UNIVERSITAT DE BARCELONA

Towards a more sustainable management of temporary rivers:

Tools for improving their conservation, biomonitoring and social recognition

Maria Soria Extremera

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Maria Soria Extremera
2021

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Soria, M. Towards a more sustainable management of temporary rivers: tools for improving their conservation, biomonitoring and social recognition. PhD Thesis. Universitat de Barcelona, Barcelona. Spain.

Covers pictures: Núria Cid and Masaru Emoto’s study.

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UNIVERSITAT DE BARCELONA

Department Department of Evolutionary Biology, Ecology and Environmental Sciences
Doctoral program in Ecology, Environmental Sciences and Plant Physiology

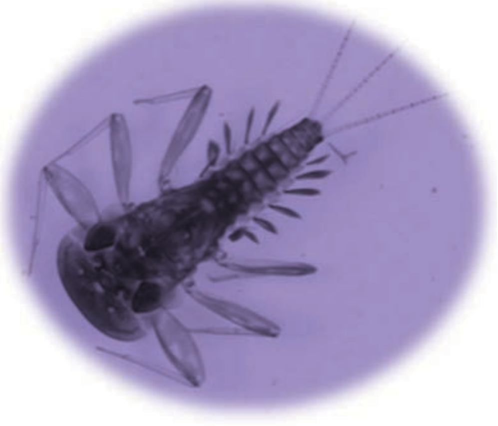
Towards a more sustainable management of temporary rivers:
tools for improving their conservation, biomonitoring and social recognition

Dissertation presented by Maria Soria Extremera to apply for the doctoral degree by the University of Barcelona

Maria Soria Extremera
Barcelona, 2020

Advisor and tutor:
Dr. Núria Bonada Caparrós
University of Barcelona

Advisor:
Dr. Núria Cid Puey
University of Barcelona



A la família i amistats d'arreu del món,

us estimo!

Vino del pueblo la abuela.

Compró una planta,

y la puso de adorno

sobre la alacena.

La planta era carnívora

¡y se nos comió la cena!

El regalo de la abuela (Gloria Fuentes)

... què faríem sense el caliu de les àvies!

AGRAÏMENTS

En primer lloc desitjo expressar el meu agraïment a les dues magnífiques directores d'aquesta tesi doctoral – Dra. Núria Bonada i Dra. Núria Cid –, per la dedicació, suport, direcció i rigor que m’han ofert al llarg d’aquests anys i que han fet possible tirar endavant aquesta tesi. Gràcies per la confiança oferta des que vaig arribar al grup de recerca. Així mateix, agraeixo als meus companys i companyes del grup de recerca FEHM, amb qui he compartit projectes i il·lusions durant aquests anys. Gràcies pel suport personal i rialles compartides al llarg d’aquests anys! Em venen al cap moments surrealistes en congressos, menjant fruita “pocha” amb la Bibi i en Bibo, o mostrejant rius als Pirineus patint pels ossos bojos, per dir-ne alguns, merci! A més, un treball de recerca és sempre fruit d'idees, projectes i esforços previs que corresponen a altres persones, així que vull agrair també a totes aquelles persones que han passat pel grup de recerca al llarg dels anys.

Quería agradecer a toda la gente del centro de investigación EULA de la Universidad de Concepción (Chile), y en especial al Dr. Ricardo Figueroa, la oportunidad de haber podido realizar diversas estadías y descubrir así ríos temporales de un país con tanta biodiversidad como es Chile. Por todas las experiencias increíbles vividas durante las cuatro estadías en Chile, como el día a día tomando once con mi familia adoptiva, muestreando empanadas (y de paso los ríos cercanos), escalando roca con el Pacífico a tocar (literalmente) los pies, (re)mirando Friends, realizando yoga, tomando cervecitas, aprendiendo algunos de los hartos chilenismos, desde los clásicos “chicotea los caracoles” o “mueve la callana”, o incluso bailando la cueca (y muriendo de vergüenza, obvio!)… gracias! A ver si en breve llega la quinta!

A todas as pessoas que tive o prazer de conhecer em Goiânia (Brasil), por todos os sorrisos compartilhados no laboratório, nas viagens, tomando uma cerveja ou fazendo pão de queijo ou brigadeiros: muito obrigada! E especialmente agradecer ao Dr. Luis Mauricio Bini e Dr. Jean Ortega por sua orientação, atenção e paciência às minhas dúvidas sobre metodologia.

I would like to thank Dr. Catherine Leigh, Dr. Thibault Datry and Dr. Rachel Stubbington for giving me the chance to work at both IRBAS and SMIRES projects.

Per acabar, vull recalcar que aquesta tesi és també fruit del suport vital de la família i amistats, sense el qual no tindria la força i energia que m’anima a créixer com a persona i com a professional. No sé ni per on començar a agrair-vos que formeu part del meu dia a dia (i em fa molta vergonya explicar aquí les mil i una aventures...), així que GRÀCIES DE TOT COR, US ESTIMO!

ADVISORS' REPORT

Dr. Núria Bonada Caparrós, Serra Húnter Associate Professor in the Department of Evolutionary Biology, Ecology and Environmental Sciences (Ecology section), at the University of Barcelona, and Dr. Núria Cid Puey, researcher at the EcoFlows lab from the "Institut national de recherche pour l'agriculture, l'alimentation et l'environnement (INRAE)" in Lyon (France) and collaborator with the Department of Evolutionary Biology, Ecology and Environmental Sciences (Ecology section), as supervisors of the Doctoral Thesis presented by Maria Soria Extremera entitled: Towards a more sustainable management of temporary rivers: tools for improving their conservation, biomonitoring and social recognition.

INFORM, that the research studies developed by Maria Soria Extremera for her Doctoral Thesis have been organized in four chapters, which correspond to four scientific papers, two already published, one under review and the last in preparation (to be sent in the next months).

And CERTIFY, that Maria Soria Extremera has actively participated on the development of the research and has lead each paper. In particular, her contribution included the following tasks: setting the objectives, conceiving and performing the analyses, handling and analysing the results and writing the manuscripts and the subsequent revisions.
Finally, we certify that the co-authors of the papers that conforms this Doctoral Thesis, will not use any of the manuscripts in other Doctoral Thesis.

Barcelona, 14th December 2020

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List and publication status of the chapters of this thesis

The list of the published chapters, indicating the Journal Impact Factor according to SCI of ISI Web of Science are:

Chapter 1: Soria, M.[1,2,3], Leigh, C.[4], Datry, T.[5], Bini, L. M.[6], Bonada, N.[1,2] (2017). Biodiversity in perennial and intermittent rivers: A meta-analysis. Oikos, 126, 1078–1089. DOI: 10.1111/oik.04118. Impact factor in 2017: 3.74 (Q1 in Ecology).

Chapter 2: Soria, M.[1,2,3], Cid, N.[1,2,7], Ortega, J.[8], Bini, L.M.[6], Acosta, R.[1], Gutiérrez-Cánovas, C.[1,2,9], Rodríguez-Lozano, P.[1,10], Fortuño, P.[1,2], Vinyoles, D.[1,2], Gallart, F.[1,3], Prat, N.[1], Bonada, N.[1,2] Contribution of intermittent rivers to beta diversity can inform freshwater conservation in the Mediterranean region (in preparation).

Chapter 3: Soria, M.[1,2,3], Gutiérrez-Cánovas, C.[1,2,9], Bonada, N.[1,2], Acosta, R.[1], Rodríguez-Lozano, P.[1,10], Fortuño, P.[1], Burgazzi, G.[11], Vinyoles, D.[1,2], Gallart, F.[1,3], Latron, J.[1,3], Llorens, P.[1,3], Prat, N.[1], Cid, N.[1,2,8] (2020). Natural disturbances can produce misleading bioassessment results: Identifying metrics to detect anthropogenic impacts in intermittent rivers. Journal of Applied Ecology, 57(2), 283–295. DOI: 10.1111/1365-2664.13538. Impact factor in 2019: 5.84 (Q1 in Ecology).

Chapter 4: Soria, M.[1,2,3], Bonada, N.[1,2], Ballester, A.[12], Verkaik, I.[1], Jordà-Capdevila, D.13, Solà, C.[14], Munné, A.[14], Jiménez-Argudo, S.[15], Fortuño, P.[1], Gallart, F.[1,3], Vinyoles, D.[1,2], Llorens, P.[1,3], Latron, J.[1,3], Estrela, T.[15], Prat, N.[1], Cid, N.[1,2,8] Adapting participatory processes in river management: insights from temporary rivers. Environmental Science and Policy (accepted the 20th August 2020 subject to major revisions). Impact factor in 2019: 4.767 (Q1 in Geography, Planning and Development; Q1 in Management, Monitoring, Policy and Law).

In addition, Maria Soria Extremera has participated in the preparation of other manuscripts related to her thesis:

Gallart, F.[3], Cid, N.[1,2,8], Latron, J.[1,3], Llorens, P.[1,3], Bonada, N.[1,2], Jeuffroy, J.[16], Jiménez-Argudo, S.[15], Vega, R.[15], Solà, C.[14], **Soria, M.**[1,2,3], Bardina, M.[14], Hernández-Casahuga, A.[17], Fidalgo A.[15], Estrela, T.[15], Munné, A.[14], Prat, N.[1] (2017). TREHS: An open-access software tool for investigating and evaluating temporary river regimes as a first step for their ecological status assessment. Science of The Total Environment, 607–608, 519–540. DOI: 10.1016/j.scitotenv.2017.06.209. Impact factor in 2017: 4.99 (Q1 in Environmental Chemistry).

Bonada, N.[1,2], Cañedo-Argüelles, M.[1,18], Gallart, F.[1,3], von Schiller, D.[18,19], Fortuño, P.[1], Latron, J.[1,3], Llorens, P.[1,3], Múrria, C.1,2, **Soria, M.**[1,2], Vintoles, D.[1,2], Cid, N.[1,2,8] (2020). Conservation and management of isolated pools in temporary rivers. Water, 12(10), 2870. DOI: 10.3390/w12102870. Impact factor in 2019: 2.544 (Q2 in Water

Science and Technology; Q2 in Aquatic Science; Q1 in Geography, Planning and Development).

Soria, M.[1,2,3], Cid, N.[1,2,8], Gutiérrez-Cánovas, C.[1,2,9], Fortuño, P.[1], Gallart, F.[1,3], Solà, C.[14], Jiménez-Argudo, S. M.[15], Munné, A.[14], Estrela, T.[15], Jorda-Capdevila, D.[13], Verkaik, I.[1], Acosta, R.[1], Prat, N.[1], Latron, J.[1,3], Llorens, P.[1,3], Bonada, N.[1,2] Lead author of the chapter: Soria, M. Tittle of the chapter: Metodologías para el estudio y evaluación del estado de los ríos temporales. Final version already submitted in May 2019. To be published next 1st october 2020.

Burfeid-Castellanos, A.[1,20], Gutiérrez-Cánovas, C.[1,9], **Soria, M.**[1,2,3], Rodríguez-Lozano, P.[1,10], Fortuño, P.[1], Cambra, J.[1], Gallart, F.[1,3], Prat, N.[1], Cid, N.[1,2,7]. Functional metrics of diatom communities as a novel approach for detecting anthropogenic impacts in intermittent rivers (in preparation).

Besides the scientific papers, the results of this Doctoral Thesis have been presented at several international and national conferences. Chapter 1 was presented as an oral presentation at the XVIII Congress of the Iberian Association of Limnology or AIL (July 2016, Tortosa, Spain), and as a poster presentation at the Interdisciplinary Meeting of Predoctoral Researchers or JIPI (February 2016, Barcelona, Spain) and at the 1st Iberoamerican Congress of Limnology or CIL (November 2016, Valdivia, Chile). Note that the CIL congress has been possible thanks to funding from AIL association. Chapter 3 was presented as an oral presentation at the 10 Symposium for European Freshwater Sciences or SEFS10 (2nd-7th July 2017, Olomuc, Czech Republic); at Annual Meeting of the Society for Freshwater Science or SFS (19-24th May 2018, Detroit, USA) and at the Science and Management of Intermittent Rivers and Ephemeral Streams (SMIRES) WG3-4 joint workshop (5-6th November 2019, Nitra, Slovakia). It was also presented as a poster at the final meeting of SMIRES (4-5th February 2020, Tirana, Albania) and at the Temporary Rivers & Streams Meeting (23rd June 2020, online). Note that SMIRES' meetings have been possible thanks to funding from the COST Action organisation.

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Funding sources of this Doctoral Thesis

Part of the work presented in this thesis has been funded by the EU project LIFE+ TRivers called "Implementing the Water Framework Directive to temporary rivers: tools for the assessment of their ecological status" (LIFE13 ENV/ES/000341). Other project related to this thesis have been the "Intermittent River Biodiversity Analysis and Synthesis–IRBAS" funded by the Centre for the Synthesis and Analysis of Biodiversity (CESAB).

In addition, this thesis has been awarded with three grants for short-term internships in two research centers, one in Chile and the other in Brasil. The first and third internship were at the EULA research center in University of Concepción (Chile), under the supervision of Dr. Ricardo de Figueroa. They were conducted from October to November 2016 and from January to May 2019, respectively. The second internship was at the Ecology Department of the Environmental Science Institute in the Federal University of Goiás (Brasil) from July to September 2018, under the supervision of Dr. Luis Mauricio Bini.

CONTENTS

ABSTRACT

Temporary rivers (TRs) are dynamic systems that typically shift between flowing, disconnected-pools and dry phases, and represent nearly 50% of the current global river network. Despite TRs support several unique and endemic aquatic and terrestrial biota, their conservation and management are still in their infancy compared to perennial rivers. Moreover, in most cases, society seems to hold these rivers in low esteem and they are often associated to environmental degradation. Considering that many perennial rivers are expected to become TRs due to global change, this thesis aims to offer new insights of how conservation and management efforts may best be directed in these ecosystems. Specifically, this thesis aimed to provide an overview on biodiversity in TRs (Chapter 1 and 2), and on how most recent approaches from a research and societal point of view can contribute to their conservation and management (Chapters 2, 3 and 4). This thesis was mainly focused on rivers in the Mediterranean Basin, where TRs constitute one of the predominant freshwater ecosystems.

Biodiversity was overall significantly higher in perennial than in TRs worldwide (Chapter 1). Moreover, our findings suggested that if perennial rivers shift to TRs, biodiversity losses may be more important for certain taxonomic groups and under particular environmental conditions. When looking at biodiversity in rivers in the Mediterranean Basin, our results showed that both taxonomic and functional richness were significantly higher in perennial rivers than in TRs (Chapter 2). However, local site contributions to taxonomic and functional β diversity (LCBD) were higher in TRs, especially during the disconnected pools phase, indicating a higher degree of ecological uniqueness of these ecosystems in terms of both species and traits composition. From a management point of view, this thesis showed that current bioassessment methods can produce misleading results when applied to TRs. In contrast, we found that functional metrics were able to detect anthropogenic impacts regardless of natural flow intermittence (Chapter 3). Finally, the thesis also emphasised the implication of citizens into the research, conservation and management of TRs. Involving citizens in the different steps of river conservation and management plans, helped to raise awareness on the biodiversity and ecological value of TRs and to promote stakeholders’ engagement (Chapter 4).

Future advances on TR’s conservation and management should (1) consider different components (alpha, beta and gamma) and dimensions (taxonomic and functional) of biodiversity, (2) consider the spatiotemporal variability of biodiversity in conservation management and especially the contribution of TRs in regional biodiversity, (3) develop new metrics to better assess the ecological status of TRs, especially in those less-studied but highly diverse phases, such as disconnected pools, and (4) involve citizens in the different steps of the current conservation and management approaches to promote a coordinated scientific and societal response to future environmental scenarios in TRs. Since Mediterranean-climate regions are considered a global biodiversity hotspot, this thesis contributes to improve and complement current conservation and management practices to halt freshwater biodiversity loss in this region.

RESUM

Els rius temporals (RTs) són sistemes dinàmics que normalment canvien entre les fases de flux, basses desconnectades i llit sec del riu, i representen gairebé el 50% de la xarxa fluvial mundial actual. Tot i que els RTs sustenten una diversitat d'espècies terrestres i aquàtiques úniques i endèmiques, la conservació i maneig d'aquests ecosistemes encara està en una fase molt inicial en comparació amb la dels rius permanents. A més, en la majoria dels casos, la societat sembla tenir en baixa estima a aquests rius i, sovint, s'associen a una degradació ambiental. Tenint en compte que s'espera que molts rius permanents es converteixin en RTs a causa del canvi global, aquesta tesi té com a objectiu oferir nous coneixements sobre com dirigir els esforços de conservació i gestió en aquests ecosistemes. En concret, aquesta tesi centra els seus esforços a proporcionar una visió general de la biodiversitat dels RTs (Capítols 1 i 2), així com a oferir nous enfocaments sobre com la recerca i la societat poden contribuir a la seva conservació i maneig (Capítols 2, 3 i 4). El camp d'estudi d'aquesta tesi se situa, principalment, en els rius de la conca mediterrània, on els RTs predominen entre els ecosistemes d'aigua dolça.

En aquesta tesi observem com, a nivell mundial, la biodiversitat és significativament major en els rius permanents que en els RTs (Capítol 1). A més, considerant que en els escenaris futurs s'espera que els rius permanents canviïn a RTs, les nostres troballes suggereixen que les pèrdues de biodiversitat poden ser més importants per a certs grups taxonòmics i sota condicions ambientals particulars. Quan ens focalitzem en la biodiversitat dels rius de la conca mediterrània, els nostres resultats mostren que tant la riquesa taxonòmica com funcional són significativament més altes en els rius permanents que en els RTs (Capítol 2). No obstant això, segons els nostres resultats, els RTs contribueixen més a la diversitat β funcional i taxonòmica (LCBD), especialment durant la fase de basses desconnectades, fet que indica un major grau de singularitat ecològica d'aquests ecosistemes en termes de composició d'espècies i trets biològics. Des del punt de vista de la gestió, aquesta tesi mostra que els mètodes d'avaluació actuals poden produir resultats poc fiables quan s'apliquen als RTs. En contrast, aquesta tesi ofereix un conjunt de mètriques funcionals que podrien ser capaces de detectar impactes antròpics independentment de la intermitència natural del flux (Capítol 3). Finalment, aquesta tesi posa de manifest la importància de la implicació de la ciutadania en la recerca, conservació i maneig dels RTs. A més, involucrar a la ciutadania en els diferents passos dels plans de gestió i conservació de conques sembla ajudar a crear consciència sobre la biodiversitat i el valor ecològic dels RTs, així com a promoure la participació de les parts interessades (Capítol 4).

Segons els resultats obtinguts, els futurs avanços en la conservació i gestió dels RTs haurien de (1) considerar diferents components (alfa, beta i gamma) i dimensions (taxonòmiques i funcionals) de la biodiversitat, (2) considerar la variabilitat espacio-temporal de la biodiversitat en la gestió de la conservació i, especialment, la contribució dels RTs a la biodiversitat regional, (3) desenvolupar noves mètriques per a avaluar millor l'estat ecològic dels RTs, especialment en aquelles fases menys estudiades però molt diverses, com són les basses desconnectades, i (4) involucrar a la ciutadania en els diferents passos de la conservació i gestió actuals per a promoure així una resposta científica i social concorde als futurs escenaris ambientals que s'esperen. Finalment, atès que les regions de clima mediterrani es consideren *hotspot* de biodiversitat mundial, aquesta tesi pretén contribuir a millorar i complementar les pràctiques actuals de conservació i gestió per a reduir la pèrdua de biodiversitat d'aigua dolça en aquesta regió.

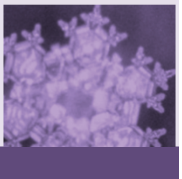
RESUMEN

Los ríos temporales (RTs) son sistemas dinámicos que normalmente cambian entre las fases de flujo, pozas desconectadas y cauce seco del río, y representan casi el 50% de la red fluvial mundial actual. A pesar que los RTs sustentan una diversidad de especies terrestres y acuáticas únicas y endémicas, la conservación y manejo de estos ecosistemas aún está en una fase muy inicial en comparación con la de los ríos permanentes. Además, en la mayoría de los casos, la sociedad parece tener en baja estima a estos ríos y, a menudo, se asocian a una degradación ambiental. Teniendo en cuenta que se espera que muchos ríos permanentes se conviertan en RTs debido al cambio global, esta tesis tiene como objetivo ofrecer nuevos conocimientos sobre cómo dirigir los esfuerzos de conservación y gestión en estos ecosistemas. Específicamente, esta tesis centra sus esfuerzos en proporcionar una visión general de la biodiversidad en los RTs (Capítulos 1 y 2), así como en ofrecer nuevos enfoques sobre cómo la investigación y la sociedad pueden contribuir a su conservación y manejo (Capítulos 2, 3 y 4). El campo de estudio de esta tesis se ubica, principalmente, en los ríos de la cuenca mediterránea, donde los RTs predominan entre los ecosistemas de agua dulce.

