitting models showed similar conditional and marginal goodness-of-fit for the three indices. However, the best one for FR showed a greater percentage of explained deviance (58.8 %) than those for SR (56.3 %) or RQI (51.5 %). The model for FR included the individual terms of agriculture, drought and flow regulation, plus the interactions between agriculture and both drought and flow regulation (Table 1). SR model included also the three individual terms together with the interactions between drought and both agriculture and flow regulation. In both cases, the individual term slopes were negative whilst pairwise interactions showed positive coefficients. The best-fitted model for RQI included the individual terms of agriculture and drought, along with the interaction between agriculture and hydrological alteration. In this model, all the slopes were negative.

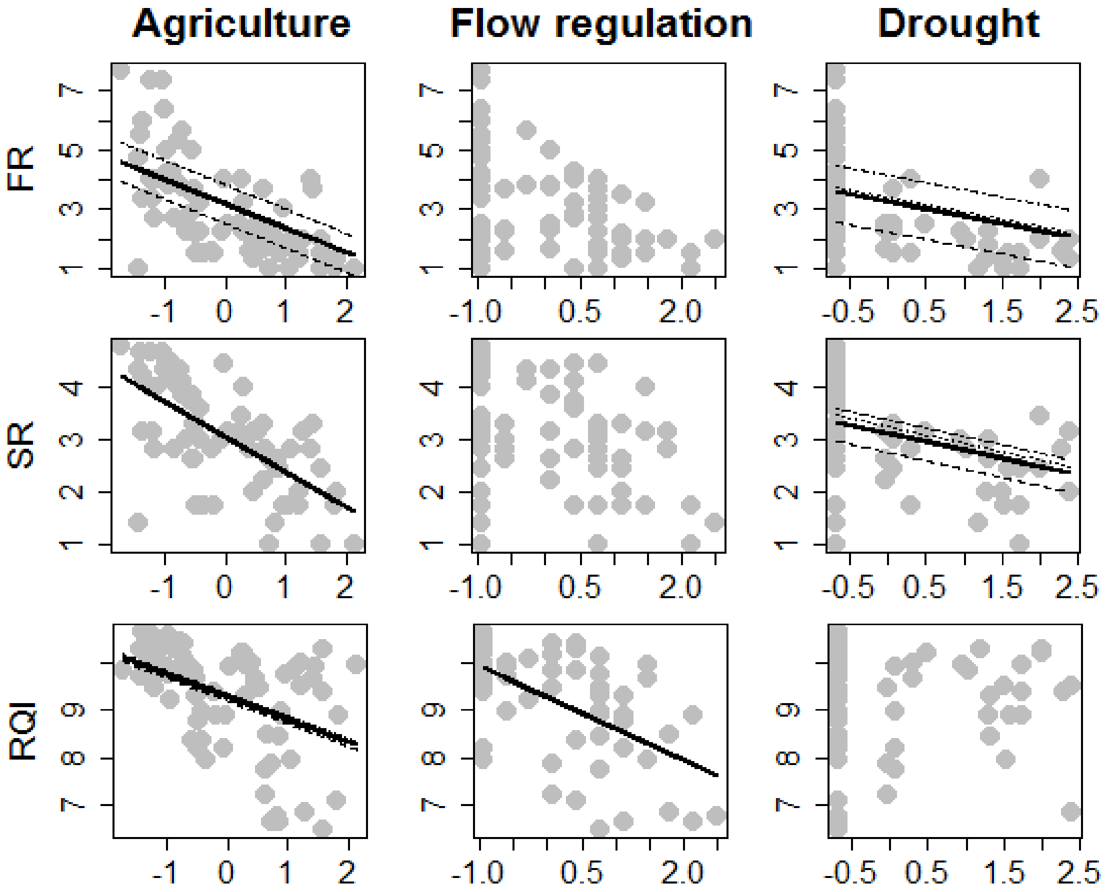


Fig. 2. Plots showing the individual response of Functional Redundancy (FR), Species Richness (SR) and Riparian Quality Index (RQI) to environmental stressors. Goodness of fit and *p*-values are available in Table 1. Black lines represent the fitted values for each LME. Solid lines represent the fitted models for each single stressor, dashed lines represent the fitted model for the low altitude 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.

Table 1. LMEs results showing the model equations, *p*-values, Bayesian Information Criterion (BIC) and the marginal (R^2m) and conditional R^2 (R^2c) for FR, SR and RQI. Interactions are represented by "*".

Indices	Model equation	*P*-value	BIC	R^2m	R^2c
	Agriculture (A)				
FR	y=3.189-0.824x	<0.001	248	0.264	0.459
SR	y=3.064-0.678x	<0.001	185.5	0.435	0.435
RQI	y=9.28-0.47x	<0.001	216.5	0.195	0.215
	Flow regulation (F)				
FR	y=3.298-0.183x	0.322	268.1	0.011	0.423
SR	y=3.148-0.2x	0.11	213.7	0.037	0.199
RQI	y=9.261-0.655x	<0.001	202.8	0.359	0.359
	Drought (D)				
FR	y=3.264-0.49x	0.004	261	0.082	0.433
SR	y=3.141-0.321x	0.006	208.9	0.098	0.236
RQI	y=9.406+0.125x	0.337	226.3	0.011	0.274
	Best-fitting models				
FR	y=2.66-0.625A-0.642D-0.475F+0.506A*D+0.354A*F		239	0.588	0.588
SR	y=2.972-0.461A-0.305D-0.239F+0.233A*D+0.179D*F		176	0.563	0.563
RQI	Y=9.325-0.463A-0.496DR-0.276A*F		185.1	0.516	0.516

ANOVA results showed significant differences in the values of FR, SR and RQI among different categories of human alteration in both perennial (*F*=13.83, *p*<0.001 for FR; *F*=7.99, *p*=0.002 for SR; and *F*=27.71, *p*<0.001 for RQI) and intermittent rivers (*F*=7.01, *p*=0.003 for FR; *F*=15.66, *p*<0.001 for SR and *F*=4.96, *p*=0.013 for RQI). Post-hoc tests (Table 2, Fig. 3) revealed that only FR showed significant differences between all alteration classes for both perennial and intermittent rivers. Contrastingly, there were no significant differences in SR between the Undisturbed and the Moderately Disturbed sites for any type of river. For RQI, we found significant differences between alteration classes for perennial rivers but not for intermittent ones.

Table 2. Post-hoc tests showing how FR, SR and RQI differ between categories of human alteration. *P*-values are given for each pairwise combination, for perennial and intermittent rivers. ns: non-significant. MRC: Mediterranean reference criteria. U: Undisturbed sites (MRC=20); MD: Moderately Disturbed (14≤MRC>19); HD: Highly Disturbed (MRC<14); ns = non-significant result.

	Perennial			Intermittent		
Human alteration	FR	SR	RQI	FR	SR	RQI
U vs. MD	< 0.05	ns	< 0.05	< 0.05	ns	ns
U vs. HD	< 0.001	< 0.01	< 0.001	< 0.001	< 0.01	ns
MD vs. HD	< 0.01	< 0.05	< 0.001	< 0.05	< 0.01	< 0.05

FR values were generally greater for perennial than for intermittent rivers whatever the category of human alteration intensity considered (Fig. 3). For Undisturbed reaches, FR values ranged mainly from 6.5 (75th percentile value) to 5.3 (25th percentile value) in perennial rivers (median value = 5.5) and from 4.2 (75th percentile value) to 4.0 (25th percentile value) in intermittent rivers (median value = 4.1, Fig. 4). Reaches showing FR values between 2.9 – 5.3 in perennial and 2.1– 4.0 in intermittent rivers were considered as moderately impacted. Reaches showing FR values below these thresholds were considered as highly impacted.

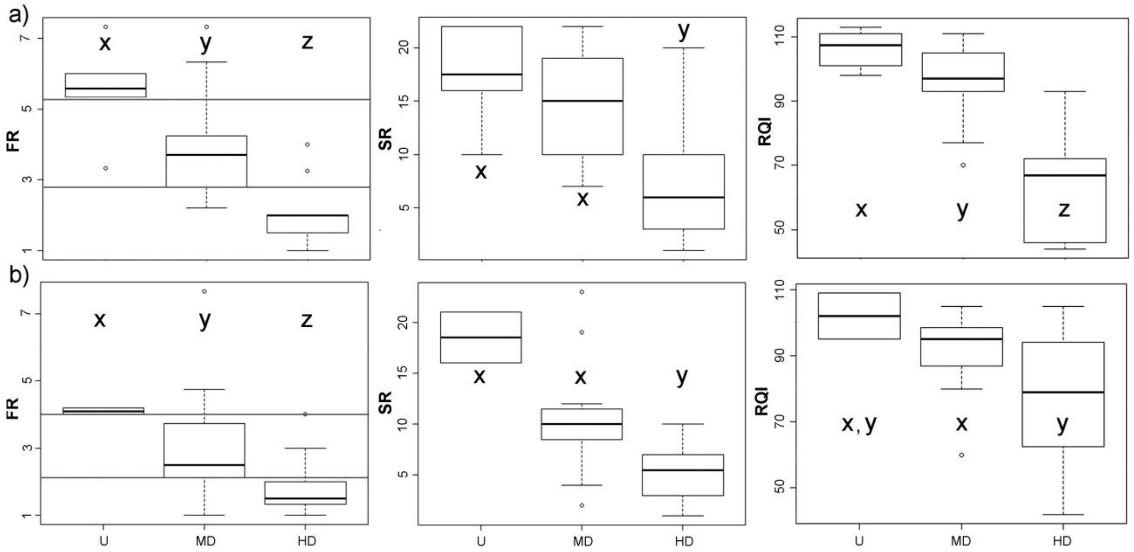


Fig. 3. Boxplots showing ANOVAs post-hoc results used to test the sensitiveness of functional redundancy (FR), species richness (SR), and riparian quality index (RQI) at different intensities of human disturbance for a) perennial and b) intermittent rivers. U: Undisturbed sites; MD: Moderately Disturbed sites; HD: Highly Disturbed sites. Grey horizontal lines represent the thresholds between the different categories for FR. Different letters (x, y, z) were assigned when alteration classes showed significant differences in the post-hoc analysis.

Finally, we mapped the human impact on the functional redundancy of riparian communities for the entire river network (Fig. 4). This map shows a clear gradient of functional impairment, increasing from unregulated rivers in natural sub-basins to regulated rivers in agricultural areas, both in perennial and intermittent rivers.

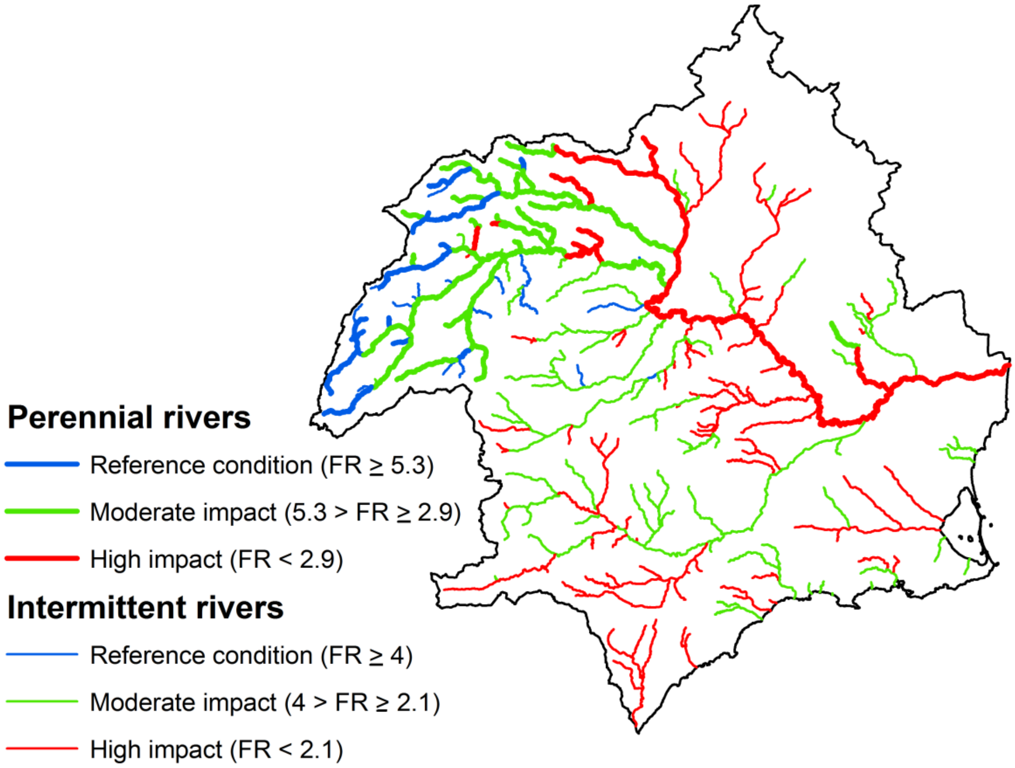


Fig. 4. Spatial patterns of the anthropogenic impact on Functional Redundancy (FR) of riparian communities for both perennial and intermittent rivers. The thresholds of FR values used to split these categories are also shown (see Methods section for further details).

Discussion

Response and sensitiveness of bioassessment indices to environmental stressors

We found that FR showed a clearer response to environmental filters than other taxonomic or ecological quality-related indices. In particular, FR was the most sensitive index to human alteration since it was able to accurately distinguish between the different categories of human disturbance. Thus, it resulted better than SR at detecting changes at low and moderate disturbance intensities and better than RQI at intermittent rivers.

Although all the indices displayed similar negative responses to single environmental stressors, FR performed better in a multi-stressor context (Table 1). Furthermore, its response to stress is non-random (tested through null models) and predictable at large scale using only coarse-grain, and remote variables, which are currently available for most regions (Chapter 3). On the other hand, all the best-fitted models for FR, SR and RQI included multiple stressors and pairwise interactions between some of them. The combined effects of several filters might push an ecosystem beyond what could be achieved through individual stress (Ban *et al*., 2014; Piggot *et al.,* 2015; Sasaki *et al*., 2015). Alternatively, antagonistic effects might be found, for instance, when the effect of two stressors is similar and species are pre-adapted to habitat filtering. Anyway, although an integrated management of catchment needs to be informed by knowledge of the combined effects of multiple stressors, either natural or anthropogenic ones, the complete understanding of such interactions is beyond our goals and should be studied in depth in future works.

Despite the better performance of FR in a multi-stressor context, the differences found in the diagnose capacities among indices, especially in the case of single stressors (e.g. only RQI was able to detect the individual effect of hydrological alteration), suggest that bioassessment should rely on multi-metric approaches. In fact, many studies have shown that different aspects of biodiversity are important for sustaining optimal levels of ecosystem functionality (e.g. Tomimatsu *et al.,* 2013). Given the scarcity of functional approaches incorporated to environmental management (Cadotte *et al.,* 2011), we advocate for the integration of FR in bioassessment toolbox to move beyond primarily descriptive biomonitoring, towards a deeper understanding of the effects of environmental change on natural systems.

Bioassessing naturally-stressed ecosystems

Our results reveal that intermittent rivers displayed lower FR compared to perennial watercourses in absence of human disturbance (reference condition). These differences are probably associated with a loss in species within some specific functional groups, such deciduous trees and an increase in sclerophyllous and evergreen shrubs (Aguiar & Ferreira, 2005). Similarly, river biomonitoring tools based on aquatic macroinvertebrates also varied differently in perennial and intermittent rivers (Sánchez-Montoya *et al.,* 2007; 2009). Therefore, in arid regions, ephemeral and intermittent streams are recognised to be significantly less diverse than perennial rivers (Tabacchi *et al.,* 1996; Bonada *et al.,* 2007b; Stromberg *et al.,* 2005), differing clearly in taxonomic and trait composition (e.g. Lite *et al.,* 2005; Bonada *et al.,* 2007a; Bruno *et al.,* 2014a). Therefore, to avoid biases in the assessment of the anthropogenic impact, the underlying natural stress must be considered in bioassessment practices. We show that FR was capable of detecting the impact of human disturbance even at naturally-stressed ecosystems such as intermittent rivers. Consequently, naturally stressed ecosystems should be assessed and managed differently to achieve a good ecological status (Gutiérrez-Cánovas *et al.,* 2008). Finally, assessing and monitoring the functional features in naturally-stressed areas could be useful to gain insights into the effect of the ongoing climate change on ecosystems, and so be able to anticipate changes in temperate European watersheds (Bonada *et al.,* 2007a), where climate change models predict an increase in the aridity (leading to higher river intermittence and drought; IPCC, 2013). Our results point to a worrying situation under such circumstances, with a potential reduction of riparian FR, which might translate into modified ecosystem functions.