En esta tesis observamos como, a nivel mundial, la biodiversidad es significativamente mayor en los ríos permanentes que en los RTs (Capítulo 1). Además, considerando que en los escenarios futuros se espera que los ríos permanentes cambien a RTs, nuestros hallazgos sugieren que las pérdidas de biodiversidad pueden ser más importantes para ciertos grupos taxonómicos y bajo condiciones ambientales particulares. Cuando nos focalizamos en la biodiversidad de los ríos de la cuenca mediterránea, nuestros resultados muestran que tanto la riqueza taxonómica como funcional son significativamente más altas en los ríos permanentes que en los RTs (Capítulo 2). Sin embargo, según nuestros resultados, los RTs contribuyen más a la diversidad β funcional y taxonómica (LCBD), especialmente durante la fase de pozas desconectadas, lo que indica un mayor grado de singularidad ecológica de estos ecosistemas en términos de composición de especies y rasgos biológicos. Desde el punto de vista de la gestión, esta tesis muestra que los métodos de evaluación actuales pueden producir resultados poco fiables cuando se aplican a los RTs. En contraste, esta tesis ofrece un conjunto de métricas funcionales que podrían ser capaces de detectar impactos antrópicos independientemente de la intermitencia natural del flujo (Capítulo 3). Finalmente, esta tesis pone de manifiesto la importancia de la implicación de la ciudadanía en la investigación, conservación y manejo de los RTs. Además, involucrar a la ciudadanía en los diferentes pasos de los planes de gestión y conservación de cuencas parece ayudar a crear conciencia sobre la biodiversidad y el valor ecológico de los RTs, así como a promover la participación de las partes interesadas (Capítulo 4).

Según los resultados obtenidos, los futuros avances en la conservación y gestión de los RTs deberían (1) considerar diferentes componentes (alfa, beta y gamma) y dimensiones (taxonómicas y funcionales) de la biodiversidad, (2) considerar la variabilidad espacio-temporal de la biodiversidad en la gestión de la conservación y, especialmente, la contribución de los RTs a la biodiversidad regional, (3) desarrollar nuevas métricas para evaluar mejor el estado ecológico de los RTs, especialmente en aquellas fases menos estudiadas pero muy diversas, como son las pozas desconectadas, e (4) involucrar a la ciudadanía en los diferentes pasos de la conservación y gestión actuales para promover así una respuesta científica y social acorde a los futuros escenarios ambientales que se esperan. Finalmente, dado que las regiones de clima mediterráneo se consideran *hotspot* de biodiversidad mundial, esta tesis pretende contribuir a mejorar y complementar las prácticas actuales de conservación y gestión para reducir la pérdida de biodiversidad de agua dulce en esta región.

GENERAL INTRODUCTION



GENERAL INTRODUCTION

GENERAL CHARACTERISTICS OF TEMPORARY RIVERS

Temporary rivers (TRs) are those in which surface flow ceases at some point in time and space (Acuña et al. 2014; Datry et al. 2014a,b; Leigh et al. 2016a,b). TRs are frequent freshwater ecosystems which are present in several climatic regions worldwide (Jacobsen 2004; Larned et al. 2010). Indeed, they have acquired popular names in different languages, such as boulevards, streams, ravines, winterbournes, wadis or oueds, among others (Datry et al. 2017a). In regions with Mediterranean (Box 1) or arid climates, TRs constitute one of the predominant freshwater ecosystems (Bonada et al. 2008; Bonada and Resh 2013; Datry et al. 2017a).

BOX 1: Mediterranean-climate rivers

are five Mediterranean-climate regions worldwide that occupy vast areas in
alia, California, South Africa, Chile and the Mediterranean Basin. Rivers in these
ns are called Mediterranean-climate rivers and there is a significant predominance
s. They are characterized by being highly seasonal and predictable, which has
ered many adaptations to resist and recover from drying conditions (Bonada et al.
a,b; Bonada and Resh 2013). Mediterranean-climate rivers are ecologically unique
ada et al. 2007a,b; Figueroa et al. 2013), but are also one of the most threaten
stems worldwide, receiving a wide variety of direct and indirect anthropogenic
cts, such as agriculture, industrial practices, human population growth or invasions
ien species (IPCC 2014; Cid et al. 2017). In fact, freshwater biodiversity in
terranean-climate rivers is declining faster than anywhere in the world (Bonada and
2013). Future scenarios in these regions predict an exacerbation of drought
tions and an increase of floods events (Döll and Schmied 2012; IPCC 2014), which
affect freshwater biodiversity, ecosystem functions and services.

The number of studies in TRs has increased in the past decades, allowing a better understanding of their hydrology and ecology which, in turn, has initiated the interest of specific conservation, biomonitoring, and/or restoration actions in these ecosystems (Leigh et al. 2016; Datry et al. 2017b). For instance, Gallart et al. (2012) defined six aquatic states to better identify the changing hydrological conditions and the available habitats in TRs over time: *Hiperrheic, Eurrheic, Oligorrheic, Arrheic, Hiporrheic* and *Edaphic* (see Fig. 1 for terms' definitions).

At the same time, challenges and limitations for TRs' bioassessment have become evident too, especially due to their high hydrological variability in both space and time (Leigh et al. 2016; Fritz et al. 2017). In this regard, several studies have classified TRs into typologies according to their flow permanence and predictability (Uys and O'Keeffe 1997; Williams 2006; Gallart et al. 2012), but there is still no consensus due to the high variability of these two factors (Datry et al. 2017a).

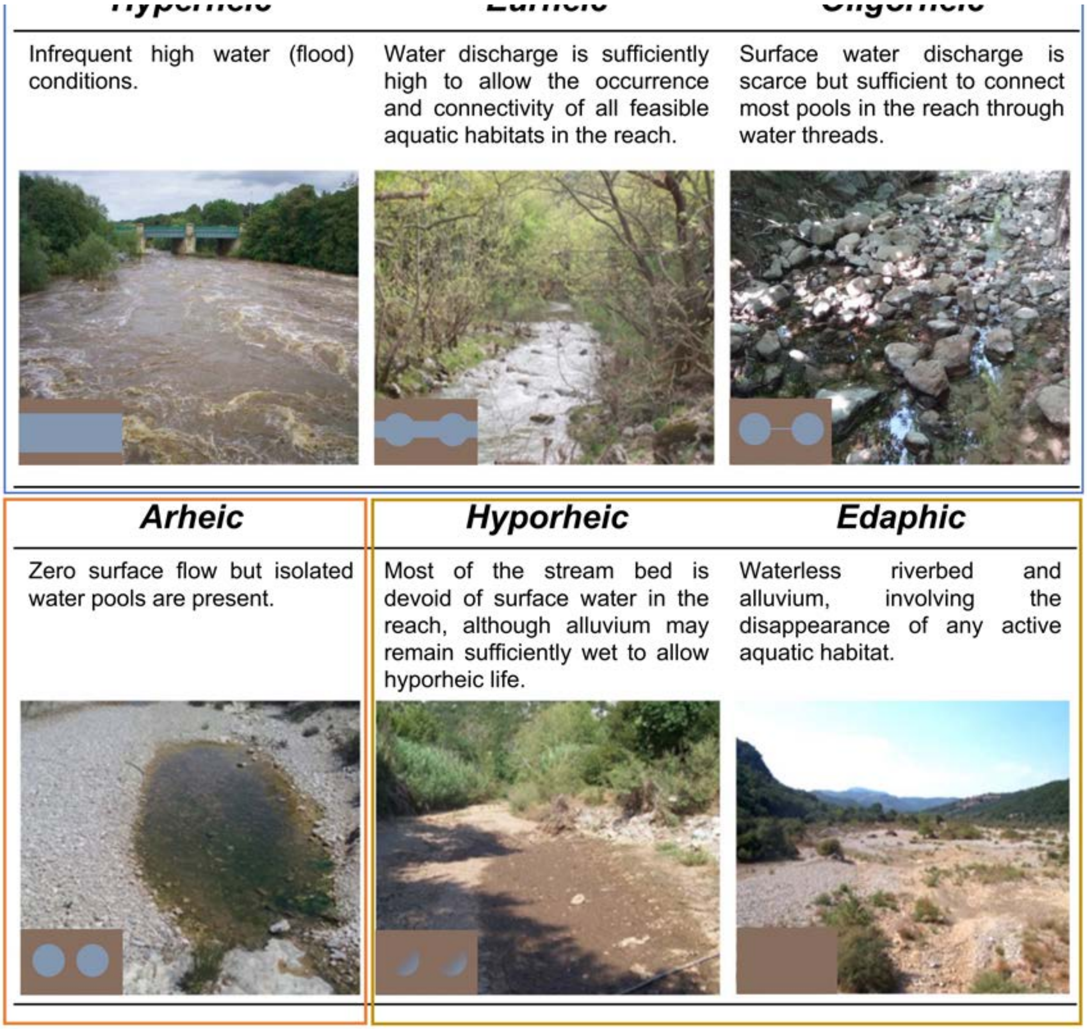


Figure 1. Six aquatic states of TRs defined by Gallart et al. (2012) and the simplification in three phases: flowing (blue), disconnected pools (orange) and dry (brown) phases. Modified from Bonada et al. (2020).

Here we consider TRs as ecosystems that typically shift among flowing, disconnected pools and dry phases (Fig.1) over space and time (Gallart et al. 2012, 2017). By taking this definition, TRs can be classified as: (1) intermittent-pools (IP), intermittent-dry (ID) and ephemeral (E) rivers (Fig. 2). IP are rivers in which flow permanence disappears during the dry season (summer) but disconnected pools always remain (Gallart et al. 2012, 2017). Instead, ID are those rivers where the riverbed dries up completely, although they can maintain subsurface water (Gallart et al. 2012, 2017).

Rivers that remain dry most of the time with a dry riverbed, without subsurface water, and that only carry water after rain events are referred as E (Gallart et al. 2012, 2017). In the last years, the term IRES (Intermittent Rivers and Ephemeral Streams) have been popularised (Datry et al. 2017a). Here we consider IRES as a synonym of TRs, and refer only to intermittent rivers (IRs) when considering TRs without E rivers (i.e. only IP and ID rivers).

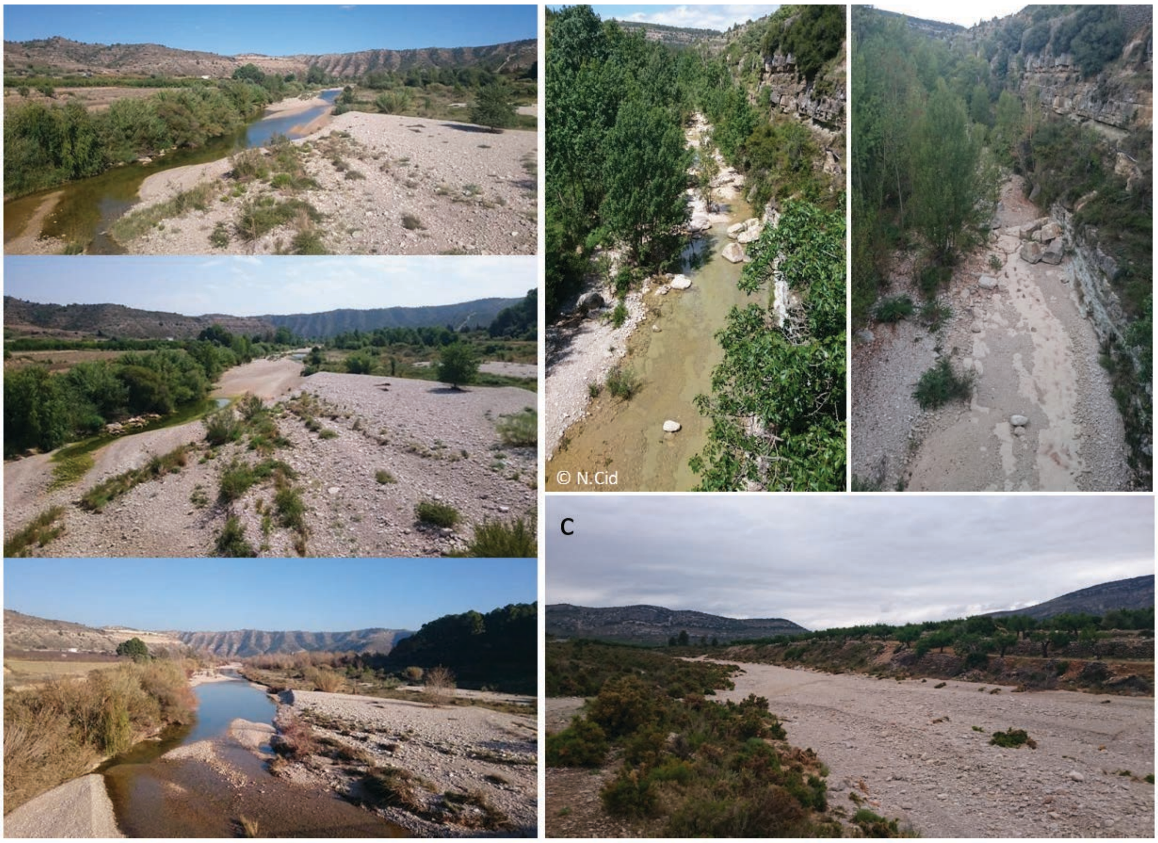


Figure 2. Examples of TRs changes over time, being (a) an intermittent river with disconnected pools (IP), (b) a dry intermittent river (ID), and (c) an ephemeral river (E). Photos: N. Cid.

TRs are also important for human wellbeing. During the flowing phase, they provide the ecosystem services typical of perennial rivers, such as freshwater, fishing and hunting products, recreation, recharging aquifers, purifying water or processing nutrients and organic matter (Postel and Carpenter 1997; Datry et al. 2017b; Koundouri et al. 2017). During the isolated pools and drying phases they still provide some of these services in the same or different form (Datry et al. 2017b; Koundouri et al. 2017). However, TRs’ ecosystem services are still rarely recognized (Boulton et al. 2014; Koundouri et al. 2017). This may be due to the low value that society places on their ecosystems services or because some threats to TRs' ecosystem services (e.g., carbon storage or release, biodiversity) are poorly documented (Datry et al. 2017b). Either way, future efforts to better understand the socioeconomic value of their ecosystem services should increase.

A great number and variety of TRs with a wide range of flow patterns occur globally, and their management is inevitably complex, involving not only environmental challenges but also socio-economic aspects (Kingsford et al. 2017). The complex and highly natural dynamic character of TRs calls for the development of adapted tools and methods for their adequate management. Nevertheless, given the predicted consequences of global change, assessment methods and management practices of these ecosystems should consider the interaction of both natural disturbances and anthropogenic impacts.

NATURAL FLOW INTERMITTENCE VS ANTHROPOGENIC IMPACTS

Ecosystems experience natural disturbances (e.g. droughts, floods or wildfires) and anthropogenic impacts (e.g. pollution, land-use changes, climate change) that affect biological communities and ecological processes (Olden et al. 2004; Dornelas 2010). Compared to natural disturbances, however, anthropogenic impacts are relatively new (<10.000 year) and may represent novel conditions for biota, threatening the stability of both biodiversity and ecosystem functioning (Olden et al. 2004).

In naturally drying TRs, flow intermittence can be considered a natural disturbance, since it has acted through evolutionary time and has resulted in species adapted to such abiotic stress (Lytle and Poff 2004; Bowman et al. 2009). Nevertheless, TRs are often also subjected to anthropogenic impacts (Chiu et al. 2017). In fact, TRs face the same anthropogenic impacts as perennial rivers, such as water extractions, geomorphology alterations and/or changes in water quality (Fig. 3) (Chiu et al. 2017). Unlike perennial rivers, however, TRs' hydrological variability often accentuates the effects of these impacts by reducing their dilution capacity (Gómez et al. 2017). TRs can also suffer extractions of aggregates and sediments (Fig. 3) or be used as passageways when the riverbed remains dry for long periods (Chiu et al. 2017). In addition, several TRs are actually perennial rivers subjected to water withdrawals for agriculture or urban uses (Datry et al. 2014a,b; Chiu et al. 2017). At the same time, some perennial rivers are actually TRs that have been "perennialized" resulting from sewage effluents or runoff from irrigation waters (Luthy et al. 2015; Chiu et al. 2017). These alterations of flow regimes may not only affect TRs' biodiversity and ecosystem functioning but result in serious declines in the provision of crucial ecosystem services (Boulton et al. 2014; Koundouri et al. 2017).

Figure 3. Examples of a TR suffering geomorphological alterations due to (a) extractions of aggregates and sediments and agriculture or (b,c) canalizations and water extractions. Photos: N. Cid and N.Bonada.

Climate change is expected to increase the frequency of droughts and to reduce mean annual discharge worldwide, altering the timing, frequency and intensity of flow intermittence in TRs (Datry et al. 2014a,b). As a result, anthropogenic impacts may either dampen differences in biodiversity between TRs and perennial rivers by homogenizing communities, or the effects in TRs' biota can be even higher than in perennial rivers because the reduction in the dilution capacity in TRs (Acuña et al. 2014; Boulton 2014). Despite the increase in scientific research in TRs, most studies on the effects of anthropogenic impacts are still focused on perennial rivers (Leigh et al. 2016a,b). In the case of TRs, a better understanding of the joint effects of flow intermittence and anthropogenic impacts on biological communities is required.

MANAGEMENT AND CONSERVATION OF TRs

Despite TRs hold unique species composition (Cid et al. 2017; Stubbington et al. 2017), these ecosystems are still among the most underprotected and poorly managed freshwater ecosystems worldwide (Leigh et al. 2019). A better management and conservation of TRs is therefore required. However, TRs are usually eluded by flow gauging networks (Gallart et al. 2016) and not always incorporated or adequately assessed in biomonitoring and conservation programs (Sanchez-Montoya et al. 2007, 2011; Stubbington et al., 2018). In fact, current bioassessment tools that can be applied in TRs are practically non-existent compared to those for perennial rivers (Datry et al. 2017a,b; Fritz et al. 2017).

Aside from improving bioassessment tools for TRs, the involvement of local citizens can result in a powerful tool for a complete understanding of their hydrological characteristics. Moreover, active participation of society is required to promote changes in legislation so that management and conservation of these ecosystems became truly effective (Leigh et al. 2016a,b; Conallin et al. 2018; Rodríguez-Lozano et al. 2020). Therefore, incorporating TRs in participatory processes is key to improve their current management. For the adequate management and conservation of TRs, it would be thus truly useful to (1) acquire a better understanding of TRs' biodiversity patterns; (2) obtain bioassessment tools capable of differentiating anthropogenic impacts from natural flow intermittence; and (3) incorporate TRs in participatory processes to promote changes in legislation.

Understanding TRs' biodiversity patterns for improving their conservation

For aquatic biological communities inhabiting TRs (e.g. algae, macrophytes, macroinvertebrates or fish), temporal and spatial changes in mesohabitats due to loss or resumption of surface flow can lead to diversity changes in species composition (Bonada and Resh 2013; Romaní et al. 2017; Stubbington et al. 2017). Loss of surface flow in TRs might imply the disappearance of species adapted to riffle habitats, but also the appearance of species that can be found exclusively in pool habitats (Fig. 4) (Bonada et al. 2006a, 2020 ; Bogan et al. 2017; Tonkin et al. 2017).

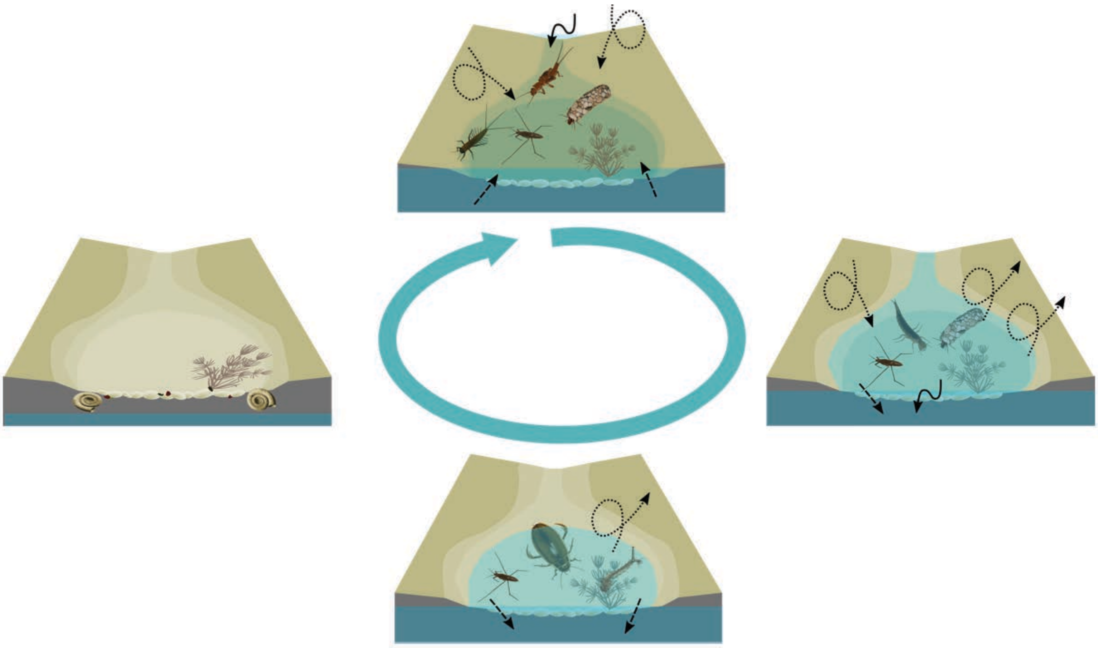


Figure 4. Changes in aquatic communities with loss and resumption of surface flow in TRs. Black arrows represent organisms that arrive or leave, either by waterway (solid line), airway (dashed line), or those that recolonize by using resistance forms to or in the hyporheic zone (segmented line). Picture from P. Fortuño.