Advantages and drawbacks on the use of FR in bioassessment

The use of FR could provide more predictable, generalisable and informative assessment than other traditionally used metrics, given their relationship with environmental change, and ecosystem functioning and stability (Hooper *et al.,* 2005; McGuill *et al.,* 2006; Guillemot *et al.,* 2011). Functional approaches link directly stressors intensity with the variation in species effect and response traits (Laliberté *et al.,* 2010; Mouillot *et al.,* 2013). In addition, the commonalities of some traits across taxa and the lower biogeographical variation of functional features (McGuill *et al.,* 2006; Bonada *et al.,* 2007a), may help to create geographically-generalised indicators. Therefore, incorporating FR to biodiversity evaluation and management may help us to anticipate the ecosystem effects caused by rapid environmental change. In a context of increasing aridity and human pressure in the Mediterranean basin, cascading effects on aquatic communities may be expected. Thus, drought reduces plants and leaf traits diversity such as specific leaf area or nutrient content (Wright *et al.,* 2001), which may affect aquatic detritus-based communities (Lecerf *et al.,* 2005). Similarly, agriculture can reduce the riparian species that produce shade, affecting to water temperature and aquatic communities (Thomas *et al.,* 2015). The ability of FR to detect the impact thresholds along disturbance gradients could serve to establish a backstop for preventing the threshold from being crossed. These perspectives can take us beyond simply invoking the precautionary principle of conserving biodiversity to a predictive science that delivers practical solutions to cope with ecological uncertainties in a changing world (Sasaki *et al.,* 2015). Previously, the accuracy and sensitivity of FR should be checked in other geographical areas, ecosystems and taxonomic groups.

In summary, FR of riparian communities fulfils most of the criteria proposed by Bonada et al. (2006) to be an "ideal" biomonitoring tool, addressing the *rationale* - since it emerges from theoretical ecology concepts, is predictable and able to assess ecological functions as well as discriminate overall and specific human impact -, *implementation* - simple and low cost sampling and taxa identification - and *performance* - large-scale applicability and reliable indication of changes caused by overall and specific human impacts -. However, there are some drawbacks that could limit the applicability of FR. First, the availability of trait databases is a clear constraint for some taxonomic groups, especially for those more diverse or small (e.g. insects, bacteria). Second, although it could be calculated directly in the field, as other indices, it requires previous statistical analysis to obtain information on functional groups and on species belonging to each of them. Third, the functional patterns could be trivially explained by taxonomic variation, and not due to any niche-driven process (Villéger *et al.,* 2008; 2011). For this reason, null models must be performed to check for the non-randomness of the relationship between functional indicators and environmental change (see Chapter 3). Fourth, FR should be treated carefully because its concept is a double-edged sword in terms of practical conservation issues. It could be wrongly assumed that species performing similar roles in ecosystems can be 'expended' with a minimal impact on ecosystem processes (Rosenfeld, 2002). However, although redundancy is a natural feature of ecosystems that may improve the amount and stability of functions (Hooper *et al.,* 2005; Pillar *et al.,* 2013), species contributing similarly to an ecosystem services may have very different tolerances to environmental change (Lavorel & Garnier, 2002; Rosenfeld, 2002; Laliberté *et al.,* 2010). In this sense, the aggregate FR value provides the mean behaviour of all the functional groups but exploring which functional traits are lost with environmental filtering is also a key question in functional ecology with direct applications to management. Accordingly, when the species belonging to a specific functional group have been progressively depleted by disturbances, ecosystem is exposed to a high risk of shifting to an undesirable state. Therefore, further research in determining the vulnerability of each functional group (i.e. how the response of each functional group to stressor relates to response diversity) seems necessary to develop mechanistic models that predict which ecosystem functions and services can be disrupted.

Concluding remarks

Our results demonstrated that FR can be a suitable indicator to evaluate and track the anthropogenic impacts on biological communities. We have detected a more accurate and sensible response of FR in comparison with traditional indicators. More concretely, FR showed a clear response to single and multiple stressors and a high sensitivity to detect both early signs of human impact in ecosystems and variations between disturbance intensity. In addition, the map showing the human impact on functional redundancy for all perennial and intermittent rivers in the basin can be a useful tool for managers, enabling a broad and dynamic assessment of the ecological condition and resilience of rivers. Therefore, given the advantages over traditional indices, functional features as functional redundancy should be used and incorporated into the bioassessment toolbox in order to help decision-makers to focus conservation and restoration efforts, as well as to anticipate changes in the amount and stability of ecosystem functions and services.

References

Aguiar, F.C. & Ferreira, M.T. (2005) Human-disturbed landscapes: effects on composition and integrity of riparian woody vegetation in the Tagus River basin, Portugal. *Environmental Conservation*, **32**, 30–41.

Allan, J.D. (2004). Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 257–284.

Bailey, R.C., Norris, R.H. & Reynoldson, T.B. (2004) *Bioassessment of Freshwater Ecosystems: Using the Reference Condition Approach*. Kluwer Academic Publishers, New York, USA.

Ban, S.S., Graham, N.A. & Connolly, S.R. (2014) Evidence for multiple stressor interactions and effects on coral reefs. *Global Change Biology*, **20**, 681–697.

Barquín, J., Fernández, D., Álvarez-Cabria, M. & Peñas, F.J. (2011) Riparian quality and habitat heterogeneity assessment in Cantabrian rivers. *Limnetica*, **30**, 329–346.

Bejarano, M.D., González del Tánago, M., Garcia de Jalón, D., Marchamalo, M.,Sordo-Ward, A. & Solana-Gutiérrez, J. (2012) Responses of riparian guilds to flow alterations in a Mediterranean stream. *Journal of Vegetation Science*, **23**, 443–458.

Belmar, O., Velasco, J. & Martinez-Capel, F. (2011) Hydrological classification of natural flow regimes to support environmental flow assessments in intensively regulated Mediterranean rivers, Segura River basin (Spain). *Environmental Management*, **47**, 992–1004.

Belmar, O., Bruno, D., Martínez-Capel, F., Barquín, J. & Velasco J. (2013) Effects of flow regime alteration on fluvial habitats and riparian quality in a semiarid Mediterranean region. *Ecological Indicators*, **30**, 52–64.

Biggs, R., Schlüter, M., Biggs, D., Bohensky, E.L., BurnSilver, S., Cundill, G., *et al*. (2012) Toward principles for enhancing the resilience of ecosystem services. *Annual Review of Environment and Resources*, **37**, 421–448.

Bonada, N., Prat, N., Resh, V.H., & Statzner, B. (2006) Developments in aquatic insect biomonitoring: A comparative analysis of recent approaches. *Annual Review of Entomology*, **51**, 495–523.

Bonada, N., Dolédec, S. & Statzner, B. (2007a) Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implications for future climatic scenarios. *Global Change Biology*, **13**, 1658–1671.

Bonada, N., Rieradevall, M. & Prat, N. (2007b) Macroinvertebrate community structure and biological traits related to flow permanence in a Mediterranean river network. *Hydrobiologia,* **589**, 91–106.

Bruno, D., Belmar, O., Sánchez-Fernández, D. & Velasco, J. (2014a) Environmental determinants of woody and herbaceous riparian vegetation patterns in a semi-arid Mediterranean basin. *Hydrobiologia*, **730**, 45–57.

Bruno, D., Belmar, O., Sánchez-Fernández, D., Guareschi, S., Millán, A. & Velasco, J. (2014b) Responses of Mediterranean aquatic and riparian communities to human pressures at different spatial scales. *Ecological Indicators*, **45**, 456–464.

Bunn, S.E., Davies, P.M., & Mosisch, T.D. (1999) Ecosystem measures of river health and their response to riparian and catchment degradation. *Freshwater Biology*, **41**, 333–345.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087.

Chillo, V., Anand, M. & Ojeda, R.A. (2011) Assessing the use of functional diversity as a measure of ecological resilience in arid rangelands. *Ecosystems*, **14**, 1168–1177.

Clapcott, J.E., Young, R.G., Goodwin, E.O. & Leathwick, J.R. (2010) Exploring the response of functional indicators of stream health to land-use gradients. *Freshwater Biology*, **55**, 2181–2199.

Díaz, S. & Cabido, M. (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, **16**, 646–655.

Díaz, A.M., Alonso, M.L.S, and Gutiérrez, M.R.V-A. 2008. Biological traits of stream macroinvertebrates from a semi-arid catchment: patterns along complex environmental gradients. *Freshwater Biology*, **53**, 1–21.