When loss of surface flow occurs, some organisms are unable to persist in the absence of water (Bogan et al. 2017). Instead, other organisms present adaptations (i.e. biological traits) to cope with it, such as emerging and completing their life cycle in the terrestrial ecosystem, migrating to other pools or to the hyporheic zone, or activating resistance forms that allow them to remain dormant in the riverbed until flow resumption (Fig. 4) (Bonada and Resh 2013; Bogan et al. 2017). Flow resumption is another key moment for biological communities, as species re-colonize TRs and communities reorganize again (Fig. 4) (Bonada et al. 2006a, 2020).

Loss and resumption of surface flow affect the structure and function of biological communities in TRs (Bonada et al. 2007a,b; Stubbington et al. 2017). Drying events act primarily as a disturbance decreasing aquatic biodiversity in TRs and, consequently, some studies found that TRs are less diverse compared to perennial rivers, where these events do not occur (Del Rosario and Resh 2000; Bogan et al. 2013). However, other studies found the opposite (Bonada et al. 2007a,b; Alexandre et al. 2013) or no difference between TRs and perennial rivers (Santos and Stevenson 2011). For instance, TRs in Mediterranean climates hold unique species composition due to their predictable flow regimes (Bonada et al. 2006; Munné and Prat 2011; Cid et al. 2017) and, thus, higher biodiversity values might be expected in these ecosystems when comparing to perennial rivers. The debate remains, thus, over whether TRs are more or less diverse than perennial rivers (Datry et al. 2011; Leigh et al. 2016a).

In addition, biodiversity differences between perennial and TRs might vary depending on environmental factors, such as climate, season, mesohabitat or longitudinal zonation. From here arises the **first chapter of the thesis,** which aims at determining whether perennial and TRs diversity differs considering also these environmental factors.

As biological communities in TRs change from flowing to drying periods, and different drying spatial patterns might be present along river networks (e.g. some networks have temporary reaches in headwaters, others in the lowlands; Datry et al. 2016a,b), a better knowledge on their spatiotemporal biodiversity patterns is required for the development of effective conservation strategies (Fig. 5). Most strategies for river conservation are currently focused on protecting the number of species within a site (taxonomic alpha diversity; α) or in a region (taxonomic gamma diversity; γ), while the variation in species composition (taxonomic beta diversity; β) is dismissed (Ruhí et al. 2017). The inclusion of β diversity in conservation strategies can contribute to the efficient selection of protected areas, the management of biological invasions or the design of wildlife-friendly landscapes (Hill et al. 2016; Socolar et al. 2016).

Protecting only taxonomic diversity, either α, β or γ, however, might provide limited insight into the impacts of disturbance on ecosystem functioning (White et al. 2018). In this context, the inclusion of functional diversity patterns to explore conservation strategies in rivers have recently increased (e.g. Villéger et al. 2013, 2017; Guitiérrez-Cánovas et al. 2015, 2019). Functional diversity connect taxonomic diversity to ecosystem functions provided by a community and, thus, refers to the biological traits possessed by taxa of this community (Mouillot et al. 2013; Villéger et al. 2013). This might be useful to clarify the resistance and/or resilience of species to environmental changes, either natural or anthropogenic. Understanding how both taxonomic and functional diversities influence ecosystem functioning, thus, is crucial to better predict the ecological consequences of biodiversity loss (Hooper et al. 2005; Flynn et al. 2011).

In this sense, the use of both taxonomic and functional β diversity, in combination with α diversity, is key. For example, they may help explaining whether communities are becoming more similar (i.e. biotic homogenisation) or what are the implications for ecosystem functioning (Hill et al. 2016; Socolar et al. 2016). Nevertheless, little is known about the processes underlying β diversity dynamics over time (i.e. temporal β diversity), hindering its incorporation into management decision-making.

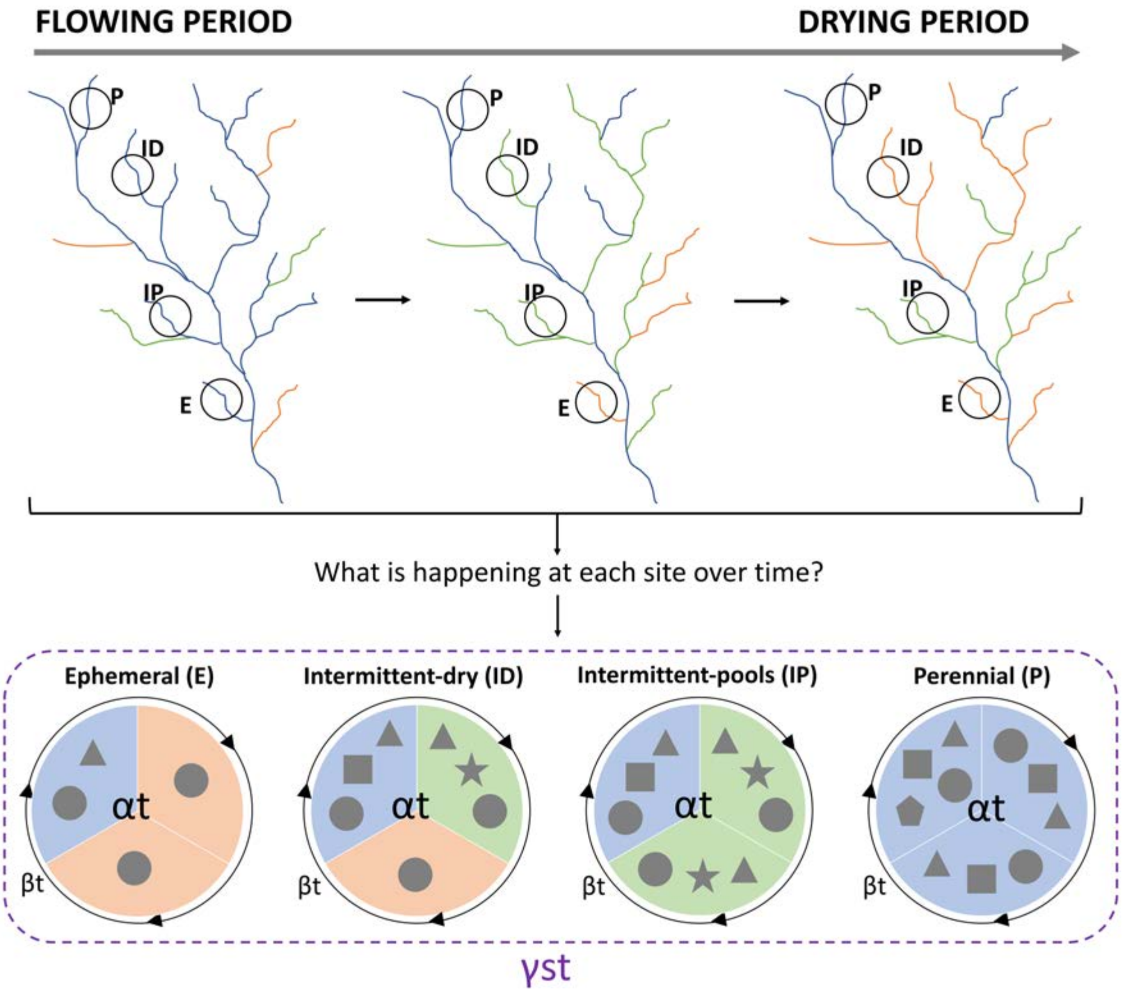


Figure 5. Spatiotemporal α, β and γ community diversity expected in Mediterranean rivers' networks including perennial rivers and different types of TRs: intermittent-pools (IP), intermittent-dry (ID) and ephemeral (E) rivers. Flowing (blue), disconnected pools (green) and dry riverbed (orange) phases. Shapes represent taxa present at each aquatic phase. During flowing and disconnected pools phases shapes represent aquatic taxa, whereas during the dry phase, they represent terrestrial taxa. Temporal α and β diversity: αt and βt, respectively. Spatiotemporal γ diversity: γst.

Despite there has been an increase of research on temporal taxonomic β diversity in TRs (e.g. Ruhí et al. 2017; Sarremejane et al. 2017; Stubbington et al. 2019b), studies of spatial β diversity still predominate. In addition, temporal dynamics remains even less quantified when applied in functional β diversity (but see Crabot et al. 2020; Sánchez-Montoya et al. 2020), which hinders to understand TRs' biodiversity variation in space and time. From here arises the **second chapter of the thesis**, which aims at analysing the contribution of TRs' aquatic macroinvertebrates to taxonomic and functional spatiotemporal β diversity from a conservation perspective in Mediterranean-climate rivers. Mediterranean-climate rivers are global biodiversity hotspots highly impaired by human impacts and, therefore, insightful and specific conservation strategies are required (Bonada and Resh 2013; Cid et al. 2017).

Biomonitoring of TRs

The ecological integrity or status in rivers is commonly determined by the assessment of the biological, chemical and physical quality (Barbour et al., 2000). Depending on the regulations of each country, measures of these three elements may differ and/or other aspects may be included. For instance, in the European Union context, the Water Framework Directive or WFD (2000/60/CE) refers to the “ecological status”, which includes the assessment of the physicochemical, hydromorphological and biological qualities (see Box 2).

BOX 2: the Water Framework Directive or WFD

WFD (2000/60/CE) aims at achieving a ‘good status’ in water bodies, which is asured in terms of chemical (i.e. concentrations of priority substances) and logical status for water bodies (Fig. 6). The WFD establishes that the assessment the ecological status must include an evaluation of the physicochemical, dromorphological and biological qualities (Fig. 6) (EC 2000).

The high hydrological variability of TRs, however, hampers the adequate essment of these ecosystems (Gómez et al. 2017; von Schiller et al. 2017). In dition, according to the guidelines of the WFD, the assessment of the ecological tus should be implemented in relation to the reference conditions established for h river type, also called ecotypes (Fig. 6) (EC 2000), which are not clear when nsidering TRs.

Beyond the water bodies diagnosis, the WFD mandates to incorporate the ticipation of stakeholders and the general public in the development and dating of the River Basin Management Plans or RBMPs (EC 2009), which cannot very attractive given that TRs are held in low consideration from a social point of w (Leigh et al. 2019).

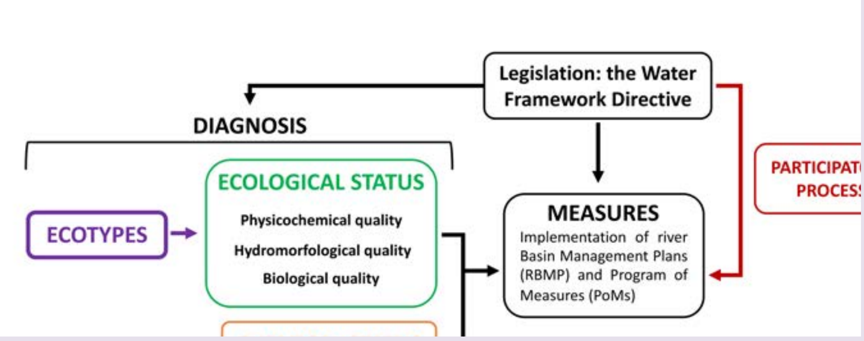


Figure 6. Outline on current factors and steps for the management and conservation of TRs within the WFD context.

Nowadays, most common tools to assess the ecological status have been developed for perennial rivers and, when applied in TRs, their reliability is generally low for both physicochemical (Gómez et al. 2017; von Schiller et al. 2017) and biological qualities (Rieradevall et al. 1999; Bonada et al. 2000; Cid et al. 2017). For the assessment of the hydromorphological quality, however, some methods have been adapted to TRs and seem to work properly. For example, this is the case of the QBR (Munné et al. 1998) and IHG (Ollero et al. 2007) hydromorphological indices, which were adapted to TRs by Suárez-Alonso and Vidal-Abarca (2000) and Ollero et al. (2011), respectively. In this context, the third and fourth chapter of this thesis have focused on methods for evaluating the biological quality of TRs, since it is one of the main current challenges in the evaluation of these ecosystems.

Typically, rivers' biological quality is assessed using metrics that compare biological communities sampled at one site with reference conditions (Hawkins et al., 2010). In TRs, however, these reference values may vary over time due to the alternation among flow-dry phases, that is, either between wet-dry periods (García-Roger et al. 2011) or years (Munné and Prat 2011). For example, studies conducted in the Mediterranean region observed that biological metrics from reference (or least disturbed) sites were highly variable (Sánchez-Montoya et al. 2010; Feio et al. 2014; Mazor et al. 2014).

Current biological metrics have been mostly developed for perennial or slightly seasonal rivers, using macroinvertebrates, aquatic flora and fish communities as biological indicators (Bonada et al. 2006b). In addition, metrics developed for the evaluation of rivers' biological quality are not only based on taxa diversity but also on their environmental tolerance. Taking into account that as flow intermittence increases, diversity decreases (Fritz and Dodds 2002; Datry et al. 2013), and that many of TRs' species are generalists with wide environmental tolerances, traditional tools may not work in these ecosystems (Prat et al. 2014). Indeed, these metrics have been calibrated to be used when water flows. Thus, when TRs are with disconnected pools or dry at the time of sampling, these metrics cannot be applied, causing many TRs remaining underassessed. In fact, even if they are applied in pristine disconnected pools, biological communities found in TRs may be significantly poorer in taxa than that in reference perennial rivers (Gallart et al. 2012). For instance, with the increase of flow intermittence, the number of taxa might decrease because taxa with greater affinity to riffle habitats, which score the best in the metrics, are lost. As time goes by, disconnected pools become colonized with species typical of these conditions, such as Odonata, Coleoptera and Heteroptera, which are rarely found in riffle habitats and have wide environmental tolerances (Boulton 2003; Bonada et al. 2006a, 2020; Cid et al. 2016). If these disconnected pools dry up, most freshwater taxa disappear. The recolonization starts just after the rewetting and the number of taxa increases with time.

Since the number of taxa and their environmental tolerances change with time in TRs, alternative methods are required for their correct assessment. Specifically, it is necessary to either calibrate current metrics or develop new ones capable of evaluating the biological quality of these ecosystems (Bruno et al. 2016a,b; Fritz et al. 2017).

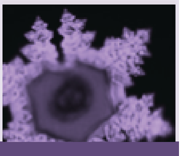
Functional metrics based on biological traits have shown to be promising tools for discriminating between multiple types of impacts and could present advantages over metrics based on taxonomy (Rosenfeld 2002; Hooper et al. 2005; Villéger et al. 2008). Among them, functional redundancy (i.e. the number of species contributing similarly to an ecosystem function) provides information on the stability, resilience and resistance of ecosystems, and seems to work better than functional diversity (Laliberté and Legendre 2010; Guillemot et al. 2011; Bruno et al. 2016a,b). Consequently, several recent studies encourage the use of metrics based on functional redundancy for TRs' biomonitoring (e.g. Gutiérrez-Cánovas et al. 2015; Bruno et al. 2016a,b; Belmar et al. 2019). From here arises the **third chapter of the thesis,** which aims at assessing the ability of traditional biomonitoring metrics and new functional ones to detect anthropogenic impacts in TRs.

PARTICIPATORY PROCESSES IN TRS MANAGEMENT

Participatory processes can help to promote a more sustainable and equitable management of water resources and engage citizens in decision-making. Effective decision-making in participatory processes, however, requires that all participants have an adequate level of knowledge about the topic addressed (Mostert et al. 2007; Moellenkamp et al. 2010; Porter and Birdi 2018). This is especially relevant in the case of TRs, as participants involved in the participatory process might not be aware of the biodiversity and ecological value of these ecosystems (Conallin et al. 2018). This lack of awareness might be partly because society holds these ecosystems in low esteem and as synonym of environmental degradation (Acuña et al. 2017; Leigh et al. 2019a). Incorporating TRs in participatory processes, thus, could contribute to increase their social recognition beyond to improve their current management. There are several participatory engagement mechanisms that can help in the effective decision-making of the process by promoting open and constructive dialogues among participants (Videira et al. 2006; Varner 2014; Mukhtarov et al. 2018). The most commonly used mechanisms are surveys, interviews, workshops and scientific dissemination (Reed 2008; Videira et al. 2006; Mostert et al. 2007), but recently some processes have also included environmental education and citizen science activities (Gray et al. 2017; Mukhtarov et al. 2018). Moreover, the ecosystem services concept has been also incorporated to increase public awareness on rivers (Grizzetti et al. 2016). For instance, several studies have incorporate the concept of ecosystem services in participatory processes of the WFD to increase public awareness on rivers and to enhance participants' engagement (Grizzetti et al. 2016; Jorda-Capdevila et al. 2016).

The WFD mandates the incorporation of stakeholders and the general public in the development and updating of the River Basin Management Plans or RBMPs using public participation (see Box 2) (EC 2009). However, as in the case of biomonitoring, the WFD implementation has been mainly focused on perennial rivers and is still rare in TRs. Considering that TRs are increasing due to global change (Döll and Schmied 2012), developing participatory processes in TRs, may help reframing and adapting current river management practices to future environmental changes. From here arises the **fourth chapter of the thesis**, which aims at reframing participatory processes in river basin management to enhance the inclusion of TRs.

OBJECTIVES



La pena llarga del
No poder mirar enre
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Saber que la mar l’espe
i no el fa córrer la n
sinó aquella aigua prime

Tan fresc és com la font e
No és vell el riu si ha arrib
És l’infant que ve can
d’abeurar joncs de ribe

(Blai Bonet i Rigo, CANÇO

OBJECTIVES

The main goal of this thesis was to contribute to the conservation and management of temporary rivers (TRs), those where surface flow ceases at some point in time and space. In the four chapters included in this thesis, the selected rivers showed a gradient of natural disturbances (flow intermittence) and anthropogenic impacts.

To obtain an overall view, in Chapter 1 we compared biodiversity between perennial and TRs worldwide considering the taxonomic groups that are usually used in management (e.g. diatoms, macroinvertebrate, fish). Instead, in Chapters 2, 3 and 4 we mainly focused on macroinvertebrates from the Mediterranean-climate region of the Iberian Peninsula. In these three chapters, we expected to contribute to TRs conservation and management by developing biomonitoring tools (Chapter 3), or testing and adapting a set of current interdisciplinary methods and approaches to improve river conservation (Chapter 2) and management (Chapters 4) (Fig. 1).

Finally, the typology of TRs used when conducting the different chapter of this thesis also varies along the thesis. In Chapters 1, 2 and 3, we excluded ephemeral rivers (E) because of lack of biological data and thus we focused on intermittent-pools (IP) and intermittent-dry (ID) rivers (hereafter referred as intermittent rivers; IRs). In chapter 4, ephemeral rivers (E) were also considered and we thus refer to TRs.

The main objectives of the four chapters of this thesis are:

- To determine whether IRs and perennial rivers biodiversity differ and whether the direction and magnitude of any difference is related to the environmental (i.e. climate, season, habitat, longitudinal zonation, anthropogenic disturbance) or biological factors (i.e. taxonomic group) hypothesised to affect biodiversity patterns in river ecosystems (**Chapter 1**).

- To analyse the contribution of IRs to the taxonomic and functional spatiotemporal β diversity of macroinvertebrates in Mediterranean-climate rivers. Specifically, spatiotemporal β diversity patterns were obtained by analysing the local contribution to β diversity of each site over time (**Chapter 2**).

- To assess the ability of biomonitoring metrics to detect anthropogenic impacts at IRs and perennial rivers, considering both flowing and disconnected pools phases of IRs. Specifically, we investigated the combined effects of natural flow intermittence (natural disturbance) and anthropogenic impacts on widely used river biomonitoring metrics (i.e. taxonomic richness and standard biological indices) and novel functional metrics based on biological traits (**Chapter 3**).

- Adapting participatory processes in river basin management to enhance the inclusion of ecosystems with low social recognition such as TRs (**Chapter 4**).