Dolédec, S. & Statzner, B. (2008) Invertebrate traits for the biomonitoring of large European rivers: an assessment of specific types of human impact. *Freshwater Biology*, **53**, 617–634.

Falcone, J.A., Carlisle, D.M. & Weber, L.C. (2010) Quantifying human disturbance in watersheds: Variable selection and performance of a GIS-based disturbance index for predicting the biological condition of perennial streams. *Ecological Indicators*, **10**, 264–273.

Ferreira, M.T. & Aguiar, F.C. (2006) Riparian and aquatic vegetation in Mediterranean-type streams (western Iberia). *Limnetica*, **25**, 411–424.

Fonseca, C.R. & Ganade, G. (2001) Species functional redundancy, random extinctions and the stability of ecosystems. *Journal of Ecology*, **89**, 118–125.

Friberg, N., Bonada, N., Bradley, D.C., Dunbar, M.J., Edwards, F.K., Grey, J., *et al*. (2011) Biomonitoring of human impacts in freshwater ecosystems: the good, the bad and the ugly. *Advances in Ecological Research*, **44**, 1–68.

González, E., González-Sanchis, M., Comín, F.A. & Muller, E. (2012) Hydrologic thresholds for riparian forest conservation in a regulated large Mediterranean river. *River Research and Applications*, **28**, 71–80.

González del Tánago, M., García de Jalón, D., Lara, F. & Garilleti, R. (2006) Índice RQI para la valoración de las riberas fluviales en el contexto de la directiva marco del agua. *Ingeniería Civil*, **143**, 97–108.

Greet, J., Cousens, R. & Webb, A. (2012) More exotic and fewer native plant species: riverine vegetation patterns associated with altered seasonal flow patterns. *River Research and Applications*, **29**, 686–706.

Guillemot, N., Kulbicki, M., Chabanet, P. & Vigliola, L. (2011) Functional redundancy patterns reveal non-random assembly rules in a species-rich marine assemblage. *PloS One*, **6**, e26735.

Gutiérrez-Cánovas, C., Velasco, J. & Millán, A. (2008) SALINDEX: A macroinvertebrate index for assessing the ecological status of saline "ramblas" from SE of the Iberian Peninsula. *Limnetica*, **2**, 299–316.

Gutiérrez-Cánovas, C., Sánchez-Fernández, D., Velasco, J., Millán, A. & Bonada, N. (2015) Similarity in the difference: changes in community functional features along natural and anthropogenic stress gradients. *Ecology*, **96**, 2458–2466.

Herberich, E., Sikorski, J. & Hothom, T. (2010) A robust procedure for comparing multiple means under heteroscedasticity in unbalanced designs. *PLoS One*, *5*(3): p.e 9788.

Herlihy, A.T. & Sifneos, J.C. (2008) Developing nutrient criteria and classification schemes for wadeable streams in the conterminous US. *Journal of the North American Benthological Society*, **27**, 932–948.

Hladyz, S., Åbjörnsson, K., Chauvet, E., Dobson, M., Elosegi, A., Ferreira, V., *et al*. (2011) Stream ecosystem functioning in an agricultural landscape: the importance of terrestrial-aquatic linkages. *Advances in Ecological Research*, **44**, 211–276.

Hooper, D.U., Chapin, F.S.III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., *et al.* (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature,* **486**, 105–108.

IPCC (2013) *Climate Change 2013: The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge, United Kingdom and New York, USA.

Kroll, S.A., Ringler, N.H., De las Heras, J., Goméz-Alday, J.J., Moratalla, A. & Briggs, R.D. (2013) Analysis of anthropogenic pressures in the Segura Watershed (SE Spain), with a focus on inter-basin transfer. *Ecohydrology*, **6**, 878–888.

Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., *et al*. (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters*, **13**, 76–86.

Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.

Lawton, J.H. & Brown, V.K. (1993) Redundancy in ecosystems. *Biodiversity and ecosystem function* (eds Schulze, E.-D & Mooney, H.A.), pp. 255–270. Springer-Verlag, Berlin, Germany.

Lite, S.J., Bagstad, K.J. & Stromberg, J.C. (2005) Riparian plant species richness along lateral and longitudinal gradients of water stress and flood disturbance, San Pedro River, Arizona, USA. *Journal of Arid Environments*, **63**, 785–813.

Mason, N.W.H., Mouillot, D., Lee, W.G. & Wilson, J.B. (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, **111**, 112–118.

Matsuzaki, S.S., Sasaki, T. & Akasaka, M. (2013) Consequences of the introduction of exotic and translocated species and future extirpations on the functional diversity of freshwater fish assemblages. *Global Ecology and Biogeography*, **22**, 1071–1082.

Menezes, S., Baird, D.J. & Soares, A.M. (2010) Beyond taxonomy: a review of macroinvertebrate trait-based community descriptors as tools for freshwater biomonitoring. *Journal of Applied Ecology*, **47**, 711–719.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, **21**, 178–185.

Monteagudo, L., Moreno, J.L. & Picazo, F. (2012) River eutrophication: irrigated vs. non-irrigated agriculture through different spatial scales. *Water Research*, **46**, 2759–2771.

Mori, A.S., Furukawa, T. & Sasaki, T. (2013) Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews*, **88**, 349–364.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, **28**, 167–177.

Navarro-Llácer, C. 2006. *Estado ecológico de los ríos de Castilla-La Mancha*. PhD dissertation, University of Castilla-La Mancha, Albacete, Spain.

Nilsson, C. & Berggren, K. (2000) Alterations of riparian ecosystems caused by river regulation. *BioScience*, **50**, 783–792.

Nippert, J.B., Butler Jr, J.J., Kluitenberg, G.J., Whittemore, D.O., Arnold, D., Spal, S.E. & Ward, J.K. (2010) Patterns of Tamarix water use during a record drought. *Oecologia*, **162**, 283–292.

Peñuelas, J., Lloret, F. & Montoya, R. (2001) Severe drought effects on Mediterranean woody flora in Spain. *Forest Science*, **47**, 214–218.

Piggott, J.J., Townsend, C.R. & Matthaei, C.D. (2015) Reconceptualizing synergism and antagonism among multiple stressors. *Ecology and Evolution,* **5**, 1538–1547.

R Development Core Team (2014) *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, Austria.

Radosevich, S.R., Holt, J.S. & Ghersa, C.M. (2007) *Ecology of weeds and invasive plants: relationship to agriculture and natural resource management*. John Wiley and Sons, New Jersey, USA.

Rosenfeld, J.S. (2002) Functional redundancy in ecology and conservation. *Oikos*, **98**,156–62.

Sala, O.E., Chapin, F.S.III, Armesto, J.J., Berlow, R., Bloomfield, J., Dirzo, R., *et al*. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

Sánchez-Montoya, M.M., Puntí, T., Suárez, M.L., Vidal-Abarca, M.R., Rieradevall, M., Poquet, J.M., *et al.* (2007) Concordance between ecotypes and macroinvertebrate assemblages in Mediterranean streams. *Freshwater Biology*, **52**, 2240–2255.

Sánchez-Montoya, M.M., Vidal-Abarca, M.R., Puntí, T., Poquet, J.M., Prat, N., Rieradevall, M., *et al.* (2009) Defining criteria to select reference sites in Mediterranean streams. *Hydrobiologia*, **619**, 39–54.

Sánchez-Montoya, M.M., Vidal-Abarca, M.R., & Suárez, M.L. (2010). Comparing the sensitivity of diverse macroinvertebrate metrics to a multiple stressor gradient in Mediterranean streams and its influence on the assessment of ecological status. *Ecological Indicators*, **10**, 896–904.

Sasaki, T., Furukawa, T., Iwasaki, Y., Seto, M. & Mori, A.S. (2015) Perspectives for ecosystem management based on ecosystem resilience and ecological thresholds against multiple and stochastic disturbances. *Ecological Indicators*, **57**, 395–408.

Sasaki, T., Katabuchi, M., Kamiyama, C., Shimazaki, M., Nakashizuka, T. & Hikosaka, K. (2014) Vulnerability of moorland plant communities to environmental change: consequences of realistic species loss on functional diversity. *Journal of Applied Ecology*, **51**, 299–308.

Stromberg, J.C., Bagstad, K.J., Leenhouts, J.M., Lite, S.J. & Makings, E. (2005) Effects of stream flow intermittency on riparian vegetation of a semiarid region river (San Pedro River, Arizona). *River Research and Applications*, **21**, 925–938.