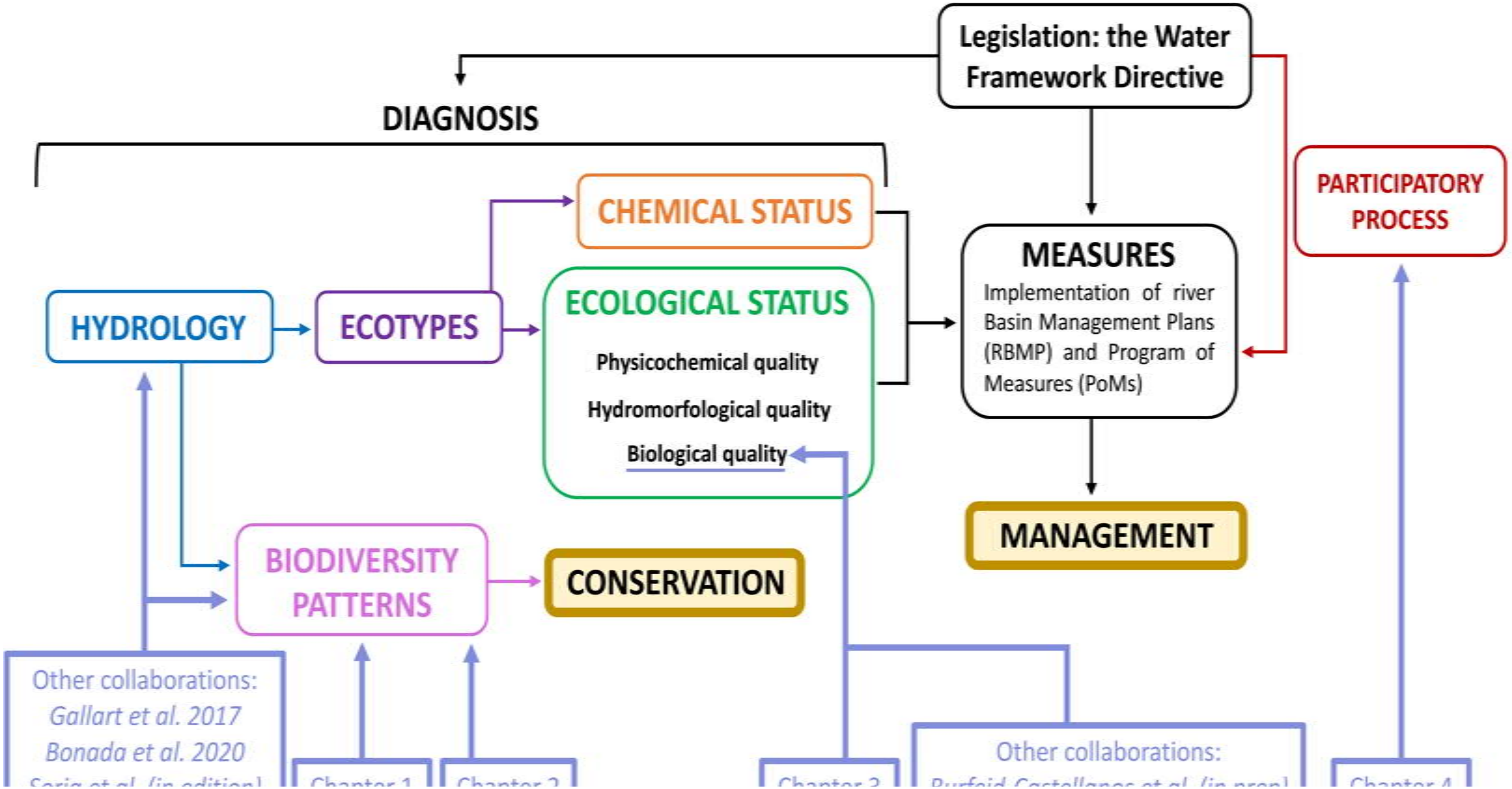
In addition to these four chapters, during my PhD I have co-authored four other manuscripts that are related to the different objectives of the thesis:

- In **Gallart et al. (2017),** we aimed at proposing updated methods for the operational monitoring, assessment and classification of the hydrological regime of temporary rivers, along with the evaluation of the degree of hydrological alteration.

- In **Bonada et al. (2020),** we aimed at providing a characterization of disconnected pools from a hydrological, geomorphological, physicochemical, biogeochemical, and biological point of view as a framework to better conceptualize, conserve, and manage these habitats.

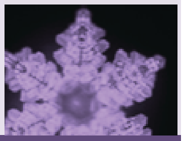
- In **Soria et al. (accepted),** we aimed at conducting a review on some of the main methods for evaluating the status of temporary rivers.

- In **Burfeid-Castellanos et al. (in preparation),** we aimed at evaluating how flow intermittence confound taxonomic and functional biomonitoring metrics for diatoms.


Legislation: the Water Framework Directive
DIAGNOSIS
PARTICIPATORY PROCESS
CHEMICAL STATUS
HYDROLOGY
ECOTYPES
ECOLOGICAL STATUS
Physicochemical quality
Hydromorfological quality
Biological quality
MEASURES
Implementation of river Basin Management Plans (RBMP) and Program of Measures (PoMs)
MANAGEMENT
BIODIVERSITY PATTERNS
CONSERVATION
Other collaborations:
Gallart et al. 2017
Bonada et al. 2020
Soria et al. (in edition)
Chapter 1
Chapter 2
Chapter 3
Other collaborations:
Burfeid-Castellanos et al. (in prep)
Chapter 4

CHAPTER 1

Biodiversity in perennial and intermittent rivers: a meta-analysis



ABSTRACT

Comprehensive knowledge of the effects of disturbances on biodiversity is crucial for conservation and management, not least because ecosystems with low biodiversity may be the most vulnerable. In rivers, the role of disturbance in shaping aquatic biodiversity has mainly focused on floods. Perennial rivers often flood, whereas intermittent rivers (IRs) flood, stop flowing and dry. Despite the recent and significant increase in research on IRs, controversy remains about whether they are more or less biodiverse than perennial rivers.

Our aim was to determine (Q1) if perennial rivers and IRs differ in biodiversity and (Q2) if the direction and magnitude of the differences (effect sizes) are related to environmental (climate, season, habitat, longitudinal zonation and anthropogenic disturbance) and/or biological factors (taxonomic group).

We conducted a meta-analysis on 44 published studies of perennial and IR biodiversity that had replicated data. We applied random effects models to the data to obtain weighted mean effect sizes for differences between perennial rivers and IRs, and their confidence intervals, by first considering all studies and then by splitting studies into groups on the basis of the above factors.

We found that biodiversity was significantly higher in PRs than in IRs (Q1). We also detected significant differences (perennial rivers > IRs) in studies of macroinvertebrates, in those conducted within arid and temperate climates, dry and wet sampling seasons, headwaters, and regions subject to different levels of anthropogenic disturbance (Q2).

Our meta-analysis suggests that the expected increase in the prevalence of IRs in certain regions of the world due to global change could result in a decrease in freshwater biodiversity. To better manage and preserve aquatic biodiversity under future global change scenarios and to avoid potential ecosystem consequences of biodiversity loss, conservation efforts should be targeted towards those environmental conditions or taxonomic groups with significant differences (perennial rivers > IRs).

INTRODUCTION

Understanding how disturbance influences biodiversity is a recurrent topic in community ecology (Pianka 1966; Huston 1979; Hughes et al. 2007). Disturbance includes a wide variety of phenomena acting at multiple temporal (e.g. from days to eons) and spatial (e.g. from local to biogeographical) scales, with multiple potential consequences for populations, communities and ecosystems (Dornelas 2010). Ecologists hypothesised many years ago that disturbance decreased biodiversity and favoured ecological succession (Clements 1916) and that intermediate levels of disturbance enhanced biodiversity (Connell 1978, but see Fox 2013). Effects of disturbance on biodiversity have been studied in many ecosystems and across multiple taxonomic groups (Horner-Devine et al. 2004; Graham et al. 2009; Barlow et al. 2016). Most studies highlight the negative effects of disturbance on biodiversity (Loreau et al. 2001; Wardle et al. 2011; Hooper et al. 2012), while only few show the contrary pattern (Thom and Seidl 2015; Brunbjerg et al. 2015). Understanding and predicting when and how biodiversity might change following disturbance is crucial for effective conservation and management (Dornelas 2010).

The role of disturbance in shaping aquatic biodiversity has focused mainly on flood and drying events (Resh et al. 1988; Giller 1996). Flood events are pulse disturbances that occur relatively quickly (Junk et al. 1989, Ward and Stanford 1995), disrupting habitat conditions and eliminating individuals (Poff et al. 1997; Lake et al. 2000). In contrast, drying events are ramp disturbances that reduce aquatic habitat and eventually result in flow cessation and/or complete loss of surface water from the streambed, and can reduce aquatic biodiversity drastically (Williams 1996; Lake et al. 2000). Floods enhance connectivity among aquatic habitats, whereas drying fragments them (Stanley et al. 1997; Boulton 2003). Although it is widely known that floods and drying events affect the structure and function of rivers (Bonada et al. 2007a; Reich and Lake 2015) and that research on drying events has significantly increased during the last decade (Leigh et al. 2016a,b), the effects of floods have been more frequently reported that those of drying events (Datry et al. 2007; Lake et al. 2007). This may be because floods occur in all river types, whereas drying events are particular to intermittent rivers (IRs), in which surface flow ceases at some point in time and space (Acuña et al. 2014; Datry et al. 2014a; Leigh et al. 2016a). In contrast, perennial rivers are characterized by continuous flow.

IRs are probably the most common fluvial ecosystems in the world (Datry et al. 2016a), and therefore drying events are probably more ubiquitous than previously thought. In addition, many perennial rivers are expected to transition to IRs in the near future as a result of global change and increased human demand for fresh water (Palmer et al. 2008; Döll and Schmied 2012), increasing the importance and relative contribution of IR ecosystems to global aquatic biodiversity. However, although research on IRs is in what has been described as a boom phase (Datry et al. 2011; Leigh et al. 2016a), debate remains over whether IRs are more or less biodiverse than PRs. Some studies find that IRs are less biodiverse (Del Rosario and Resh 2000; Storey and Quinn 2008; Bogan et al. 2013), whereas others find the opposite (Dieterich and Anderson 2000), or no difference between IR and perennial biodiversity (Miller and Golladay 1996; Casas and Langton 2008; Santos and Stevenson 2011). Clearly, a more thorough understanding and test of the biodiversity difference between perennial rivers and IRs is required.

Biodiversity between perennial rivers and IRs might differ depending on several factors. First, biodiversity in IRs can depend on how flow regime characteristics, which change among climatic zones, forge adaptations to drying (Boulton 2003; Lytle and Poff 2004). For example, the higher number of unique taxa in IRs than perennial rivers in Mediterranean climates has been related to their predictable flow regimes (Bêche et al. 2006; Munné and Prat 2011). Second, biodiversity between PRs and IRs can vary seasonally. During the wet season, when both PRs and IRs flow, their biodiversity is more likely to be similar (Delucchi 1988; García-Roger et al. 2011), whereas during the dry season, IRs will likely have lower aquatic habitat availability than perennial rivers, and thus lower aquatic biodiversity. Third, as biodiversity varies among habitats in perennial rivers and IRs (García-Roger et al. 2013), habitat type is another relevant factor to consider. Riffles in IRs might host a lower biodiversity than in perennial rivers because this habitat is the first to disappear during drying (Bonada et al. 2006a), whereas pools might show the contrary pattern if isolated pools remain in IRs during drying (Bonada et al. 2006a; Leigh and Sheldon 2009; Boersma et al. 2014). Fourth, biodiversity differences between perennial rivers and IRs may vary with longitudinal zonation. IR headwaters might have lower biodiversity than perennial headwaters because their greater isolation might hamper recolonization after drying (Finn et al. 2011; Datry et al. 2016b, c), whereas no significant landscape barriers would affect recolonization of middle reaches (of free-flowing rivers, at least). However, and fifthly, anthropogenic disturbance may dampen differences in biodiversity between perennial rivers and IRs by homogenizing and simplifying communities (Rahel 2002) regardless of flow regime, climate, habitat, season, or the taxonomic group considered. Finally, the magnitude of change between biodiversity in perennial rivers and IRs may vary depending on the taxonomic group considered (i.e. macroinvertebrates, fish, algae or macrophytes) because despite some taxa within all groups having traits of resistance and/or resilience to drying (Bonada and Resh 2013), their evolutionary history, species biodiversity and ecological tolerance varies. For example, although algae and macrophyte species are much more widespread than other freshwater groups, they have a limited set of biological adaptations to flow variation (e.g. see Lange et al. 2016 for algae in comparison to Tachet et al. 2002 for macroinvertebrates).

Here, we investigated the above hypotheses by comparing biodiversity in perennial rivers and IRs using a meta-analytic approach. Specifically, we sought to determine (Q1) whether perennial and IR biodiversity differ and (Q2) whether the direction and magnitude of any difference is related to the environmental (i.e. climate, season, habitat, longitudinal zonation, anthropogenic disturbance) or biological factors (i.e. taxonomic group) hypothesised to affect biodiversity patterns in river ecosystems. For our main question (Q1), we hypothesized that biodiversity should be lower in IRs than in perennial rivers (Fritz and Dodds 2002; Storey and Quinn 2008; Bogan et al. 2013) because IRs are subject to drying events that act primarily as a disturbance decreasing aquatic biodiversity (Leigh and Datry 2016). However, if this loss of taxa in IRs is compensated by taxa with resistance and resilience traits to cope with drying (Bonada et al. 2007b; Grubbs 2011; Vander Vorste et al. 2016), biodiversity in perennial rivers and IRs may be similar or IR biodiversity may be higher. Assessing the differences in biodiversity between perennial rivers and IRs and understanding the conditions under which those differences differ is increasingly important for predicting aquatic biodiversity changes in the face of global change.

METHODS

Data selection

We identified published studies that recorded biodiversity of perennial rivers and IRs from an ISI Web of Knowledge (<www.accesowok.fecyt.es/>) literature search considering a time span from the 1900s to the 21 of August 2014 (Leigh et al. 2016a). Leigh et al (2016a) used a comprehensive search string of multiple terms for IRs which resulted in 10 800 records and then filtered these publications using further search terms associated with key topics of research on IR ecology and management: invertebrate ecology, fish ecology, biogeochemistry and ecological and hydrological assessment. They then screened the resultant groups of records manually to ensure relevancy to the topics and IR research more generally (e.g. removing studies in the medical field), obtaining 1237 publications (see Table S2 in Leigh et al. 2016a for full details of search parameters and screening criteria).

For this study, we re-screened each of the 1237 publications to select those relevant for the meta-analysis according to the following criteria: the publication had to discuss or provide direct insight into the ecology and/or management of perennial rivers and IRs, the sampling design had to include sites which were not located along the same river (i.e. sites must be hydrologically independent), and the publication had to include means and standard deviations (SDs) of biodiversity measures (e.g. taxonomic richness, Shannon–Wiener diversity index) for each river type (perennial rivers and IRs) or enough information to calculate these values. This selection resulted in a total of 63 publications, 44 with replicated data (i.e. studies with more than one perennial and IR each from which the means and SDs were obtained) and 19 with non-replicated data (i.e. only one perennial or IR from which biodiversity data was obtained) (see Supplementary Material Appendix 1 and 2 for the full reference details of these publications). Most studies were conducted in North America, Europe and Australia. Very few studies were from Africa and Asia, and none were from South America (Fig. 1). For studies investigating biodiversity in more than one distinct region (e.g. South Africa and Australia) we derived biodiversity data separately for each region, whereas for studies which investigated multiple groups of organisms (e.g. fish, invertebrates, diatoms), we randomly chose one group only. Each of these individual investigations are referred to and counted as one study for simplicity.

Figure 1. Distribution of publications, identified from an ISI Web of Knowledge literature search by Leigh et al. (2016a), that examined biodiversity in hydrologically independent perennial and intermittent rivers (perennial rivers and IRs, respectively). White stars refer to studies with non-replicated data for perennial rivers and/or IRs (n = 19), whereas black stars refer to studies with replicated data for perennial rivers and IRs (n = 44).

We most commonly extracted means, SDs, and number of sites (n) directly, computed them from text and/or tables in the studies (27 studies), or obtained them directly from authors (26 studies). For the remaining 10 studies, we extracted data from figures using Plot Digitiser (<www.plotdigitizer.sourceforge.net/>). Where multiple measures of biodiversity (e.g. taxonomic richness, evenness, Shannon–Wiener diversity index) were available, we preferentially extracted richness data due to it being the most commonly reported measure across all studies. Only one study reported the Shannon–Wiener diversity index alone. We included both these measures (i.e. richness and the Shannon–Wiener diversity index) together in our analysis because our aim was to provide a general summary of the difference in biodiversity among groups (i.e. perennial rivers and IRs) (Scheiner and Gurevitch 2001). Then, for each individual publication, we obtained information on site or sampling characteristics. In particular, we considered the following six factors, each with several levels within: climate, sampling season, habitat, longitudinal zonation, level of anthropogenic disturbance, and taxonomic group (Table 1, Supplementary material Appendix 3). We created different subsets of data using the levels of these factors and analysed them separately.

Effect size estimate

For replicated studies (with n > 1 perennial rivers and n > 1 IRs, nPR and nIR, respectively), we obtained effect sizes using Hedge's g, which corresponds to the difference between the means of biodiversity in perennial rivers and IRs ( ) divided by the pooled standard deviation (S_{within}) and with a correction for small sample bias (J) (Rosenberg et al. 2000, Borenstein et al. 2009):

$$g = \frac{\overline{PR} - \overline{IR}}{S_{within}} J,\ S_{within} = \sqrt{\frac{(n_{PR} - 1)SD_{PR}^{2} + (n_{IR} - 1)SD_{I}^{2}}{n_{PR} + n_{IR} - 2}}$$

$$J = 1 - \frac{3}{\quad}$$

The variance of g was given by:

$$V_g = \left[\frac{n_{PR} + n_{IR}}{n_{PR} n_{IR}} + \frac{\left[\frac{\overline{PR} - \overline{IR}}{S_{within}} \right]^2}{2(n_{PR} + n_{IR})} \right] J^2$$

For non-replicated studies, where means and standard deviations were not available, we obtained effect sizes using log(PR/IR), known as the response ratio. Following Hedges et al. (1999; see also Eq. 4.30 and 4.31 in Borenstein et al. 2009), we also computed the response ratio for replicated studies for comparison with the non-replicated studies, but we did not include it in the estimation of weighted effect sizes.

Table 1. Description of the environmental and biological factors and levels within each factor, identified from individual publications and used in our meta-analysis with replicated data.

Climate	B, C, D, E, Multi	Dominant climate of each system was determined according to the Köppen classification of Peel et al. (2007), which considers 5 general climates: tropical (A), arid (B), temperate (C), cold (D), and polar (E). No studies were carried out in the tropical (A) climate and thus it is not included here. Multiple includes a combination of these climates.
Habitat	Riffles, Pools, Stones, Multiha	Multihabitat includes riffles and pools. Stones refer to rock fragments of more than 25 cm.
Longitudinal Zonation	Headwaters, Mi Multiple	Middle refers to reaches with a catchment area between 100 and 1000 km^2 or a stream order of 4-6. Large refers to a catchment area >1000km^2. Multiple includes headwaters, middle and large reaches.
Anthropogenic disturbance	Low, Medium-H	distinguishspecific types of disturbance (e.g. hydrological vs morphological). Low levels were distinguished from Medium-High levels on the basis of information available in the published studies (e.g. Low levels were assigned to sites within reserves; Medium-High to sites in urban areas). Medium and high levels of disturbance were difficult to differentiate based on information provided in studies and were thus combined .

Weighted mean effect size

We used random effects models in all cases because we assumed that the true effect sizes vary among studies (Borenstein et al. 2009). This assumption is justifiable as our meta-analysis included a wide variety of studies that, for example, investigated different organisms or were conducted using different sampling methods. Statistically, this choice of meta-analytic model consists in estimating 1) the between-studies variance (T^2; see Eq. 12.2, 12.3, 12.4 and 12.5 in Borenstein et al. 2009) and 2) the total variance ($V_i = V_g + T^2$) to 3) assign the weight of each study ($W_i = 1/V_i$). Model outputs included the weighted mean effect size (wES) and its confidence interval, and a test of the hypothesis that the true wES is zero, following standard methods described in Borenstein et al. (2009).

We estimated wES for the entire dataset (e.g. considering all replicated data in the one random effects model) and for each of the subsets of data separated by the six factors listed above (Table 1). For these subset analyses, the models were estimated without the intercept (Viechtbauer 2010). With this parameterization, a pooled value of T^2 was used, a procedure recommended by Borenstein et al. (2009) to increase the accuracy of the estimate of the between-studies variance.

We used a forest plot to illustrate the results of the meta-analysis. This plot shows the effect sizes and confidence intervals of each study and the wES (Gates 2002). A significant model (or a wES whose confidence interval does not include zero) indicates a significant difference between perennial and IR biodiversity. The magnitude of the wES indicates the amount of difference between the two river types. Here, a positive wES indicates that biodiversity in perennial rivers is higher than in IRs.

Publication bias

First, we visually assessed publication bias in the replicated studies using a funnel plot of effect size against a measure of study size or precision (e.g. the standard error of the effect size) (Sterne et al. 2011). Visually asymmetrical funnel plots usually indicate publication bias, whereas symmetrical ones indicate negligible publication bias. Second, we calculated the fail-safe number according to Orwin’s equation (Orwin 1983), which gives the number of studies needed to reduce the average effect size to a pre-specified value, which is considered unimportant. We tested a range of values (with steps of 0.2) from 0.2 to 0.8 (corresponding, approximately, to half of the unweighted mean effect size). Third, we calculated the fail-safe number according to Rosenthal’s approach (‘file drawer analysis’). This indicates the number of missing studies (i.e. those unpublished or available but not captured by the literature search and selection process) needed to be retrieved and incorporated in the analysis to eliminate bias (Borenstein et al. 2009). A high value indicates that a meta-analysis (i.e. estimated effect size) is robust to publication bias, given that we would need a large number of studies to nullify the effect size. Finally, as a sensitivity analysis, we applied the trim-and-fill method (Duval and Tweedie 2000a, b). This method estimates and adjusts meta-analysis results for the numbers and outcomes of missing studies.