Tabacchi, E., Planty-Tabacchi, A., Salinas, M.J. & Décamps, H. (1996) Landscape structure and diversity in riparian plant communities: a longitudinal comparative study. *Regulated Rivers: Research and Management*, **12**, 367–390.

Thomas, S.M., Griffiths, S.W., Ormerod, S.J (2015) Beyond cool: adapting upland streams for climate change using riparian woodlands. *Global Change Biology*, **60**, 64–77.

Tomimatsu, H., Sasaki, T., Kurokawa, H., Bridle, J.R., Fontaine, C., Kitano, J., *et al*. (2013) Sustaining ecosystem functions in a changing world: a call for an integrated approach. *Journal of Applied Ecology*, **50**, 1124–1130.

Vandewalle, M., De Bello, F., Berg, M.P., Bolger, T., Dolédec, S., Dubs, F., et al. (2010) Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation*, **19**, 2921–2947.

Villarreal, M.L., Drake, S., Marsh, S.E. & McCoy, A.L. (2012) The influence of wastewater subsidy, flood disturbance and neighbouring land use on current and historical patterns of riparian vegetation in a semi-arid watershed. *River Research and Applications*, **28**, 1230–1245.

Villéger, S., Mason, N.W. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**, 2290–2301.

Villéger, S., Novack-Gottshall, P.M. & Mouillot, D. (2011) The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecological Letters*, **14**, 561–568.

Walker, B.H. (1992) Biodiversity and ecological redundancy. *Conservation Biology*, **6**, 18–23.

Werren, G. & Arthington, A.H. (2002) The assessment of riparian vegetation as an indicator of stream condition, with particular emphasis on the rapid assessment of flow-related impacts. *Landscape Health of Queensland* (eds Playford, J. Shapcott, A. & Franks, A.), pp. 194–222. Royal Society of Queensland, Brisbane, Australia.

Wright, I.J., Reich, P.B. & Westoby, M. (2001) Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology*, **15**, 423–434.

Supporting Information

Appendix 4.1. Functional effect trait information.

Appendix 4.2. Spatial patterns of species richness, functional redundancy, riparian quality index and MRC.

Appendix 4.3. R code and data files. Available at: https://www.dropbox.com/s/kxc9swbaqz8o2m5/Appendix%204.3.rar?dl=0

Appendix 4.1. Effect traits considered to characterise the functional features of the woody riparian species. C=continuous, SC=semi-continuous, CAT=categorical.

Trait	**Type**	**Units/Categories**
Plant size	CAT	Trees / Large shrubs / Small shrubs / Lianas
Raunkiaer	CAT	Macrophanerophytes / Mesophanerophytes / Nanophanerophytes / Chamaephytes / Epiphyte
Plant height	C	m
Growth rate	SC	Fast / Moderate / Slow
Specific leaf area	C	$cm^2 g^{-1}$
Leaf size	SC	Large / Moderate / Small
Leaf thickness	SC	Gross / Medium / Thin
Leaf type	CAT	Broadleaf / Needle / Scaly / Palm
Leaf compoundness	CAT	Simple / Compound
Leaf deciduousness	CAT	Evergreen / Deciduous/ Marcescent
P leaf concentration	SC	%
N leaf concentration	SC	%
C : N ratio	SC	High / Medium / Low
Nitrogen fixation capacity	CAT	Nitrogen fixer / Non fixer
Photosynthesis pathway	CAT	C3 / C4
Flower colour	CAT	Coloured / Not coloured
Lateral spread	SC	High / Medium / Low
Ramification	SC	High / Medium / Low
Rooting depth	SC	Deep / Moderate / Shallow

References: Data sources used to obtain the functional trait values.

Aguinagalde, I., Hampe, A., Mohanty, A., Martín, J.P., Duminil, J. & Petit, R.J. (2005) Effects of life-history traits and species distribution on genetic structure at maternally inherited markers in European trees and shrubs. *Journal of Biogeography*, **32**, 329-339.

Antúnez, I., Retamosa, E.C. & Villar, R. (2001) Relative growth rate in phylogenetically related deciduous and evergreen woody species. *Oecologia*,**128**, 172-180.

Aranda, I., Pardo, F., Gil, L. & Pardos, J.A. (2004) Anatomical basis of the change in leaf mass per area and nitrogen investment with relative irradiance within the canopy of eight temperate tree species. *Acta Oecologica*, **25**, 187-195.

Bejarano, M.D., González del Tánago, M., de Jalón, D.G., Marchamalo, M., Sordo-Ward, Á. & Solana-Gutiérrez, J. (2012) Responses of riparian guilds to flow alterations in a Mediterranean stream. *Journal of Vegetation Science*, **23**, 443-458.

Bell, L.W. (2005) Relative growth rate, resource allocation and root morphology in the perennial legumes, Medicago sativa, Dorycnium rectum and D. hirsutum grown under controlled conditions. *Plant and Soil*, **270**, 199-211.

Borghi, M., Tognetti, R., Monteforti, G. & Sebastiani, L. (2008) Responses of two poplar species (Populus alba and Populus x canadensis) to high copper concentrations. *Environmental and Experimental Botany*, **62**, 290–299.

Castro-Díez, P., Villar-Salvador, P., Pérez-Rontomé, C., Maestro-Martínez, M. & Montserrat-Martí, G. (1997) Leaf morphology and leaf chemical composition in three Quercus (Fagaceae) species along a rainfall gradient in NE Spain. *Trees*, **11**, 127-134.

Castro-Díez, P., Montserrat-Martí, G. & Cornelissen, J.H.C. (2003) Trade-offs between phenology, relative growth rate, life form and seed mass among 22 Mediterranean woody species. *Plant Ecology*, **166**, 117-129.

Castro-Díez, P., González-Muñoz, N., Alonso, A., Gallardo, A. & Poorter, L. (2009) Effects of exotic invasive trees on nitrogen cycling: a case study in Central Spain. *Biological Invasions*, **11**, 1973-1986.

Castroviejo, S. (coord). 1986-2012. *Flora iberica* 1-8, 10-15, 17-18, 21. Real Jardín Botánico, CSIC, Madrid, Spain. Available at: http://www.floraiberica.org/.

Ceballos, L. & Ruíz-de-la-Torre, J. (1971) *Árboles y arbustos de la España peninsular*. E.T.S.I. Montes, Madrid, Spain.

Cornelissen, J.H.C., Díez, P.C. & Hunt, R. (1996) Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology*, **84**, 755-765.

Domínguez, M.T., Marañón, T., Carpio, M., Manuel, J., Hidalgo, J.M. & Madejón, P. (2004) Crecimiento y morfología foliar de especies leñosas en las reforestaciones del Corredor Verde del Guadiamar (Sevilla). *Cuaderno de la Sociedad Española de Ciencias Forestales*, **20**, 173-179.

Domínguez, M.T., Aponte, C., Pérez-Ramos, I.M., García, L.V., Villar, R. & Marañón, T. (2012) Relationships between leaf morphological traits, nutrient concentrations and isotopic signatures for Mediterranean woody plant species and communities. *Plant and Soil*, **357**, 407-424.

Escudero, A., Del Arco, J.M., Sanz, I.C. & Ayala, J. (1992) Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. *Oecologia*, **90**, 80-87.

Escudero, A. & Mediavilla, S. (2003). Decline in photosynthetic nitrogen use efficiency with leaf age and nitrogen resorption as determinants of leaf life span. *Journal of Ecology*, **91**, 880-889.

Fitter, A.H. & Peat, H.J. (1994) The Ecological Flora Database. *Journal of Ecology*, **82**, 415-425. Available at http://www.ecoflora.co.uk.

González, E., Muller, E., Comín, F.A. & González-Sanchís, M. (2010) Leaf nutrient concentration as an indicator of Populus and Tamarix response to flooding. *Perspectives in Plant Ecology, Evolution and Systematics*, **12**, 257–266.

Gracia, C., Burriel, J.A., Ibáñez, J.J., Mata, T. & Vaydera, J. (2000-2004) *Inventari Ecològic i Forestal de Catalunya. Obra completa*. CREAF, Bellaterra, Spain. http://www.creaf.uab.es/iefc.

Gulías, J., Flexas, J., Mus, M., Cifre, J., Lefi, E. & Medrano, H. (2003) Relationship between Maximum Leaf Photosynthesis, Nitrogen Content and Specific Leaf Area in Balearic Endemic and Non-endemic Mediterranean Species. *Annals of Botany*, **92**, 215-222.