We checked our meta-analysis against the quality criteria provided by Koricheva et al. (2013). We fulfilled all applicable criteria. We computed all statistics using the R ver. 3.3.1 (<www.r-project.org>) and the libraries metaphor (Viechtbauer 2010) and rmeta (Lumley 2012).

RESULTS

Overall differences between IRs and perennial rivers

The overall meta-analysis revealed a statistically significant difference in perennial and IR biodiversity (considering all replicate studies together), with a positive overall effect size (wES = 0.879, Table 2), thus indicating a significantly higher biodiversity in perennial rivers than in IRs (Fig. 2). Positive effect sizes for the individual studies ranged from 0.01 to 7.95; negative effect sizes were smaller, ranging from –1.10 to –0.04 (Fig. 2). Accordingly, heterogeneity among studies was highly significant (Q = 89.317, df = 43, p < 0.0001).

Table 2. Results of the random effects models for the overall design (with and without trim-and-fill) and for the levels of the six factors. Bold typeface indicates p = 0.005. n = number of studies considered in each level; wES = weighted mean effect size; SE = standard error of the estimates; ci.lb and ci.ub = confidence interval (lower and upper limits, respectively). See Table 1 for a description of the factors and levels.

OVERALL DESIGN		0.879	0.169	**).0001**	1.209
Climate					
	E	1.369	1.204	2556	3.729
Sampling					
	Multiple	0.719	0.222	**0012**	1.155
	Headwaters	0.988	0.263	**0002**	1.504
Longitudi zonation					
Anthropo disturban	**Medium-High**	1.016	0.293	**0005**	1.590

Log response ratios estimated for replicated (weighted mean effect size [log(PR/IR)] = 0.38 ± 0.05 SE) and non-replicated (unweighted mean effect size [log(PR/IR)] = 0.25 ± 0.08 SE) studies were also positive (Supplementary material Appendix 4). The majority of non-replicated studies had effect sizes located in the positive side of the forest plot (Supplementary material Appendix 4), again indicating that biodiversity in perennial rivers was, in most cases, higher than in IRs.

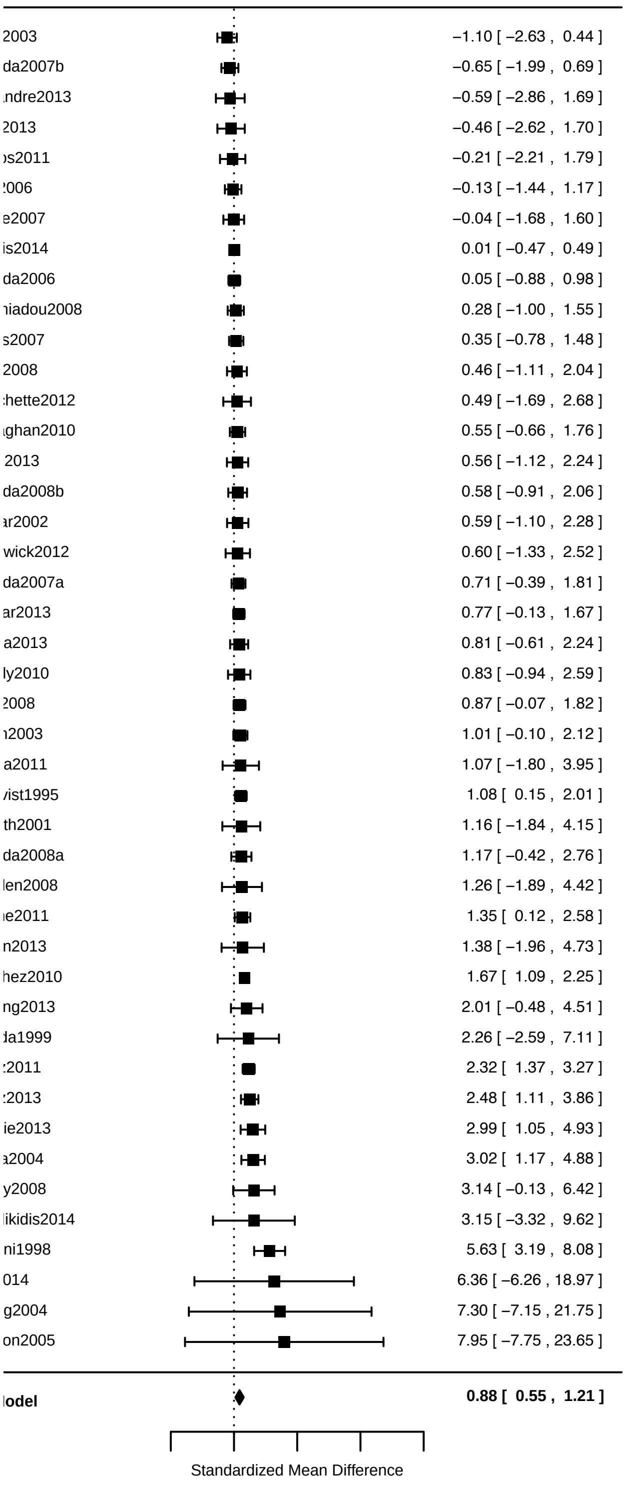


Figure 2. Forest plot for the overall design of the original model (without trim-and-fill) considering the 44 replicated studies ordered by increasing effect size from the top to the bottom. Each study is indicated in the left column with the first author and the year of publication (see Supplementary material Appendix 4 for the complete reference). Effect sizes of each study (using the standardized mean difference) with their corresponding confidence intervals are displayed in the centre of the plot with the exact values on the right. The filled diamond at the bottom shows the weighted mean effect size (wES) estimated by the model with the edges of the diamond showing the corresponding confidence interval.

Specific differences in biodiversity between IRs and perennial rivers

For most levels of the six factors, wES was significantly positive (Table 2), indicating higher biodiversity in perennial rivers than IRs. We detected differences between perennial and IR biodiversity for studies conducted within arid (B), temperate (C), cold (D) or multiple climate zones; within studies that considered dry, wet, or multiple seasons; a multi-habitat sampling regime; samples from headwaters or multiple longitudinal zones; sites subject to low and medium-high levels of anthropogenic disturbance; and that included macroinvertebrates (Table 2). We found non-significant results for polar climates (E); riffle, pool, and stone habitats; middle reaches; fish, algae and macrophytes (Table 2).

Publication bias

Although the funnel plot visually approached asymmetry (Fig. 3a), fail-safe numbers and the sensitivity analysis indicated minimal bias. According to Orwin's method, even if a substantial effect size (0.8) is conservatively assumed as unimportant, a large number of unpublished studies would still be needed (Orwin's fail safe N = 38 studies) with no differences between the types of rivers for the estimated effect size to be reduced to an 'unimportant' value. As expected, this number increases substantially when lower effect sizes (i.e. 0.6, 0.4 and 0.2) are used in Orwin's equation (Orwin's fail safe N = 67, 124 and 295, respectively)

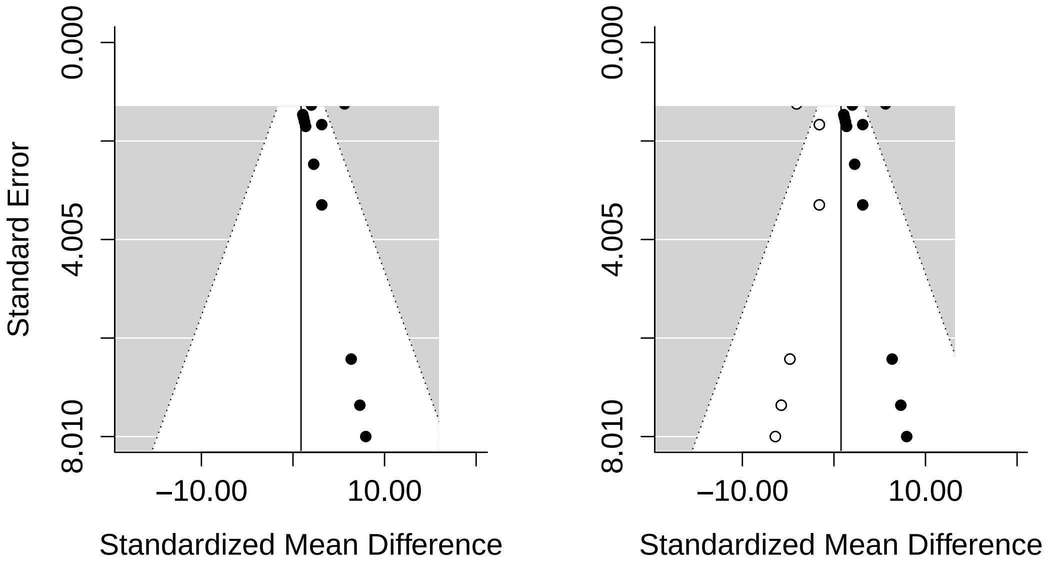


Figure 3. Funnel plots for the overall design using replicated studies without and with trim-and-fill, (a) and (b) panels, respectively. Filled circles represent the individual replicated studies, whereas open circles represent the missing studies required to produce a symmetrical plot.

According to Rosenthal’s approach, the fail-safe number was 1352, suggesting that a large number of studies with non-significant differences between types of rivers would be needed to reverse the conclusion that PRs were more biodiverse than IRs. According to the trim and fill approach, only six studies were potentially missing from our analysis that if present would produce a symmetrical funnel plot (Fig. 3b). The wES estimated by this method was similar to the one reported above (trim and fill wES = 0.776 ± 0.178; 95% CI = 0.427 to 1.125).

DISCUSSION

The studies analysed here compared biodiversity in perennial rivers and IRs across a wide range of environmental conditions. We found a significantly higher biodiversity in perennial rivers than in IRs, which confirmed our primary hypothesis. This finding agrees with individual studies showing that perennial rivers are more species-rich than IRs and that flow intermittence is a disturbance that constrains aquatic biodiversity (Del Rosario and Resh 2000; Storey and Quinn 2008; Bogan et al. 2013). However, several individual studies included in our meta-analysis found similar values of biodiversity in perennial rivers and IRs; in these cases, the characteristic taxa found in IRs during the dry period compensated for the loss of taxa present during flow (Miller and Golladay 1996; Casas and Langton 2008; Santos and Stevenson 2011). Few of the studies analysed here had higher biodiversity in IRs than in perennial rivers (Price et al. 2003; Bonada et al. 2007a, Alexandre et al. 2013). The persistence of isolated pools during the dry season in IRs, which favours the presence of a wide variety of species found exclusively in lentic waters and/or that prefer such habitat, may have increased IR biodiversity in these cases (Bonada et al. 2006a).

Although we found overall support for the hypothesis that perennial biodiversity is higher than IR biodiversity, IRs occur throughout the globe, including many in regions in Africa, Asia or South America not covered by our meta-analysis (Datry et al. 2016a; Leigh et al. 2016a). In addition, most of the papers analysed here consider the most commonly studied taxonomic groups in river ecology (i.e. macroinvertebrates, fish, algae and macrophytes); no papers examining other highly diverse groups such as microbes (Palmer et al. 2000) fulfilled our selection criteria. To increase the robustness of our meta-analysis, there is a need for future research on studies comparing perennial rivers and IRs biodiversity in regions beyond those included here and across a wider variety of taxonomic groups. This would provide a more comprehensive view of the effects of flow intermittence on aquatic biodiversity and the potential effects of current and future global change.

Our finding that perennial biodiversity was higher than IR biodiversity within cold, arid and temperate (which includes Mediterranean) climates agrees with several studies from arid (Beugly and Pyron 2010; Leigh 2013; De Jong et al. 2013) and Mediterranean-temperate regions (Progar and Moldenke 2002; Roux et al. 2008; Storey and Quinn 2008). Flow predictability, which is related to climate predictability, plays an important role in shaping species adaptations and thus biodiversity (Lytle and Poff 2004); highly predictable environments (e.g. in predictably seasonal Mediterranean-climate regions) are considered to support higher biodiversity than less predictable ones. However, despite dry riverbeds providing habitat and refuge for terrestrial organisms (Steward et al. 2012; Corti et al. 2013; Corti and Datry 2016) and their disconnected pools acting as refuges for aquatic organisms (Bonada et al. 2007a, b; Sheldon et al. 2010; Datry et al. 2014a), flow intermittence is a strong disturbance even in predictable climates (Datry et al. 2014b; Leigh and Datry 2016). Indeed, although some aquatic organisms have traits to cope with flow intermittence (Bêche et al. 2006; Bonada et al. 2008; Blanchette and Pearson 2012), resistance traits acquired through evolution as a response to drying are much less frequent than resilience traits in IRs (Datry et al. 2014b; Leigh et al. 2016a; Vander Vorste et al. 2016), which would explain our overall result. Of particular concern is our finding of comparatively low biodiversity in arid-zone IRs given aridity is projected to increase in several regions of the world (e.g. the already arid southwest region of USA; Seager et al. 2013).

Our results do not support the view that differences in biodiversity between perennial rivers and IRs are negligible during the wet season. However, despite the low number of studies considered, we did find support for the hypothesis that biodiversity in perennial rivers is higher than in IRs during the dry season. In this latter case, the low habitat availability in IRs compared to perennial rivers will reduce biodiversity unless isolated pools remain for long periods allowing many species to colonize and increase community variability among pools within reaches (Bonada et al. 2006a; Leigh and Sheldon 2009). By contrast, during the wet season, despite IRs having similar habitat availability as perennial rivers, some studies have also shown that biodiversity may remain relatively low in IRs because fewer species may be available and able to colonize these habitats and/or because of alterations to food web structure and dimensions (Datry 2012; McHugh et al. 2015).

Aquatic organisms (i.e. macroinvertebrate, fish, algae and macrophytes) have adaptations to particular instream habitats, from riffles to pools (Bonada et al. 2006a, 2008; Dallas 2007). Most likely due to the small number of studies in the subsets, our hypothesis regarding habitat (i.e. biodiversity in perennial riffles may be higher than in IR riffles, whereas the opposite pattern may be observed in pools) was not supported. However, studies sampling multiple habitats showed a higher biodiversity in perennial rivers than in IRs, which agrees with findings from Graça et al. (2004), Belmar et al. (2013)

and Leigh et al. (2013a). Multi-habitat sampling may be a better method to account for biodiversity of rivers (Leitão et al. 2014) because species characteristic of individual habitats may not occur across all habitat types (Bonada et al. 2006b; Cid et al. 2016).

The aquatic biodiversity of a particular reach not only depends on instream habitat characteristics, but also on the regional biodiversity and the balance between dispersal and abiotic/biotic factors. The river network structure plays an essential role for the dispersion of aquatic organisms and thus helps determine aquatic biodiversity patterns (Altermatt 2013). In perennial rivers, biodiversity in lowland reaches is driven by mass effects whereas abiotic/biotic factors are considered more important in their headwaters (Brown and Swan 2010). In IRs, the relative role of dispersal versus abiotic/biotic factors depends not only on the hydrological phase of the reach (i.e. flowing, non-flowing, dry) but also on where the drying event occurs along the river network (Datry et al. 2014b, 2016c, d). We were unable to test how different configurations of drying events affect aquatic biodiversity but, although more studies are needed for middle reaches, our results on longitudinal zonation agreed with our initial hypothesis. Flow and river characteristics change with longitudinal zonation and, according to the River continuum concept, alpha-diversity is expected to peak at middle reaches (Vannote et al. 1980; Finn et al. 2011). Indeed, the low alpha biodiversity in headwaters and their high isolation make them highly vulnerable to biodiversity loss by flow intermittence and hampers recolonization after flow resumption unless communities in IR headwaters are dominated by resistance strategies to drying (Datry et al. 2014b, 2016a). In contrast, middle reaches have higher alpha biodiversity and less isolation (Finn et al. 2011), resulting in no differences between perennial rivers and IRs. On the other hand, headwaters make up a large proportion of all river networks (Naiman 1983; Benda et al. 2005) and the studies included in our analyses that were conducted in multiple reaches also included a higher proportion of headwater sites, supporting the hypothesis that perennial rivers have a higher biodiversity than IRs when examined across multiple reaches (i.e. at large spatial scales). We suggest, however, that these interpretations should be viewed with caution due to the small number of studies in middle reaches.

Anthropogenic disturbances often decrease biodiversity by homogenising communities (Rahel 2002). Despite this, we found higher biodiversity in PRs than in IRs regardless of the level of anthropogenic disturbance (i.e. low or mediumhigh). We acknowledge, however, that our categorization of anthropogenic disturbances was coarse and more studies comparing biodiversity in perennial rivers and IRs under more explicit and different disturbance categories are needed. The effect of anthropogenic disturbances on IRs is a relatively novel topic that is being considered in terms of management and conservation of river ecosystems (Skoulikidis et al. 2017). Current bioassessment methods are designed to detect the impacts of anthropogenic disturbances (Bonada et al. 2006b) but typically fail when applied to IRs. This means that the lower biodiversity of IRs compared to perennial rivers cannot simply be interpreted as indicative of anthropogenic impairment. New methods for IR bioassessment must be designed that can disentangle natural from anthropogenic disturbances (Prat et al. 2004; Leigh et al. 2013b).

Biodiversity has been related to ecosystem resilience (defined by Holling 1973, “as the magnitude of disturbance that a system can experience before it shifts into a different state”), however, there is uncertainty about how ecosystem resilience will respond to increases in levels of anthropogenic disturbance and consequent impacts on biodiversity (Steffen et al. 2004). Walker and Meyers (2004) suggested that ecosystems might respond gradually to biodiversity loss, whereas Gunderson and Pritchard (2002) suggested that ecosystems will respond strongly, because crossing the threshold of biodiversity loss will produce sudden and dramatic changes in the responding state factors. Indeed, higher numbers of species are expected to increase the ability to recover from disturbances (Holling 1978; Folke et al. 2004). If IRs have significantly lower biodiversity than perennial rivers, as found by us, ecosystem resilience could be affected. However, IR taxa have particular adaptations for surviving and recovering from drying (Lake 2011; Blanchette and Pearson 2012; Leigh et al. 2016b), which may help to mitigate the effects of future co-occurring disturbances (Mori et al. 2013; Vander Vorste et al. 2016). Although a growing number of studies on IRs consider ecosystem resilience (e.g. using functional characteristics of species; Bruno et al. 2016; Vander Vorste et al. 2016), the ecosystem effects of biodiversity loss in these systems needs to be investigated.

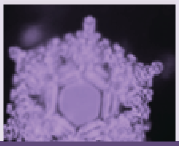
As a result of global change, extreme climatic events are expected to increase in frequency and intensity, with an increase in drying frequency, duration, and/or intensity in many regions (Beniston et al. 2007; Palmer et al. 2008; Döll and Schmied 2012). Some regions will experience shifts from perennial rivers to IRs, whereas other regions will show the contrary pattern (Döll and Schmied 2012). If these hydrological regime shifts occur faster than the evolutionary scale at which species acquire adaptive traits (Filipe et al. 2013), dramatic effects on aquatic biodiversity and ecosystem processes and services will result (Datry et al. 2014a; IPCC 2014; Ledger and Milner 2015). In regions where perennial rivers will shift to IRs, loss of species poorly adapted to dry conditions can be expected (Phillipsen and Lytle 2013; Jaeger et al. 2014). Our findings suggest such losses may be particularly relevant for certain taxonomic groups (i.e. macroinvertebrates) and under particular environmental conditions or in certain regions (e.g. in arid and temperate climate zones, and in headwaters). However, IRs communities of species with strong dispersal capacity and high fecundity may be minimally affected and able to colonize these novel IRs (Arscott et al. 2010; Datry et al. 2014a, b). In regions where IRs will shift to perennial rivers, the expected increase in biodiversity in these novel perennial rivers will ultimately depend on the connectivity to other perennial rivers. Perennial rivers highly connected to novel perennial rivers might maintain biodiversity, whereas the biodiversity in of highly isolated perennial rivers may decline. As highly dynamic metacommunities are expected to dominate in this future scenario of IRs shifting to perennial rivers and *vice versa* (Datry et al. 2016b), conservation efforts to reduce the risk of undesired hydrological regime shifts should be prioritized to avoid effects on ecosystem resilience (Folke et al. 2004) and could be targeted towards those environmental conditions or taxonomic groups with significant differences between perennial and IR biodiversity.

ACKNOWLEDGEMENTS

We thank all authors that provided original data: Antoni Munné, María del Mar Sánchez, Esther Mas-Martí and Oscar Belmar. This work is one aspect of the international research project “Intermittent River Biodiversity Analysis and Synthesis” (IRBAS, irbas.cesab.org). The IRBAS research project is supported by the Center for Synthesis and Analysis of Biodiversity (CESAB), which is funded jointly by the French Foundation for Research on Biodiversity (FRB) and the French National Agency for Water and Aquatic Environments (ONEMA). Financial support was received from the Centre for Synthesis and Analysis of Biodiversity (CESAB) and the Intermittent River Biodiversity Analysis and Synthesis working group (IRBAS).