Han, W., Fang, J., Guo, D. & Zhang, Y. (2005) Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. *New Phytologist*, **168**, 377-385.

Herrera, C.M. (1987) Vertebrate-dispersed plants of the Iberian Peninsula: a study of fruit characteristics. *Ecological monographs*, **57**, 305-331.

Herrera, J. (1991) The reproductive biology of a riparian Mediterranean shrub, Nerium oleander L. (Apocynaceae). *Botanical journal of the Linnean Society*, **106**, 147-172.

Hill, M.O., Preston, C.D. & Roy, D.B. (2004) *PLANTATT-Attributes of British and Irish Plants: status, size, life history, geography and habitats*. Centre for Ecology & Hydrology, Monks Wood, United Kingdom.

Hladyz, S., Gessner, M.O., Giller, P.S., Pozo, J. & Woodward, G. (2009) Resource quality and stoichiometric constraints on stream ecosystem functioning. *Freshwater Biology,* **54**, 957–970.

Karrenberg, S. & Suter, M. (2003) Phenotypic trade-offs in the sexual reproduction of Salicaceae from flood plains. *American Journal of Botany*, **90**, 749-754.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., *et al*. (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology*, **96**, 1266–1274.

Lefèvre, F., Barsoum, N., Heinze, B., Kajba, D., Rotach, P., De Vries, S.M.G. & Turok, J. (2001) *EUFORGEN Technical Bulletin: In situ conservation of Populus nigra*. International Plant Genetic Resources Institute, Rome, Italy.

Martínez-Sánchez, J.J., Franco-Leemhuis, J.A. & Vicente-Colomer, M.J. (2008) *Especies silvestres mediterráneas con valor ornamental: selección, producción, viverística y utilización en jardinería*. Dirección General de Medio Natural, Consejería de Agricultura y Agua, Murcia, Spain.

Martínez-Vilalta, J., Mencuccini, M., Vayreda, J. & Retana, J. (2010) Interspecific variation in functional traits, not climatic differences among species ranges, determines demographic rates across 44 temperate and Mediterranean tree species. *Journal of Ecology*, **98**, 1462–1475.

Mediavilla, S., Santiago, H. & Escudero, A. (2002) Stomatal and mesophyll limitations to photosynthesis in one evergreen and one deciduous Mediterranean oak species. *Photosynthetica*, **40**, 553-559.

Mediavilla, S. & Escudero, A. (2003) Relative growth rate of leaf biomass and leaf nitrogen content in several Mediterranean woody species. *Plant Ecology*, **168**, 321-332.

Mediavilla, S., García-Ciudad, A., García-Criado, B. & Escudero, A. (2008) Testing the correlations between leaf life span and leaf structural reinforcement in 13 species of European Mediterranean woody plants. *Functional Ecology*, **22**, 787-793.

Milla, R., Reich, P.B., Niinemets, Ü. & Castro-Díez, P. (2008) Environmental and developmental controls on specific leaf area are little modified by leaf allometry. *Functional Ecology*, **22**, 565-576.

Ministerio de Medio Ambiente (1997-2007) *Tercer Inventario Forestal Nacional*. Dirección General de Conservación de la Naturaleza, Madrid, Spain.

Navarro, R. & Galvez, C. (2002) *Manual para la identificación y reproducción de semillas de especies vegetales autóctonas*. Junta de Andalucía, Cordoba, Spain.

Navarro, T., Nieto-Caldera, J.M., Pérez-Latorre, A.V. & Cabezudo, B. (1993) Estudios fenomorfológicos en la vegetación del sur de España. III: Comportamiento estacional de una comunidad de badlands (Tabernas, Almería. España). *Acta Botánica Malacitana*, **18**, 189-198.

Navas, M.L., Roumet, C., Bellmann, A., Laurent, G. & Garnier, E. (2010) Suites of plant traits in species from different stages of a Mediterranean secondary succession. *Plant Biology*, **12**, 183-196.

Niinemets, Ü. & Valladares, F. (2006) Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs,* **76**, 521–547.

Paula, S., Arianoutsou, M., Kazanis, D., Tavsanoglu, Ç., Lloret, F., Buhk, C., *et al.* (2009) Fire-related traits for plant species of the Mediterranean Basin. *Ecology,* **90**, 1420.

Paula, S. & Pausas, J.G. (2013) *BROT: a plant trait database for Mediterranean Basin species*. Version 2013.06. http://www.uv.es/jgpausas/brot.htm

Petisco, C., García-Criado, B., de Aldana, B.V., Zabalgogeazcoa, I. & Mediavilla, S. (2005) Use of near-infrared reflectance spectroscopy in predicting nitrogen, phosphorus and calcium contents in heterogeneous woody plant species. *Analytical and Bioanalytical Chemistry*, **382**, 458-465.

Prada, M.A. & Arizpe, D. (2008) *Manual de propagación de árboles y arbustos de ribera, Una ayuda para la restauración de riberas en la región mediterránea*. Generalitat Valenciana, Valencia, Spain.

Pujol, J.A., Calvo, J.F. & Ramírez-Díaz, L. (2001) Seed germination, growth, and osmotic adjustment in response to NaCl in a rare succulent halophyte from southeastern Spain. *Wetlands*, **21**, 256-264.

Qu, X.-X., Huang, Z.-Y., Baskin, J.M. & Baskin, C.C. (2008) Effect of temperature, light and salinity on seed germination and radicle growth of the geographically widespread halophyte shrub Halocnemum strobilaceum. *Annals of Botany,* **101**, 293–9.

Reich, P.B. & Oleksyn, J. (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 11001-11006.

Reich, P.B., Wright, I.J. & Lusk, C.H. (2007) Predicting leaf physiology from simple plant and climate attributes: a global GLOPNET analysis. *Ecological Applications*, **17**, 1982-1988.

Rodríguez-Pérez, J., Riera, N. & Traveset, A. (2005) Effect of seed passage through birds and lizards on emergence rate of Mediterranean species: differences between natural and controlled conditions. *Functional Ecology*, **19**, 699-706.

Royal Botanic Gardens Kew (2014) *Seed Information Database (SID)*. Version 7.1. Available from: http://data.kew.org/sid/

Ruíz de la Torre, J. (1984). *Árboles y arbustos de España*. Salvat Editores, Barcelona, Spain.

Ruíz de la Torre, J. (2006) *Flora mayor*. Dirección general para la biodiversidad. Ministerio de Medio Ambiente, Madrid, Spain.

Sack, L. (2004) Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation?. *Oikos*, **107**, 110-127.

Sack, L., Grubb, P.J. & Marañón, T. (2003) The functional morphology of juvenile plants tolerant of strong summer drought in shaded forest understories in southern Spain. *Plant Ecology*, **168**, 139-163.

Schweitzer, J.A., Martinsen, G.D. & Whitham, T.G. (2002) Cottonwood hybrids gain fitness traits of both parents: a mechanism for their long-term persistence?. *American Journal of Botany*, **89**, 981-990.

Silva, J.S. & Rego, F.C. (2004) Root to shoot relationships in Mediterranean woody plants from Central Portugal. *Biologia*, **59**, 1-7.

Silva, J.S., Rego, F.C. & Martins-Loução, M.A. (2003) Root distribution of Mediterranean woody plants. Introducing a new empirical model. *Plant Biosystems*, **137**, 63-72.

Stock, W.D. & Verboom, G.A. (2012) Phylogenetic ecology of foliar N and P concentrations and N : P ratios across Mediterranean-type ecosystems. *Global Ecology and Biogeography*, **21**, 1147–1156.

USDA, NRCS. (2015) *The PLANTS Database* (http://plants.usda.gov). National Plant Data Team, Greensboro, North Carolina, USA.

Villar, R., Ruíz-Robleto, J., Quero, J.L., Poorter, H., Valladares, F. & Marañón, T. (2004) Tasas de crecimiento en especies leñosas: aspectos funcionales e implicaciones ecológicas. *Ecología del bosque mediterráneo en un mundo cambiante* (ed Valladares, F.), pp. 191-227. Ministerio de Medio Ambiente, EGRAF, S.A., Madrid, Spain.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., *et al*. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821-827.

Appendix 4.2. Spatial patterns of the Mediterranean Reference Criteria (MRC) and the taxonomic (species richness), functional (functional redundancy) and quality (riparian quality index) indices.

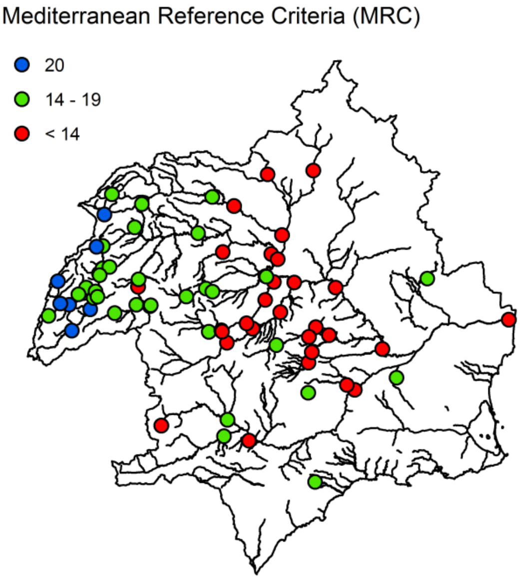


Fig. S4.2.1. MRC values for the river reaches sorted by three categories of human disturbance: Undisturbed (U, MRC=20 criteria), Moderately Disturbed (MD, MRC within 14-19 criteria) and Highly Disturbed sites (HD, MRC<14 criteria).

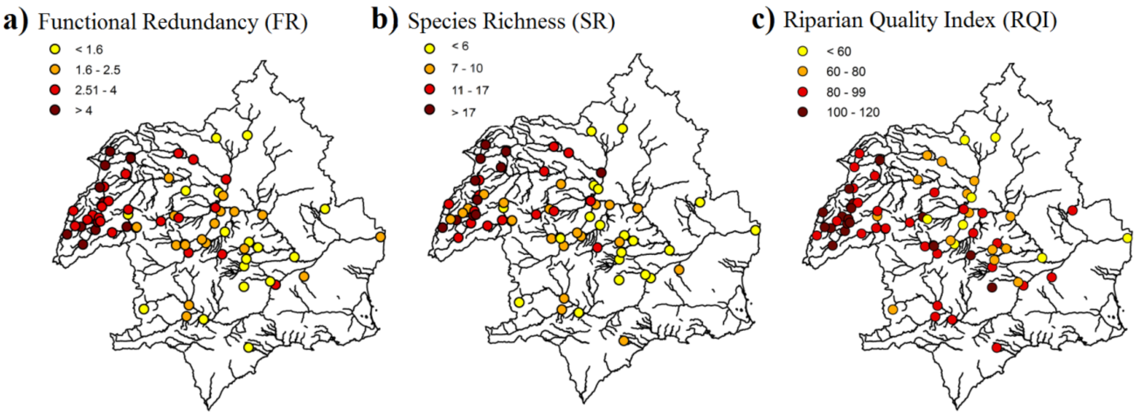


Fig. S4.2.2. Values of the functional, taxonomic and quality indices obtained for each sampling site, classified by quartiles: a) FR, b) SR, or ecological status categories: c) RQI.

General Conclusions

Hydropower dam in the Zumeta river (Jaén)

Chapter 1

1. Riparian woody and herbaceous communities showed a progressive longitudinal change in species composition and richness from headwater streams to lowland reaches, following the strong environmental and anthropogenic longitudinal gradient. Theses gradients were clearer for woody than for herbaceous species. Headwaters were the most favourable areas for riparian species due to the absence of anthropogenic pressures and milder environmental conditions.

2. Variables related with hydrogeomorphology and land use, especially agriculture, were the most important ones in explaining species composition and richness distribution of riparian species in the Segura basin.

3. Given the notable congruence in the composition and species richness patterns of both groups and in the main types of variables explaining them, a global approach considering both groups jointly or even selecting only one of them could be suitable when studying Mediterranean riparian communities.

Chapter 2

4. Human pressures negatively influenced both riparian and aquatic communities, regardless of the spatial scale considered (basin or reach), the nature of the human pressure (agriculture or hydromorphological alteration) or the type of indicator used (ecological condition or biodiversity).

5. In general, agriculture seemed to be the most important disturbance for riparian woody plants, whereas hydromorphological alteration showed a clearer relationship to aquatic macroinvertebrates.

6. Human pressures acting at basin scale had an effect at least comparable to or even greater than those operating at local scale.

7. Ecological condition indices (RQI and IBMWP) resulted more sensitive to human pressures than biodiversity ones (riparian and water beetles taxonomic richness).

8. Land use and hydrological planning at basin scale are essential complements to conservation and restoration efforts, traditionally carried out at reach scale, in order to maintain stream ecosystem integrity and biodiversity.

Chapter 3

9. Functional Redundancy of Mediterranean riparian communities showed a non-random reduction in response to increased individual and multiple stressors, meaning that increased stress could jeopardise stability, resistance and resilience of these systems.

10. Although both Functional Redundancy and all functional diversity measures (i.e. Functional Richness, Evenness and Divergence) responded similarly to environmental filters, Functional Redundancy proved to be more sensible than the other functional diversity measures.

11. Functional Redundancy can be considered as an ecologically-sound measure, providing additional and complementary information to taxonomic richness on how biological communities respond to stress.

12. The response of Functional Redundancy can be predicted from large-scale geographic variables for entire river networks, constituting a useful potential tool for biomonitoring and environmental management.

Chapter 4

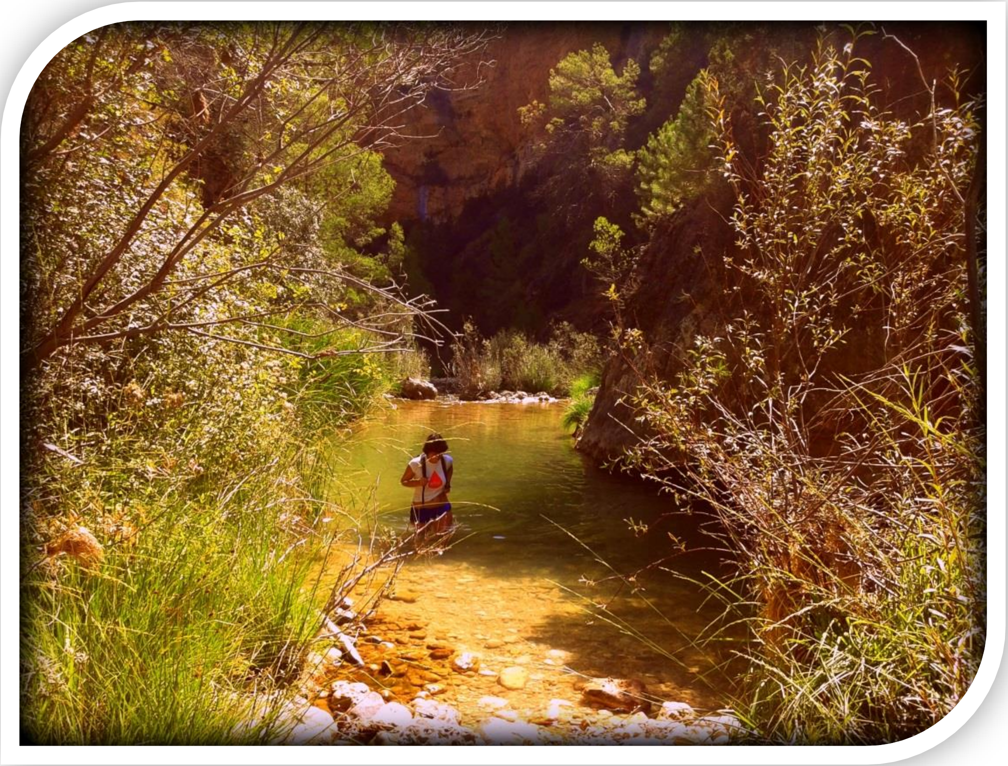
13. Functional Redundancy shows clear advantages over traditional biomonitoring taxonomic (Species Richness) and ecological status (Riparian Quality Index) indices. More concretely, FR has a clear response to single and multiple stressors and high sensitivity to detect early signs of human impact in both perennial and intermittent river reaches.

14. A map showing the human impact on riparian Functional Redundancy can be obtained for entire river network based on predicted values and the thresholds defined for perennial and intermittent rivers. This can assist decision-makers in setting goals and designing strategies for conservation and restoration at wide scale.

15. Functional Redundancy can be used as indicator to assess and predict the impact of natural (drought duration) and anthropogenic stressors (flow regulation and agriculture) on riparian communities. It could be incorporated as a complementary tool in a multi-metric bioassessment context considering various ecological aspects such as diversity, functionality and quality of riparian ecosystems, allowing a better assessment and prediction of ecosystem responses to environmental changes.