CHAPTER 2

Contribution of intermittent rivers to beta diversity can inform freshwater conservation in the Mediterranean region



ABSTRACT

In Mediterranean-climate areas, intermittent rivers (IRs) are frequent, and hold highly dynamic communities that typically change among flowing, disconnected pools and dry phases. From a conservation point of view, including both spatial and temporal biodiversity patterns are key to capture the full variation in their community composition. Using taxonomic measures alone to protect biodiversity might provide limited insight into the impacts of disturbance on ecosystem functioning. Information on the contribution of key sites and moments to both regional taxonomic and functional diversity could help to develop effective conservation strategies.

We analysed the spatiotemporal contribution of aquatic macroinvertebrates from perennial and IRs to taxonomic and functional beta diversity in the western Mediterranean Basin. Local site contributions to beta diversity (LCBD) were compared within each site and over five sampling times in relation to flow intermittence, local environmental variability and anthropogenic impacts.

When considering all sampling times, taxonomic and functional richness over time were significantly higher in perennial than in IRs, while taxonomic and functional LCBD were higher in IRs. Despite some of the highest LCBD values found in IRs corresponded to anthropogenic impacted sites, flow intermittence was the main predictor explaining spatiotemporal patterns of both taxonomic and functional LCBD. When comparing the sites over time, higher values of taxonomic and functional LCBD corresponded mostly to IRs during the disconnected pool phase.

Our results highlight the importance of IRs to biodiversity conservation of Mediterranean-climate rivers, especially during the disconnected pool phase, suggesting that these ecosystems cannot be ignored in conservation planning strategies.

INTRODUCTION

Incorporating relevant information on community composition is crucial to developing effective biodiversity and ecosystem conservation strategies (Pereira et al. 2013; Hill et al. 2016). Commonly, conservation efforts have focused on protecting the number of species within a site (taxonomic alpha diversity; α) or region (taxonomic gamma diversity or regional diversity; γ), while efforts to characterize and incorporate the variation in species composition (taxonomic beta diversity; β) are more recent (Koleff et al. 2003; Anderson et al. 2011; Socolar et al. 2016). Taxonomic β diversity can be measured as the compositional dissimilarity in species assemblages, either in space (Baselga 2010; Anderson et al. 2011) or in time (Legendre and Gauthier 2014; Shimadzu et al. 2015). While links between α, β and γ spatial taxonomic diversity have been widely explored, their temporal dynamics have been overlooked (Anderson et al. 2011; Legendre and Gauthier 2014). Temporal taxonomic β diversity inform about how the community variation, influenced by environmental variables, changes through time (Legendre and Gauthier 2014; Legendre and Condit 2019).

Functional diversity components can provide more insight into the impacts of disturbance on ecosystem functioning than taxonomic measures (Graham and Fine 2008; Villéger et al. 2013, 2017; Mazel et al. 2018). In comparison with taxonomic diversity, the use of functional diversity allows clarifying the role of each species in ecosystem processes and their resistance and/or resilience to environmental changes, either natural or anthropogenic (Tobias and Monika 2011; Mouillot et al. 2013; Villéger et al. 2013, 2017). Since the increase of multiple anthropogenic impacts is undermining the stability of ecosystems, understanding how both taxonomic and functional diversity influence ecosystem functioning can contribute to better predict the ecological consequences of biodiversity loss (Hooper et al. 2005; Flynn et al. 2011; Gutiérrez-Cánovas et al. 2015, 2019). As for taxonomic β diversity, functional β diversity can be defined as the compositional dissimilarity in trait assemblages across space (Villéger et al. 2013; Aspin et al. 2018) and time (Baselga et al. 2015; Magurran et al. 2019). Despite such functional β diversity measures provide information on what are the implications of spatiotemporal changes in trait community composition for ecosystem functioning (Korhonen et al. 2010; Baselga et al. 2015; Magurran et al. 2019), their temporal dynamics still remain poorly quantified (Korhonen et al. 2010; Stegen et al. 2013; Crabot et al. 2020).

Intermittent rivers (IRs) are highly dynamic ecosystems that typically shift among flowing, disconnected pools and dry phases (Gallart et al. 2012, 2017). Flow intermittence exerts a primary control on IRs ecosystem structure and function over time and, consequently, biodiversity patterns typically follow these changes (Datry et al. 2014a,b; Stubbington et al. 2017). In the case of aquatic macroinvertebrates, surface flow cessation and the subsequent formation of disconnected pools imply the disappearance of species adapted to riffles and the appearance of pool-like species (Bonada et al. 2006a; Bogan et al. 2017; Tonkin et al. 2017). With the complete drying of the riverbed, some taxa may emerge, move to other wet habitats, to the hyporheic zone, or enter in a desiccation-resistant life stage (Bogan et al. 2017; Stubbington et al 2019a,b). Shifts from dry to flowing phases following rewetting favour recolonization, contributing to the recovery of local communities in IRs (Leigh et al. 2016b; Bogan et al. 2017). IRs communities are highly variable in time, with species and trait composition changing from one period to another (Datry et al. 2014a,b; Bogan et al. 2017). Therefore, assessing spatiotemporal taxonomic and functional β diversity patterns might be even more important compared to other relatively more stable ecosystems (Leigh et al. 2019b; Crabot et al. 2020). Considering that climate change and increased human demands for water are altering IRs' biodiversity patterns and functional processes (Datry et al. 2014a,b), a better understanding of their contribution to biodiversity is timely (Ruhí et al. 2017; Sánchez-Montoya et al. 2020).

In comparison to IRs from other climatic regions, those in Mediterranean-climate areas are characterised by being highly predictable in terms of seasonality, resulting in clear community shifts between flowing and non-flowing phases (Hershkovitz and Gasith 2013; Tonkin et al. 2017). In addition, Mediterranean-climate IRs are global biodiversity hotspots, i.e. regions holding high levels of endemism and also being particularly vulnerable to anthropogenic impacts (Bonada and Resh, 2013; Cid et al. 2017). Considering their high spatiotemporal variability, identifying key sites and moments that contribute the most to regional diversity could be informative for conservation management (Ruhí et al. 2017, Sánchez-Montoya et al. 2020).

Here, we studied riverine aquatic macroinvertebrates taxonomic and functional spatiotemporal β diversity in 20 rivers of the western Mediterranean Basin by analysing the local contribution to β diversity (LCBD; Legendre and De Cáceres 2013) of each site over time. Specifically, perennial rivers and IRs were sampled along gradients of natural flow intermittence and anthropogenic impacts to investigate their influence on LCBD. Our first hypothesis (H1) was that LCBD would be higher in IRs than in perennial rivers because IRs macroinvertebrate communities are subjected and adapted to higher spatiotemporal variability (Bonada and Resh 2013; Tornés and Ruhí 2013; Leigh et al. 2019b). Our second hypothesis (H2) was that anthropogenic impacts would reduce differences between IRs and perennial rivers contributions, as they are known to simplify and homogenize communities (Tonkin et al. 2017). Finally, our third hypothesis (H3) was that LCBD of IRs would be higher during disconnected pools than during the flowing phase because IRs hold unique species adapted to non-flowing conditions (Bonada et al. 2006a, 2020).

METHODS

Study sites and sampling design

The study was conducted in 20 river sites located in the Mediterranean-climate region of the Iberian Peninsula. Ten sites were intermittent and ten were perennial. The study area is characterized by Mediterranean climate, with high seasonal and inter-annual variability in precipitation and flow regime (Bonada and Resh 2013; Cid et al. 2017). Sites ranged from 6 to 1100 m.a.s.l., with discharges ranging from 0 to 0.417 m^3/s. For further details on the study area, see Soria et al. (2020).

Biological dataset

Macroinvertebrates were collected during flowing and disconnected pools phases, sampling five times per site at six-week intervals between April and December 2015: April-May (t1), June (t2), July-August (t3), September (t4), December (t5). Therefore, sampling included both drying and rewetting periods. Because five sites were dry between one and three occasions, a total of 91 samples were obtained. Our sampling procedure followed the official quantitative standardized protocol used by water agencies in Spain (MAGRAMA 2013). Samples were collected using a 250 μm-mesh D-net across all available microhabitats and preserved them in 4% formaldehyde. Macroinvertebrates were identified to the lowest taxonomic resolution possible, usually genus, but with some Chironomidae and Ceratopogonidae identified to subfamily or tribe. Overall, 194 macroinvertebrate taxa were identified (Soria et al. 2020).

In addition to taxonomy, resistance and resilience traits related to flow intermittence were also considered (Lytle and Poff 2004; Bogan et al. 2017; Stubbington et al. 2017). Overall, 35 categories of seven specific traits were selected: type of reproduction, resistance forms, respiration, locomotion, life cycle duration, reproduction cycles per year, and dispersal (Tachet et al. 2010).

Predictors of spatiotemporal β diversity

Hydrology, anthropogenic impacts and general physico-chemistry of the studied rivers were included as predictors of LCBD. The TREHS (Temporary Rivers Ecological and Hydrological Status) software (http://www.lifetrivers.eu/products/trehs-software/; Gallart et al. 2017) was used to classify rivers hydrological regime and to differentiate river sites affected by natural flow intermittence from those with human-driven flow intermittence.

To infer the IRs' phases (i.e. flow, disconnected pools, dry riverbed), two temperature data loggers (UA-002 HOBO) were installed at each river site and recorded data during the 30-week study period (see details in Soria et al. 2020). Based on temperature data collected from temperature data loggers, thermal amplitude was used to infer two hydrological predictors: the accumulated zero-flow days (i.e. disconnected pools or dry riverbed) since the last flow resumption occurred (ZF_a), and the accumulated number of days with disconnected pools since the last flow resumption occurred (DP_a). ZF_a and DP_a were used to address hypotheses H1 and H2, respectively.

Anthropogenic impacts were measured at each river site by using the number of impacts according to the Mediterranean Reference Criteria (MRC index) (Sánchez-Montoya et al. 2009). The MRC index includes information on invasive species, diffuse pollution sources, land-use intensity, riparian vegetation, river geomorphology, instream habitat conditions and hydrological alterations, and ranges from 0 (highly impacted) to 20 (non-impacted). To facilitate interpretation, the inverse of the MRC index values were used (i.e. from 0 = non-impacted, to 20 = highly impacted, hereafter number of impacts; see Soria et al. 2020). In addition, the number of impacts were also separated in two main categories: unimpacted or least impacted (number of impacts between 0 and 5; hereafter least impacted) and medium-high impacted (number of impacts between 6 and 20; hereafter impacted).

For each sampling site and time, the following physico-chemical parameters were measured in situ: conductivity (µS/cm), pH, temperature (ºC), dissolved oxygen (both percentage and mg/l), chemical parameters (i.e. HCO_3, Ca, TOC, Mg, SO_4; μg/l) and chlorophyll-a (Chl; mg/m^2). From this data, environmental heterogeneity (EH) of each sampling site was calculated by two proxies considering the variables conductivity, pH, temperature, dissolved oxygen and chemical parameters measured during each sampling time. First, the sum of the coefficient of variation of these variables was calculated. Then, standardised Euclidean distances (between sampling times of each site) in a Permutational Analysis of Multivariate Dispersions (Anderson 2006) were calculated to obtain the average distances to the centroid. The higher was the average distance to the centroid, the higher EH (Bini et al. 2014; Siqueira et al. 2020). All variables were previously standardised. The Chl predictor was not further used because its correlation with the number of impacts (Soria et al. 2020).

Statistical analysis

Taxonomic and functional LCBD of each site (hereafter T-LCBD and F-LCBD, respectively) were estimated for each sampling time (Legendre and De Cáceres 2013; Legendre and Gauthier 2014). The T-LCBD was calculated with taxa abundances (columns) by sites (rows) matrix (Legendre and De Cáceres 2013). The F-LCBD was also calculated with the proportion of each category trait (columns) by sites (rows) matrix (Rodrigues-Capítulo et al. 2009). The proportion of each category trait was obtained by multiplying the abundance of taxa (columns) X sites (rows) matrix obtained from the field samples by the traits (columns) X taxa (rows) matrix created from Tachet et al. (2010). T-LCBD and F-LCBD values indicate the degree of ecological uniqueness of each site at each sampling time in terms of species or traits composition, respectively (Legendre and De Cáceres 2013). According to the procedures described by Legendre and De Cáceres (2013), T-LCBD and F-LCBD were estimated after using Hellinger standardization and the significance of each site in each sampling time were tested by permutation (999 runs). T-LCBD and F-LCBD values higher than the community average were considered to reflect higher contributions to overall β diversity (Landeiro et al. 2018; Sánchez-Montoya et al. 2020). Indeed, the higher the T-LCBD or F-LCBD value of a given site, the rarer the taxa or trait composition, respectively.

For a first descriptive analysis, community dynamics were compared between perennial and IRs using changes in local taxonomic and functional richness (α diversity) through time. Functional richness was obtained from Soria et al. (2020) and estimated as suggested by Villéger et al. (2008). Beta regression was conducted to relate T-LCBD and F-LCBD with taxonomic and functional richness, respectively. The non-parametric Kruskal-Wallis test was applied to compare perennial rivers and IRs considering all sampling times, while post-hoc pairwise analyses using a Tukey's HSD test were applied to compare perennial rivers and IRs at each sampling time. When using the subset of data including only IRs, the non-parametric Kruskal-Wallis was applied to compare flowing and disconnected pools phases considering all sampling times, while post-hoc pairwise analyses were applied to compare least impacted and impacted IRs during their flowing and disconnected pools phases.

Linear mixed-effect models (LME) were used to test for the correlation of T-LCBD and F-LCBD with the different environmental predictors. To account for the non-independence of samples collected from the same site a Gaussian error distribution was used, and sites were included as a random factor. Predictors were included as fixed factors. Models always included the number of impacts and one of the two hydrological predictors (i.e. ZF_a or DP_a) but differed among the EH predictor, which resulted in two main models (Table S1). Overall, four sub-models were tested, which resulted from testing each of the two main models to both T-LCBD and F-LCBD response variables. For models including the ZF_a predictor, the whole dataset was used. For models conducted with the DP_a predictor, a subset of data including only IRs was included.

The Akaike Information Criterion (AIC; Burnham and Anderson 2001; Zuur et al. 2009) was used to select the best models (i.e. models with the lowest AIC values). Multicollinearity was assessed in models by calculating Pearson's correlations between the predictors and the variance inflation factor (VIF), in which we adopted a threshold of VIF > 2.0 (Zuur et al. 2010). Normality was also assessed in models by applying the Shapiro-Wilk test (Quinn and Keough 2002). Interactions between the selected predictors were tested in the initial 4 sub-models, but excluded because of models' multicollinearity (VIF > 2.0).

All analyses were conducted in R version 3.6.2 (R Core Team 2015), using the packages "ade4" (Dray et al. 2007), "vegan" (Oksanen et al. 2013), "betapart" (Baselga et al. 2013), "car" (Fox and Weisberg 2011) and "nlme" (Pinheiro et al. 2016). The code and functions used to run these analyses are available at Data Accessibility Statement.

RESULTS

Comparing community dynamics between perennial rivers and IRs

Overall, when comparing perennial and IRs, significantly higher values were observed in perennial rivers than IRs for both taxonomic and functional richness (KW = 10.821, P = 0.001 and KW = 3.866, P = 0.049; respectively; Fig. S1a,b). For T-LCBD and F-LCBD significantly higher values were observed in IRs than perennial rivers (KW = 5.853, P = 0.016 and KW = 4.408, P = 0.036; respectively; Fig. S1c,d). When considering individual sampling times, post-hoc analyses showed significantly higher values in IRs than perennial rivers for T-LCBD (P > 0.05) during t3-summer and t4-summer sampling times (Fig. 1c, Table S3). No significant differences were observed among perennial and IRs for taxonomic (Fig. 1a) and functional richness (Fig. 1b) or for F-LCBD (Fig. 1d) at any sampling time (Table S3). T-LCBD and F-LCBD increased significantly with decreasing taxonomic and functional richness (Table S4).

When considering all sampling times, the highest T-LCBD values over time (i.e. above the community average; T-LCBD > 0.043) were observed in five least impacted and one impacted perennial rivers, and in two least impacted and four impacted IRs (Table S5). However, when looking into each sampling time, significant values of T-LCBD were only found in five IRs corresponding to the disconnected pool phase (Fig. 2a, Table S5).

The highest F-LCBD values over time (F-LCBD > 0.034), when considering all sampling times, were observed in two least impacted and two impacted perennial rivers, and three least impacted and five impacted IRs (Table S5). When considering individual sampling times, significant values of F-LCBD were observed in one least impacted perennial river, and in seven IRs at one specific sampling time (Fig. 2b, Table S5). From these seven IRs, two corresponded to the flowing phase and five to the disconnected pools phase.

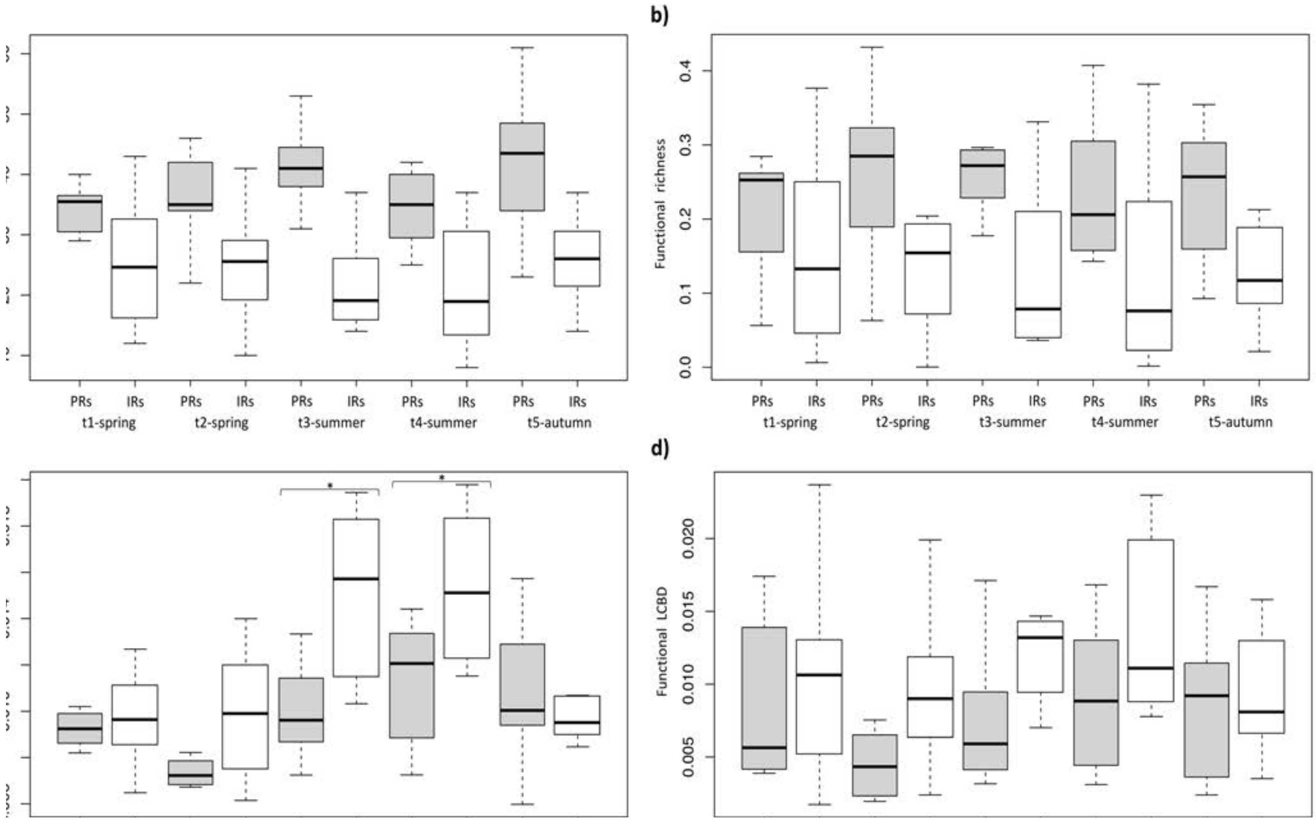


Figure 1. Boxplots showing taxonomic and functional local richness (a and b, respectively) and LCBD (c and d, respectively) over the five sampled times: spring (t1-t2), summer (t3-t4) and autumn (t5). Full boxes represent perennial rivers (PRs) and empty ones IRs. The * are displayed for significant differences between PRs and IRs (*P* > 0.05).

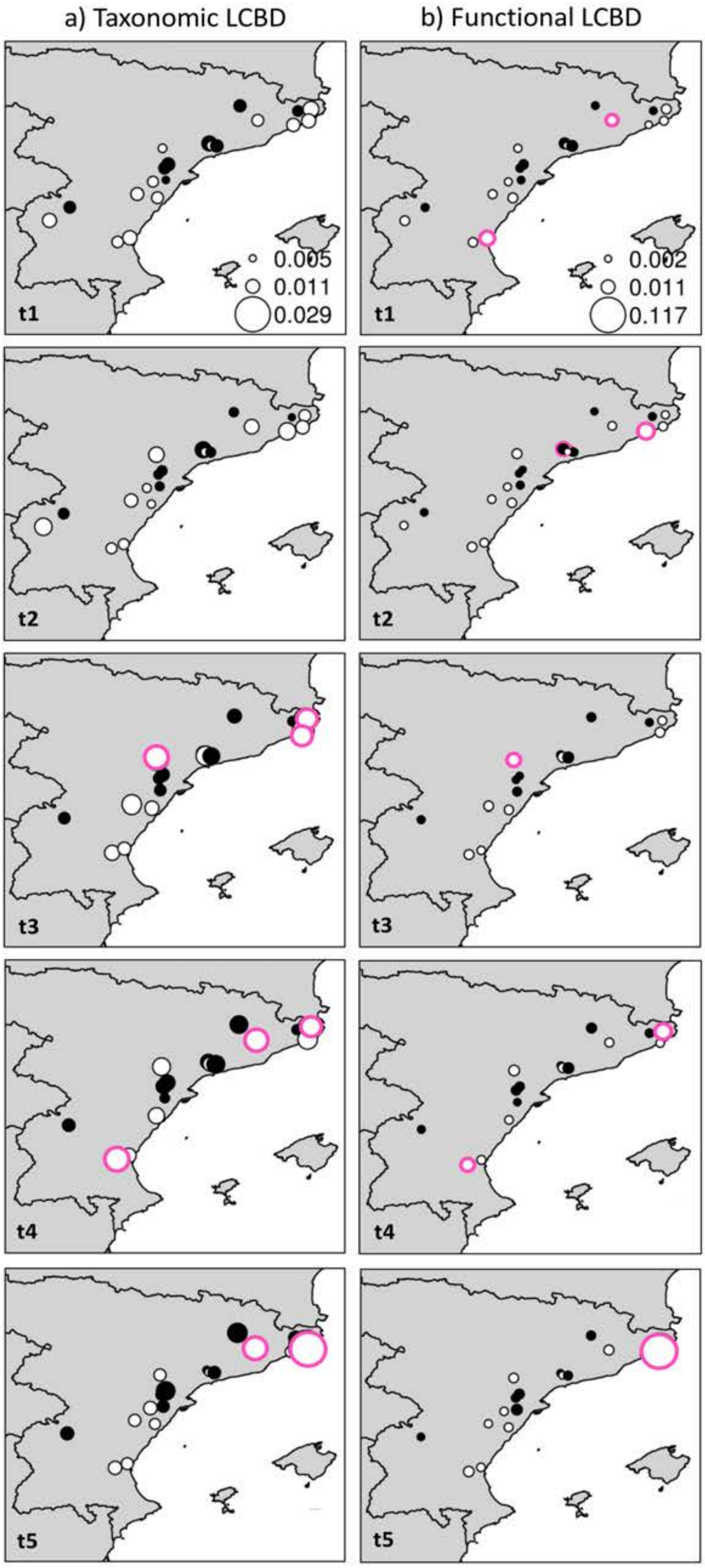


Figure 2. Taxonomic (a) and functional (b) LCBD plots of each site through the five sampled times: spring (t1-t2), summer (t3-t4) and autumn (t5). Circle size is proportional to the contribution to overall β diversity. Black circles: perennial rivers; white circles: intermittent rivers. Significant sites (*P* < 0.05) are indicated in pink. See Table S5 for further details.

IRs’ contribution during the disconnected pools phase

Overall, IRs during the disconnected pools phase had significantly higher values of T-LCBD than during flowing phase (KW = 9.521, *P* = 0.002; Fig. 3a), but no significant differences were observed in F-LCBD (KW = 1.9623, *P* = 0.1613; Fig. 3b). For T-LCBD, the post-hoc analysis showed significantly higher values in impacted IRs during the disconnected pools phase than in impacted IRs during the flowing phases (*P* = 0.041; Fig. 3c). Moreover, significant higher T-LCBD values were also observed in impacted IRs during the disconnected pools phase than in least impacted IRs during flowing phase (*P* = 0.020). No significant differences were observed in F-LCBD (Fig. 3d).

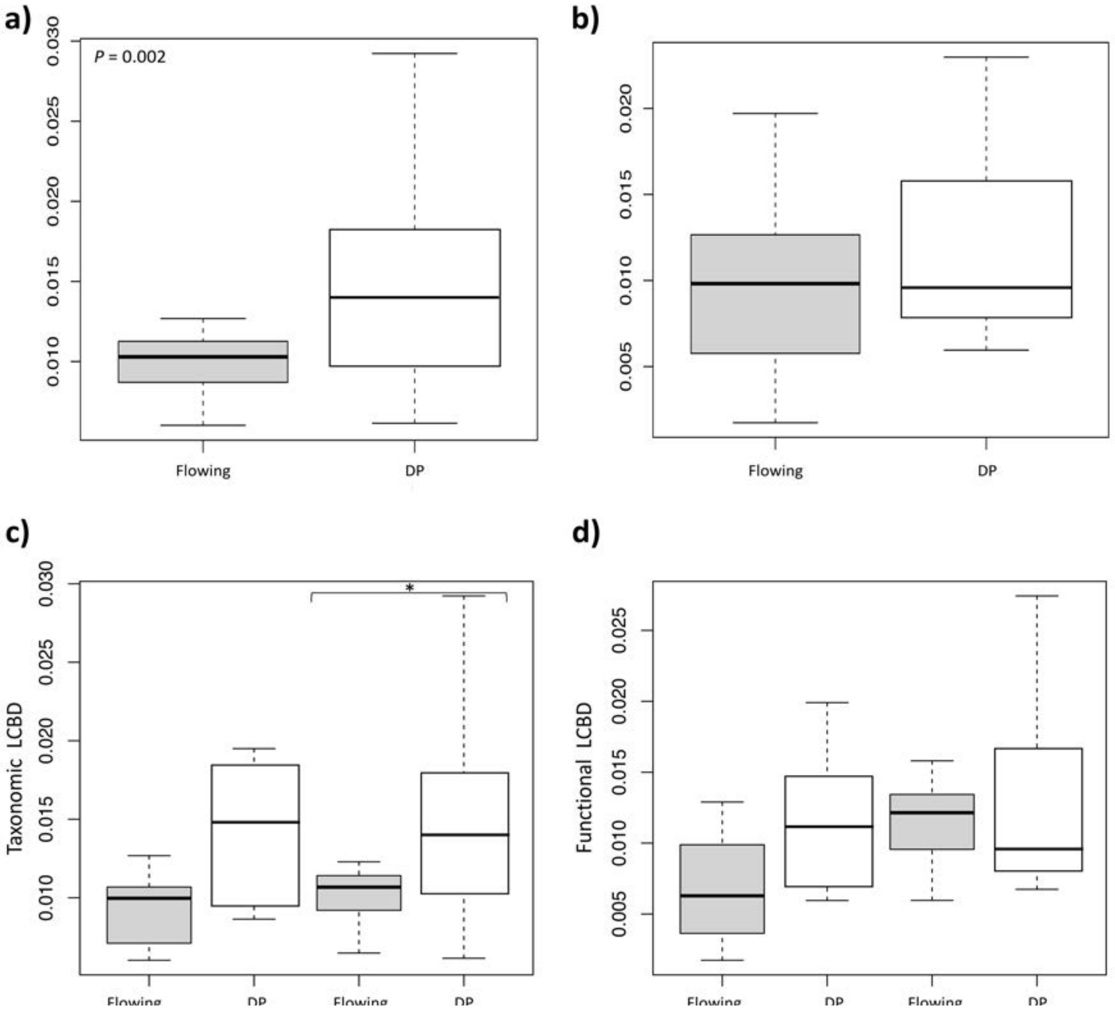


Figure 3. Boxplots showing taxonomic (a,c) and functional (b,d) LCBD patterns of IRs considering all five sampled times. Plots show least impacted and impacted IRs during flowing (grey) and disconnected pools (DP; white) phases. *P* values are displayed for significant differences between flowing and disconnected pools phases applying the Kruskal-Wallis test, while * are displayed for significant differences (*P* > 0.05) between least impacted and impacted IRs.

Environmental predictors explaining the ecological uniqueness of rivers

The main explanatory predictors of T-LCBD best model (AIC = -768.01) were ZF_a, EH and the number of impacts, while for F-LCBD best model (AIC = -547.64) were ZF_a and the number of impacts (Table 1, Fig. S2a-e). T-LCBD and F-LCBD increased significantly with increasing ZF_a ($t = 4.986$, $P < 0.001$ and $t = 4.593$, $P < 0.001$, respectively), but no significant patterns were observed for the rest of predictors.

Table 1. Partial regression coefficients of the explanatory predictors variables used in LME best models of T-LCBD and F-LCBD (i.e. lowest AIC, including models with ΔAIC < 2; see Table S1). Models tested the hypothesis 1 by using the accumulated zero flow days since the last flow resumption occurred (ZF_a) hydrological predictor. The greater the t-value, the greater the evidence against the null hypothesis (i.e. there is a significant difference). Significant predictors ($P < 0.05$) are indicated in bold. EH: environmental heterogeneity. Nº impacts: number of impacts.

LCBD	**AIC**	**Predictors variables**	**SE**	**t-value**	
		ZF_a	0.00001	**4.986**	.001
F-LCBD	-547.64	Intercept	0.004	3.163	02
		Nº impacts	0.0003	1.146	267

Similarly, when using the subset of data including only IRs, the main explanatory predictors of T-LCBD best model (AIC = -409.23) were DP_a, EH and the number of impacts (Table 2, Fig. S3a-c). The T-LCBD increased significantly with increasing DP_a ($t = 3.530$, $P = 0.001$), but the number of impacts and EH predictors were not significant. The main explanatory predictors of F-LCBD best model (AIC = -277.93) were DP_a and the number of impacts (Table 2, Fig. S3d-e). The F-LCBD increased significantly with increasing DP_a ($t = 3.429$, $P = 0.002$), but the number of impacts were not significant.

Table 2. Partial regression coefficients of the explanatory predictors variables used in LME best models of T-LCBD and F-LCBD i.e. lowest AIC, including models with ΔAIC < 2; see Table S2). Models tested the hypothesis 2 by using the accumulated number of days with disconnected pools since the last flow resumption occurred (DP_a) hydrological predictor. The greater the t-value, the greater the evidence against the null hypothesis (i.e. there is a significant difference). Significant predictors (P < 0.05) are indicated in bold. EH: environmental heterogeneity. Nº impacts: number of impacts.

Nº impacts	00002	0.114	0.911
Nº impacts	.00001	-0.082	0.937
DP_a	0002	**3.429**	0.002
DP_a	0002	**3.346**	0.002

DISCUSSION

Overall, our results showed that taxonomic and functional richness were significantly higher in perennial than in IRs, while taxonomic and functional LCBD were higher in IRs. Moreover, LCBD values were negatively related to richness, as found in other studies conducted with macroinvertebrates (e.g. Heino et al. 2017; da Silva et al. 2018; Valente-Neto et al 2020) and other biological groups (e.g. Legendre and De Cáceres 2013; Vilmi et al. 2017; Landeiro et al. 2018). This negative relationship indicates that sites with unique species or trait composition had lower taxonomic and functional richness, respectively (Heino et al. 2017; da Silva et al. 2018). In our study, there was a decrease in taxonomic and functional richness in IRs with the loss of surface flow at the beginning of summer, which can be explained by the disappearance of species adapted to riffle habitats during this period (Bogan et al. 2017; Tonkin et al. 2017). Yet, over the disconnected pools phase in summer, there was an increase of taxonomic and functional LCBD in IRs, which can be related to the appearance of species with specific traits adapted to cope with such conditions (Bonada et al. 2006a, 2020). Hence, unlike in perennial rivers, IRs are characterized by a higher gain/loss of species and traits throughout the year (Tornés and Ruhí 2013; Leigh et al. 2019b). From a conservation point of view, including these biodiversity temporal patterns are key to capture the full variation in community composition present in these highly dynamic ecosystems (Ruhí et al. 2017).

Despite some of the highest LCBD values found in IRs corresponded to anthropogenic impacted sites, flow intermittence was the main explanatory predictor explaining spatiotemporal patterns of both taxonomic and functional LCBD. IRs can be subjected to constant shifts in their community composition resulting from both the effect of anthropogenic impacts (Legendre and Gauthier 2014) and their natural flow intermittence (Tornés and Ruhí 2013; Ruhí et al. 2017; Stubbington et al. 2019b). However, mediterranean IRs hold unique species composition adapted to natural flow intermittence, such as a dominance of pool-like species during the disconnected pools phase (Bonada et al. 2006a, 2020; Cid et al. 2017), that might give them capacity to resist and to recover from drying and, at the same time from anthropogenic impacts (i.e. a phenomenon known as co-tolerance; Boulton et al. 2000). In the long term, however, if anthropogenic impacts remain or even increase, they might negatively affect the competitive ability of species that have evolved to utilize specific temporal niches in IRs, which could cause significant declines in their temporal taxonomic and functional β diversity (Tonkin et al. 2017).

When comparing perennial rivers and IRs over time, higher values of taxonomic and functional LCBD corresponded mostly to IRs during the disconnected pool phase. Despite the main community shifts occurring in IRs corresponded to the formation of disconnected pools, the complete drying of the riverbed and the flow resumption (Datry et al. 2014; Bonada et al. 2020), our results suggested that the disconnected pools phase was the most relevant to LCBD. Due to the shift from lotic to lentic habitats that occurs with the formation of disconnected pools, taxa related to the flowing phase disappear, while others progressively colonize from nearby sites that are drying up, such as Odonata, Coleoptera and Hemiptera (Bogan et al. 2017; Bonada et al. 2020). Disconnected pools are refuges for maintaining aquatic taxa such as fish or amphibians during IRs' dry season, which can recolonize the river network upon flow resumption (Hermoso et al. 2013; Gallart et al. 2017). In addition, for some species of macroinvertebrates or amphibians, disconnected pools are also used as stepping-stones for their dispersal or as key sites for laying eggs and, thus, complete their life cycle (Bonada et al. 2006a, 2020; Stubbington et al. 2017). Local specific management actions should therefore be implemented for biodiversity conservation purposes of disconnected pools and to mitigate their possible existing impacts (Bonada et al. 2020). This is even more relevant with the predictions of IRs increasing worldwide because of climate-change and increased water demand (Döll and Schmied 2012), which, in turn, might also increase the frequency of disconnected pools (Gallart et al. 2017; Bonada et al. 2020).

Considering that IRs have been commonly ignored in conservation planning (Bogan and Lytle 2007; Leigh et al. 2019a), providing complementary measures to adequately assess their biodiversity is timely. In this sense, the LCBD approach shows a high potential to be used for conservation purposes, as the ecological uniqueness of a site can be compared with other sites sampled in a region and can be correlated with environmental variables (Legendre and De Cáceres 2013; da Silva et al. 2018; Valente-Neto et al 2020). In highly dynamic systems such as IRs, temporal patterns should also be considered to better identify key sites (Ruhí et al. 2017). Despite there has been an increase of research on temporal taxonomic β diversity in IRs (e.g. Ruhí et al. 2017; Rogosch and Olden 2019; Stubbington et al. 2019b; Sánchez-Montoya et al. 2020), studies of spatial β diversity still predominate. In addition, due to the unprecedented increase of multiple human impacts that are undermining the stability of riverine ecosystems (Leigh et al. 2016b, 2019a,b; Villéger et al. 2017), considering only species richness and community composition, even over time, might not be sufficient to protect the processes that maintain their ecosystem functioning. Our results suggest that conservation planning in rivers should attempt to assess temporal dynamics in IRs quantifying also functional β diversity. Such metric has shown to be informative for assessing spatiotemporal biodiversity in IRs (Leigh et al. 2019b; Crabot et al. 2020), but it still remains unapplied in freshwater conservation. Therefore, considering both IRs' hydrological variability and the increasing anthropogenic impacts, freshwater conservation planning should consider monitoring the temporal variability of both taxonomic and functional biodiversity in these ecosystems. This might be even more relevant in Mediterranean-climate regions worldwide where IRs constitute one of their predominant freshwater ecosystems (Bonada and Resh 2013; Cid et al. 2017). Special attention should also be given to the disconnected pools phase, as this is key to maintain local and regional aquatic biodiversity (Gallart et al. 2017; Bonada et al. 2020). In this regard, some tools have recently developed to better predict the temporal and spatial occurrence of disconnected pools across IRs networks (Gallart et al. 2017), as well as to assess their priority as biodiversity refuge and incorporate them into the conservation planning process (Hermoso et al. 2013). The integration of these tools in conservation management of IRs, together with the use of new metrics able to capture their spatiotemporal biodiversity patterns, could contribute to improve freshwater conservation in the Mediterranean region.

ACKNOWLEDGEMENTS

The study was supported by the LIFE+ TRivers (LIFE13 ENV/ES/000341) project and the Fundació Universitària Agustí Pedro i Pons. NC was supported by the French research program Make Our Planet Great Again.

CHAPTER 3

Natural disturbances can produce misleading bioassessment results: Identifying metrics to detect anthropogenic impacts in intermittent rivers

ABSTRACT

Ecosystems experience natural disturbances and anthropogenic impacts that affect biological communities and ecological processes. When natural disturbance modifies anthropogenic impacts, current widely used bioassessment metrics can prevent accurate assessment of biological quality.

Our aim was to assess the ability of biomonitoring metrics to detect anthropogenic impacts at both perennial and intermittent sites, and in the latter including both flowing and disconnected pool aquatic phases. Specifically, aquatic macroinvertebrates from 20 rivers were sampled along gradients of natural flow intermittence (natural disturbance) and anthropogenic impacts to investigate their combined effects on widely used river biomonitoring metrics (i.e. taxonomic richness and standard biological indices) and novel functional metrics, including functional redundancy (i.e. the number of taxa contributing similarly to an ecosystem function, here a trophic function) and response diversity (i.e. how functionally similar taxa respond to natural disturbance and anthropogenic impacts).

Only the widely used IBMWP index (Iberian Biological Monitoring Working Party) was able to detect anthropogenic impacts in intermittent rivers when used during flowing phases. Several functional metrics also detected anthropogenic impacts regardless of flow intermittence. Besides, functional redundancy of the entire community remained effective even in disconnected pools.

Our results therefore show that natural flow intermittence can confound river bioassessment, and that a set of new functional metrics could be used as effective alternatives to standard metrics in naturally disturbed intermittent rivers. Our findings suggest that water managers should incorporate alternative functional metrics in the routine biomonitoring of naturally disturbed rivers.

INTRODUCTION

Ecosystems experience natural disturbances and anthropogenic impacts that affect biological communities and ecological processes (Turner et al. 2003; Dornelas 2010). Natural disturbances (e.g. droughts, floods, wildfires) have acted through evolutionary time and have resulted in species adapted to such abiotic stress (Lytle and Poff 2004; Bowman et al. 2009). In contrast, anthropogenic impacts (e.g. pollution, land-use changes, biological invasions, and recently, climate change) are relatively new (<10,000 year), and may represent novel conditions for biota, impacting both biodiversity and ecosystem functioning (Olden et al. 2004; Hooper et al. 2012). Given the predicted consequences of global change, both natural disturbances and anthropogenic impacts may increase in many regions worldwide (Olden et al. 2004). Urgent action is thus needed to develop suitable assessment methods and management practices that consider the interaction of both type of impacts (Elliott and Quintino 2007; Ghazoul et al. 2015).

Biomonitoring methods detect anthropogenic impacts using metrics based on aspects of ecosystem structure and function (Bonada et al. 2006b; Pereira et al. 2013). These metrics underpin biomonitoring programmes that aim to halt and reverse biodiversity loss, to maintain and enhance the quality of ecosystems, and to assess the effectiveness of conservation and restoration measures, such as the Water Framework Directive (WFD; European Commission 2000), the Convention on Biological Diversity (CBD 2010) or the International Union for Conservation of Nature (IUCN 2016). Problematically, few current metrics integrate the effects of natural disturbances, which can confound the assessment of anthropogenic impacts and thus lead to inappropriate management actions (Tockner et al. 2010; Gutiérrez-Cánovas et al. 2019; Pitacco et al. 2019).

Functional metrics based on biological traits have shown to be promising tools for detecting anthropogenic impacts in different types of ecosystems (Laliberté et al. 2010; Statzner and Beche 2010; Mouillot et al. 2013), and to be more accurate for the biomonitoring of naturally disturbed systems (Bruno et al. 2016; Belmar et al. 2019). However, studies assessing the combined effects of natural disturbances and anthropogenic impacts on the functional composition of biological communities remain limited (e.g. Elliott and Quintino 2007; Mouillot et al. 2013; Bruno et al. 2016). Additionally, the response of functional metrics might improve when incorporating traits responding to environmental changes (i.e. response traits), and to the effect of such changes on ecosystem functioning (i.e. effect traits; Suding et al. 2008; Laliberté et al. 2010). Consequently, approaches that more directly link community dynamics to ecosystem functioning are emerging.