Acknowledgements

(Agradecimientos)



Upper sector of Tús river (Albacete)

En la realización de esta tesis doctoral han participado directa o indirectamente tantas personas y lugares que ya adelanto que va a ser difícil no dejarme algún agradecimiento en el tintero, no por ello menos merecido ni menos sentido que los que a continuación menciono.

No sería justo empezar esta sección sin agradecer a mis padres, Diego y María Julia por su infinita fe en mí, su cariño y apoyo incondicional y por transmitirme su amor por la naturaleza. Sin esos viajes y excursiones de parque natural en parque natural y el espíritu de superación y lucha que me habéis inculcado, esta tesis no habría sucedido. A mi hermano Javi por su gran y noble corazón y ser compañero de aventuras a lo largo de los años que espero continuemos con mayor intensidad si cabe (con la incorporación de Xena en estos últimos años). A mi yaya Primitiva, sin duda una segunda madre para mí, gracias por la educación y cariño que me has dado durante toda mi formación como persona e investigador; este éxito es también tuyo. A mis abuelos, padrino, madrina, tíos, tías, primos, primas y sus familias por tantos buenos momentos que hemos pasado juntos entre risas, comidas, calistradas, canciones y celebraciones, ¡gracias por estar ahí!

A mi segunda casa, el Departamento de Ecología e Hidrología de la Universidad de Murcia, por haberme permitido formar parte del mismo, aprender e iniciarme como investigador. Concretamente, a Pepa y Andrés por su confianza e introducirme en el fascinante mundo de la investigación en general, y la ecología acuática en particular. Os doy las gracias no solo por vuestro asesoramiento científico, sino también por vuestra calidad humana y apoyo personal en momentos difíciles. El ambiente sano (no siempre fácil de encontrar en un mundo tan competitivo) y el equipo maravilloso e inigualable de los que os habéis rodeado no son casualidad. Una pieza clave y precursor del mismo ha sido y es David, que ha hecho posible que esta tesis vea la luz a través de su omnipresente ayuda y asesoramiento estando siempre ahí para lo que fuera necesario. Eres un ejemplo a seguir personal y profesionalmente.

Dentro de este equipo de Ecología Acuática especial mención a Pedro Abellán por hacer posible que las personas que hemos llegado después tuviéramos ya mucho hecho. Qué decir de mis compadres, Tano, Félix, Simone,

Carbo, Óscar, Paula, Susana, Maridol, Piedad, Laura y María. No tengo palabras chicos, sois cojonudos. Mi vida estos años no habría sido igual sin vosotros. Por el bien de la ciencia y la sociedad española, espero que este país no os deje escapar. Si lo hace, no tengo duda de que tendréis éxito allá donde vayáis. Y si todo falla, siempre nos tendremos ahí los unos a los otros para embarcarnos en las aventuras que hagan falta. ¡Ecoaqua rules! Me gustaría también destacar a gente que ha dejado huella en el grupo como Vanessa, Nat, Lázaro, Javi y Carlos por crear ese ambiente tan bueno en el laboratorio.

Aunque previamente mencionados, merecen un agradecimiento especial mis infatigables compañeros de muestreo Óscar Belmar, José A. Carbonell y Simone Guareschi, juntos hemos conocido y vivido lugares y experiencias inigualables. Tano y Félix (junto a Elena), por haberme abierto las puertas de la Ecomandanga de par en par y hacerme partícipe de tan bonito e interesante proyecto.

Quiero hacer extensible mi agradecimiento a todos los profesores y personal del departamento de Ecología e Hidrología con los que he compartido muestreos, clases, seminarios, consejos, comidas y mucho más. Muchas gracias a todos, en especial a Zapati, Pablo, Mario, Paqui, Vicente, Pereñíguez, Rubén, Marisa, Delphine, Javi, María, Ilu, Vicky, Gabi, Rosa, Juan, Pepa, Chari y Charton.

A Maria Teresa Ferreira y Christer Nilsson por abrirme las puertas de sus grupos de investigación en mis estancias en Lisboa y Umeå, respectivamente. Quiero agradecer a todas aquellas personas que me facilitaron dichas estancias. Así me gustaría dar las gracias a Paulo Branco, Maria Rosario Fernandes, Pedro Segurado, José Maria Santos, Francisca Aguiar, António Albuquerque, Maria Dolores Bejarano, Álvaro Sordo, Liga Liepa, Micael Jonsson, Juddith Sitters, Daniela Figueroa, Lenka Kuglerová, Lina Polvi y Anouschka Hof. Mención especial para el *dream team* ibérico que dominaba la vida social lisboeta en aquellos tiempos. Gracias Pablo, Itxaso, Naira, Lucía, Isa, Ramón, Ruka y compañía por hacer de esta estancia una experiencia personal irrepetible.

A los compañeros de AJIUM (Asociación de Jóvenes Investigadores de la Universidad de Murcia) por su labor desinteresada en defensa de los jóvenes investigadores. En particular a David Verdiell, María, Lucía, Carlos, Elvira, Fátima, Gala, Ana, Mª Ángeles y resto de buena gente, así como a Pepe Carrasco por su inestimable colaboración, además de los ecólogos ya mencionados en párrafos anteriores. Juntos, somos más fuertes.

A todas las personas que generosamente me han ayudado a identificar especies y ayudado a descubrir la diversidad fluvial de la Cuenca del Segura. Muchas gracias a Pedro Sánchez Gómez, Segundo Ríos y Félix Picazo. Agradecer también la aportación de datos ambientales por parte de la Confederación Hidrográfica del Segura, Instituto Geográfico Nacional e Instituto Geológico y Minero de España, así como a Cayetano Gutiérrez-Cánovas y Núria Bonada por sus comentarios constructivos sobre algunos de los artículos en los que se basa esta tesis.

Agradecer a María del Mar Sánchez Montoya, Rossano Bolpagni y Virginia Garófano por prestarse a revisar la tesis.

A Melissa Crim, Javier Lloret, Antonio Aledo y María Sánchez Tornel por revisar el inglés de diversas partes de la tesis.

A los referees anónimos que han revisado y mejorado de manera altruista parte del trabajo aquí presentado porque sin ellos y pese a las editoriales, la ciencia no avanzaría.

A mis compañeros de la Confederación Hidrográfica del Segura, Universidad, ANSE, Comunidad Autónoma, Ayuntamientos de Cieza y Calasparra integrantes del proyecto europeo LIFE+ RIPISILVANATURA de restauración de riberas por su buen hacer e ilusión y darme la oportunidad de formar parte del equipo.

A los grandes compañeros de piso (o casi) y andanzas murcianas que he tenido a lo largo de estos años en Murcia y con los que he compartido y comparto parte de la que dicen es la mejor fase de la vida: Fany, Lojo, Chiwi, Sara, Mara, Eddy, Miñi, Pai, Hauribor, Mike, Emilie, Juanlu, Fran, Pablo, Puro, Willy, Barbas, Fer, Almu, Emma, Baldo, Adri y mucha gente más.

No puedo olvidarme de mis amigos, los que siempre están ahí, por el tiempo robado y la atención no prestada. En especial a mi equipo cartagenero y miembros de la TPT, entre ellos, Alen, Arzur, Bea, Carol, Chasis, Goyo, Largo, Marta, Piti, Pollo, Raquel, Ruru, Sergio y resto de *people*. Dicen que los 30 son los nuevos 20, así que esto acaba de empezar chicos (pese a la plaga de envejecimientos prematuros que está asolando el grupo).

Finalmente, a ti, Ana, mi compañera de este viaje que es la vida. Echo la vista atrás, y ha sido todo tan intenso que parece que fue ayer cuando empezamos a compartir vivencias. Qué alegría haberte encontrado en un océano tan grande. La vida a tu lado, sabe mejor. De hecho me ha permitido conocer a la maravillosa gente que te rodea (Domingo, Manolo, Ana, Pedro, Vero, Lara, Acen, Maite, Yiya, Gonzalo, Inesica y todos los demás) y que ya considero como míos. ¡Por todas las aventuras y desventuras que hemos vivido y quedan por vivir!

Para concluir, agradecer a la FJI y a todos los que luchan y alzan la voz contra el actual desmantelamiento del sistema público de investigación español porque aunque ello pueda parecer tiempo perdido en un mundo tan extremadamente competitivo como el científico, es importante recordar que:

"Sin ciencia, no hay futuro"


FACU


rom Murcia