Nearly 50% of the current global river network has intermittent flow (Datry et al. 2014a,b). Intermittent rivers, also known as temporary rivers in a broad sense, are dynamic systems that typically shift between flowing, disconnected-pools and dry periods, named hereafter as aquatic phases (Gallart et al. 2012, 2017). Repeated shifts between aquatic phases reorganize biological communities and, therefore, flow intermittence represents a natural disturbance (Lake 2000; Leigh and Datry 2017). Intermittent rivers also experience anthropogenic impacts, such as hydrological alterations (flow regulation, surface and/or groundwater extractions), geomorphological impacts (e.g. sediment extraction and physical habitat modifications), pollutants (e.g. heavy metals and nutrient additions) and biological invasions (Chiu et al. 2017). Detection of these impacts at intermittent rivers is challenging because the reliability of standard biomonitoring metrics is generally uncertain for such naturally disturbed systems (Chiu et al. 2017; Cid et al. 2017). As the global extent of intermittent rivers increases due to climate change and water resource pressures (Döll and Schmied 2012), understanding the combined effects of natural flow intermittence and anthropogenic impacts on widely used and novel river biomonitoring metrics is needed to underpin reliable biological quality assessments.

Our aim was to assess the ability of biomonitoring metrics to detect anthropogenic impacts at both perennial and intermittent sites, and in the latter including both flowing and disconnected pool aquatic phases. Specifically, aquatic macroinvertebrates from 20 rivers were sampled along gradients of natural flow intermittence (natural disturbance) and anthropogenic impacts to investigate their combined effects on widely used river biomonitoring metrics (i.e. taxonomic richness and standard biological indices) and novel functional metrics based on biological traits. Different types of responses to natural and anthropogenic gradients were used to assess the reliability and calibration requirements of potential metrics to both perennial and intermittent rivers (Fig. 1). A single response effect occurs when a metric respond to anthropogenic impacts but not to natural flow intermittence (Fig. 1a), indicating high reliability without calibration. An additive effect occurs when the effects of natural flow intermittence add to those of anthropogenic impacts but effects do not interact (Fig. 1b), indicating that this metric could be reliable after proportional calibration with a constant term (i.e. adapting reference conditions). Finally, interactive responses occur when the effects of natural flow intermittence reduce, enhance or oppose those of anthropogenic impacts, and leads to antagonistic (Fig. 1c), synergistic (Fig. 1d) or opposing (Fig. 1e) interactions, respectively (Feld et al. 2016). Metrics with these interactive responses could be reliable only after non-proportional calibration (i.e. adapting reference conditions and response gradient to anthropogenic impacts).

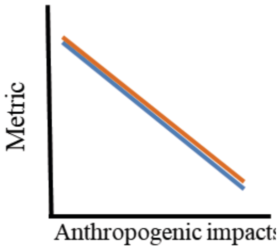
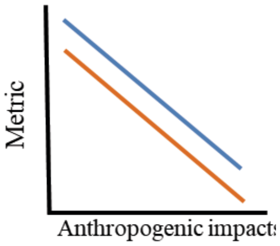
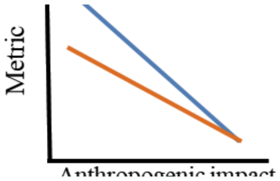
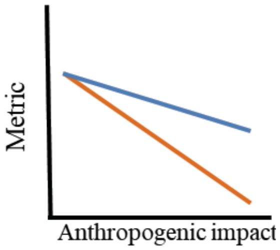
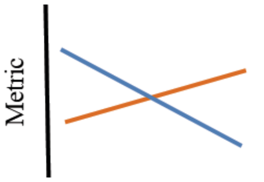
Type of effect and description		Reliability of the metric in biological assessments	Designation of the
(a) Single No effect of natural disturbance. The effect c anthropogenic impacts w be the same under the effect of natural disturbance.		The metric is reliable and can be used both in ecological systems affected and not affected by natural disturbance (e.g. perennial and intermittent rivers). No calibration needed.	Universal
(b) Additive The effect of natural disturbance adds to the effect of anthropogenic impacts, but they do not interact.		The metric could be reliable in ecological systems affected by natural disturbance only after proportional calibration with a constant term	Flexible
Two-way interaction. Th effect of natural disturbance reduces the effect of anthropogenic impacts.		systems affected by natural disturbance only after non-proportional calibration.	
(d) Synergistic Two-way interaction. Th effect of natural disturbance enhances the effect of anthropogenic impacts.			
Two-way interaction. Th effect of natural disturbance is the opposi of anthropogenic impact			

Figure 1. Potential effects of natural disturbances and anthropogenic impacts on a biomonitoring metric and the associated reliability for its use in bioassessment, with a special focus on intermittent rivers. Colours indicate communities not affected (blue) and affected (orange) by natural disturbance.

METHODS

Study area

The study was conducted in 20 river sites in the north-eastern Iberian Peninsula (Fig. S1). The area has a Mediterranean climate (i.e. Csa and Csb; Kottek et al. 2006), with high seasonal variability in precipitation and thus streamflow (Bonada and Resh 2013; Cid et al. 2017). Ten of the sites are intermittent and 10 are perennial. Sites were located in different sub-basins in the Ebro, Júcar and Catalan catchments and experience different degrees of anthropogenic impact and river regime. Sites ranged from 6 to 1,100 m a. s. l. and drained calcareous catchments with discharges ranging from 0 to 417 L/s.

Macroinvertebrate data

Macroinvertebrates were collected five times per site (i.e. n = 100 samples) at six-week intervals between April and December 2015, to capture the assemblages present during flowing phases and in disconnected pools. In total, 91 samples were taken because five sites were dry between one or three occasions. Samples were collected using a 250 µm-mesh D-net across all available microhabitats (i.e. different mineral and organic substrates), following the national standard quantitative sampling protocol (MAGRAMA 2013). Samples were preserved in 4% formaldehyde, and the macroinvertebrates identified to the lowest taxonomic resolution possible, usually genus, but with some Chironomidae and Ceratopogonidae identified to subfamily or tribe. Overall, 194 macroinvertebrate taxa were identified.

Macroinvertebrate effect and response traits were characterized. Effect traits describe the potential contribution of macroinvertebrate organisms to ecosystem functioning through the trophic transfer of resources and energy from basal to higher organisms (Suding et al. 2008). Response traits characterize the resistance and resilience of communities to disturbances and, thus, inform on community responses to environmental changes (Suding et al. 2008; McLean et al. 2019). For the effect traits, trophic characteristics of each genus (i.e. grazers, miners, xylophagous, shredders, gatherers, active and passive filterers, predators, parasites and others) were gathered from the Freshwater Information Platform (http://www.freshwaterecolo gy.info; Moog 2002; Schmidt-Kloiber and Hering 2015). Response traits were compiled from Tachet et al. (2010; Table S1). For each genus, traits were assigned using a fuzzy coding approach (i.e. a degree of affinity assigned to each trait category, according to the frequency of occurrence within the genus; Chevenet et al. 1994).

For genera without traits or for taxa not identified to genus, the averaged data from other genera within the same family or from family-level traits were used. This was the case for 24 taxa identified to genus, as well as for the Chironomidae and Ceratopogonidae identified to subfamily or tribe (see Data Accessibility Statement). Prior to analysis, fuzzy-coded data were converted into percentages of affinity for each trait.

Characterization of flow intermittence and anthropogenic impacts

The degree of flow intermittence at each site was obtained from different descriptors. First, TREHS (Temporary Rivers Ecological and Hydrological Status) software (http://www.lifet rivers.eu/products/trehs-software/; Gallart et al. 2017) was used to classify the rivers' regime and to identify potential hydrological alterations (Table S2) to differentiate sites affected by natural flow intermittence from those with human-driven flow intermittence.

The degree of flow intermittence during the study period (i.e. from April 2015 until December 2015) was calculated from temperature data loggers (UA-002 HOBO), from which is possible to infer the aquatic phases (Gungle 2006). Two data loggers were installed at each site: one in a riffle, to determine the day flow ceased and resumed, and one in a pool, to identify the day the reach dried completely. Data were used to calculate two descriptors of flow intermittence for each site: the number of days in the disconnected pool phase since the last sample was taken (DP_i), and the total number of zero-flow days (i.e. disconnected pool or dry riverbed) during the 30-week study period (ZF_T).

The extent of anthropogenic impacts at each site was measured using the number of impacts in the Mediterranean reference criteria (MRC), which include invasive species, diffuse pollution sources, land-use intensity, riparian vegetation, river geomorphology, instream habitat conditions and hydrological alterations (Sánchez-Montoya et al. 2009). To facilitate interpretation, the number of MRC index impacts (i.e. 0 = non-impacted, to 20 = extremely impacted) was used as a descriptor variable (hereafter, number of impacts; see Table S3 for more details). Physicochemical parameters of each river were also measured in every sampling occasion, and were the following: dissolved oxygen, conductivity, temperature, phosphates, nitrates and Chl-a (Table S2). However, only the number of impacts was used as it represented a broad spectrum of impacts and was correlated with most of the physicochemical parameters in our dataset (Table S2) and elsewhere (Sánchez-Montoya et al. 2009).

Metrics calculation

Two types of metrics were calculated for each sample to characterize biotic responses to flow intermittence and the anthropogenic impacts: widely used and functional. As widely used metrics, taxonomic richness based on invertebrate families (Sfam) or genera (Sgen) and several tolerance-based biological indices used in the Iberian Peninsula were calculated: IBMWP (Alba-Tercedor et al. 2002), IASPT (Jáimez-Cuéllar et al. 2002), and IMMi-T (Munné and Prat 2009; Table 1).

For the functional metrics, functional redundancy (i.e. FR; the number of taxa or individuals contributing similarly to an ecosystem function, here a trophic function) and response diversity (i.e. RD; how functionally similar taxa respond to natural disturbance and anthropogenic impacts; Suding et al. 2008) were calculated (Figure 2). For FR metrics, using a classification of macroinvertebrates into functional trophic groups (i.e. effect traits; see Appendix 1) was used to obtain the average abundance (ab) and trait richness (i.e. presence–absence; pa) for the entire community and each trophic group: omnivorous, shredders, predators, grazers, gatherers and filterers (Figure 2, Table 1). For RD, traits related to resilience and resistance strategies (i.e. response traits; see Appendix 1) were used to estimate functional richness (FRic, Villéger et al. 2008) and functional dispersion (FDis, Laliberté and Legendre 2010; hereafter, RD) for the whole community and each trophic group, all of them using abundance (ab) measures (Figure 2, Table 1).

Statistical analysis

Two datasets were analysed. One considered all data collected during aquatic phases (i.e. flow and disconnected pools), to identify metrics that respond to anthropogenic impacts independently of flow. The second dataset included only flowing-phase samples, as required in current river biomonitoring protocols. To determine the reliability of each metric to detect anthropogenic impacts across a gradient of flow intermittence, linear mixed-effects models (LME) were fitted with a Gaussian error distribution to model all metric responses. Before analyses, to reduce distribution skewness and improve linearity, a square-root-transformation was applied to Sfam, Sgen and IBMWP, and a log- or square-root-transformation was applied to almost all functional metrics. Predictor variables (i.e. the number of impacts, DP_i and ZF_T) were standardized to mean = 0 and SD = 1 to allow for model coefficient comparison.

Table 1. Community metrics used in this study. Functional redundancy (FR) and response diversity (RD) metrics were calculated using effect and response traits, respectively. Type of data: FR and RD were calculated as the average abundance (ab) and/or richness (i.e. presence–absence; pa) for each functional trophic group and for the entire community. Omnivorous taxa had mixed feeding habits, including a variety of shredding, grazing and gathering affinities. See Section 2 for further details.

Widely used	MWP	Iberian Biological Monitoring Working Party (Alba-Tercedor et al., 2002)	pa
		Functional redundancy of the entire community	pa, ab
Functional redundancy	.predators	Functional redundancy of the predator functional group	pa, ab
	.gatherers	Functional redundancy of the gatherer functional group	pa, ab
	.omnivorous	Response diversity of the omnivorous functional group	ab
Response diversity	.grazers	Response diversity of the grazers functional group	ab
	ic	Functional richness of the response traits	ab

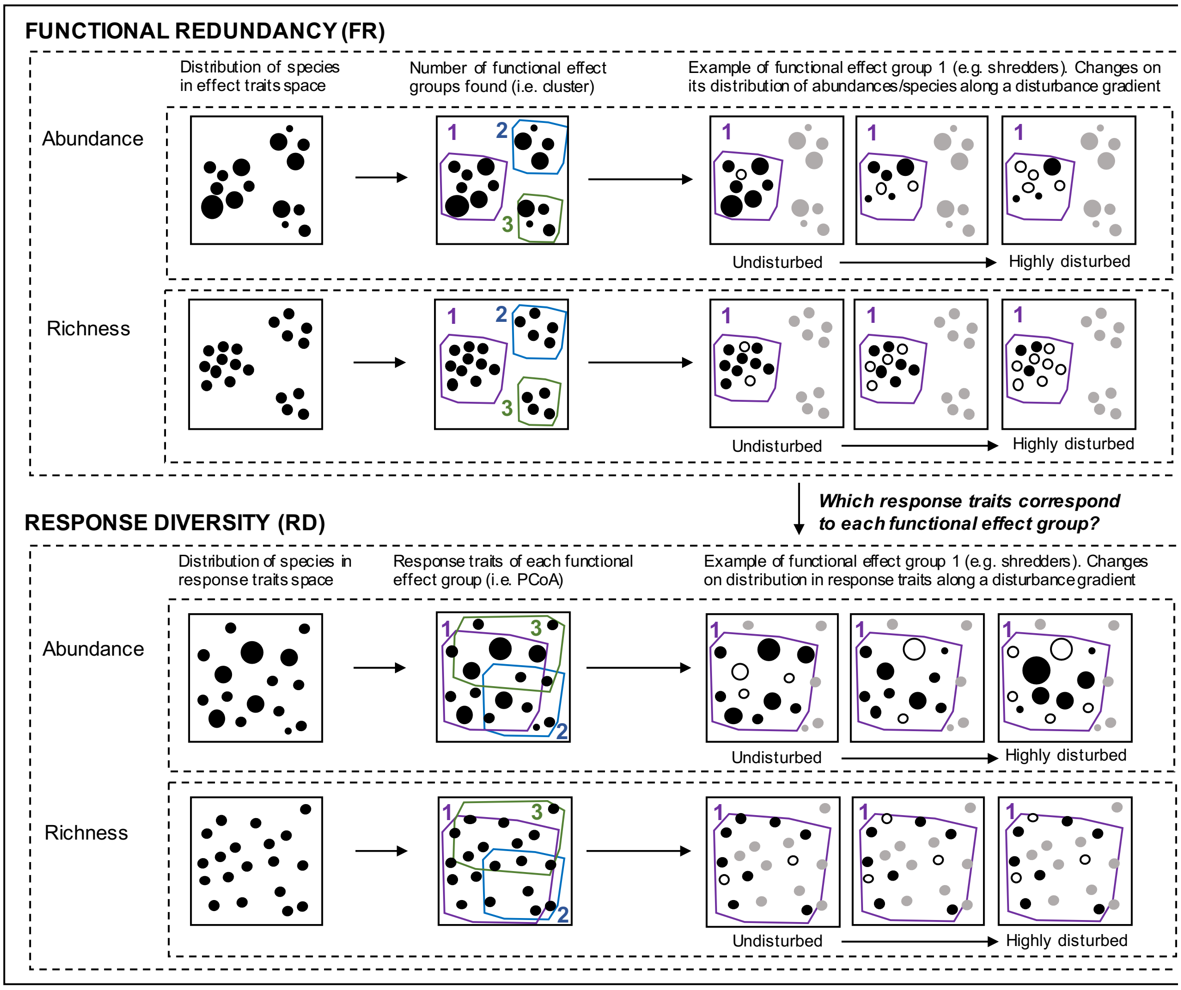


Figure 2. Analytical framework for the functional metrics used in this study (i.e. functional redundancy, FR, and response diversity, RD). For FR functional trophic groups were used as effect traits. For RD biological traits related to resilience and resistance strategies were used as response traits (Table S1). Both FR and RD are represented as the average abundance (ab) or trait richness (i.e. presence–absence; pa) for each functional group. Circle size is proportional to abundance. Black circles: species present; white circles: species absent; grey circles: species not included in the functional effect group of the example (i.e. shredders). PCoA, Principal Coordinate Analysis.

For all the aquatic phases dataset, the LMEs were fitted using the number of impacts, DP_i and ZF_T and their pairwise interactions as fixed factors (i.e. DP_i × number of impacts, and ZF_T × number of impacts). For the flowing-phase dataset, the same analysis was performed, but excluding DP_i. All models included site as a random factor to account for the non-independence of samples collected from the same location. A multimodel inference approach was adopted to quantify the predictor's standardized effect sizes and significance. See Appendix 2 for more details.

For each metric, the combined effect type was determined using the regression coefficient sign (+ or −) and p-value of individual predictors and their interactions (Feld et al., 2016). Under this framework, a non-significant interaction term and one significant predictor coefficient indicate a single effect, whereas two or more significant single predictor coefficients indicate an additive effect. Interactive (antagonistic, synergistic or opposing) effects were identified by a significant ($p < 0.05$) or potential (p-value between 0.05 and 0.25) interaction and a single interaction explaining the conditional goodness of fit (rc^2) ≥ 5% of variance. Negative coefficients for individual predictors with a positive interaction coefficient indicated an antagonistic effect. Negative individual predictor and interaction coefficients indicated a synergistic effect. Different coefficient signs between individual predictors indicated an opposing effect. Effective metrics should be responsive to anthropogenic impacts (i.e. explaining a high percentage of total variance and the marginal goodness of fit or $r^2m > 0.20$), and show a similar pattern across a gradient of flow intermittence, which is reflected by non-interactive responses. For all predictors (i.e. number of impacts, ZF_T and DP_i), null models were used to determine whether observed functional metric responses to anthropogenic impacts reflected taxonomic variation (i.e. the probability of finding more or fewer abundance or trait categories due to the number of taxa; see Appendix 3).

All analyses were conducted in R version 3.4.1 (R Core Team 2015), using the packages “lme4” (Bates et al. 2015), “MuMIn” (Barto’n 2017) and “variancePartition” (Hoffman and Schadt 2016). The code and functions used to run these analyses are available at Data Accessibility Statement.

RESULTS

Overall, metrics decreased with increasing the number of impacts and with flow intermittence predictors (i.e. DP_i and ZF_T; Table 2 and Table 3). However, responses varied between metrics and between datasets (i.e. flowing phase and all aquatic phases).

Widely used metrics

All widely used metrics were negatively related to the number of impacts, explaining >50% of total variance (Tables S4 and S5). A single effect of the number of impacts on the flowing phase dataset (but not all the aquatic phases dataset) was found for IBMWP (Figure 3h, Table 3). For other widely used metrics, the most common effect was the antagonistic (Figure 3, Tables 2 and 3). All widely used metrics from both datasets were identified as responsive metrics ($r^2m > 0.20$), with r^2m values ranging from 0.39 to 0.54 for all the aquatic phases dataset (Table 2) and from 0.24 to 0.43 for flowing phase samples (Table 3). According to the criteria in Figure 1, IBMWP is reliable for flowing phase assessments in both perennial and intermittent rivers (i.e. universal metric; Table 4), whereas other widely used metrics would require calibration before use in intermittent rivers.

Table 2. LME results from the all aquatic-phases dataset. R^2m: marginal goodness of fit. R^2c: conditional goodness of fit. (-): not selected in the top model. ns: non-significant effect. Significant p-values (< 0.05) are indicated as * for all variables. Potential p-values (i.e. between 0.05 and 0.25) are also indicated for interactions as (.). Nº impacts: number of impacts. DP_i: number of days in the disconnected pool phase since last sample was taken. ZF_T: total number of zero flow days. See Table 1 for further details about metrics.

	Intercept	Nº impacts	ZF_T	DPi	Nº impacts × ZF_T	Nº impacts x DP_i	R^2m	R^2c	Effect type: Nº impacts x ZF_T	Effect type: Nº impacts x DPi
Sfam	5.488	-0.105 *	-2.725	-0.003	0.262 (.)	-	0.39	0.77	antagonistic	single
Sgen	6.392	-0.135 *	-3.529	-0.006	0.355 (.)	-0.0001	0.45	0.75	antagonistic	single
IBMWP	0.973	-0.024 *	-0.379	-0.002	0.056 (.)	0.0001	0.31	0.82	antagonistic	single
IASPT	0.982	-0.032 *	-0.762	-0.004 *	0.083 (.)	0.0003	0.44	0.73	antagonistic	additive
IMMiT	1.045	-0.045 *	-1.116 *	-0.005 *	0.126 *	0.0002	0.54	0.86	antagonistic	additive
FR.pa	1.316	-0.006	-0.265	0.001	-0.031 (.)	-0.0002	0.22	0.22	synergistic	ns
FR.ab	3.949	0.064 *	1.481	-0.005	0.187	-	0.23	0.47	single	single
FR.omnivorous.pa	1.453	-0.085 *	-2.332 *	-0.004	0.278 *	-	0.32	0.62	antagonistic	single
FR.shredders.pa	1.093	-0.043 *	-0.272	-0.01	-	0.001 (.)	0.23	0.36	single	antagonistic
FR.predators.pa	3.913	-0.092 *	-3.085 *	0.001	0.244 (.)	-	0.39	0.65	antagonistic	single
FR.grazers.pa	1.671	-0.016	-0.161	-0.005 *	-	0.0004	0.10	0.57	ns	single
FR.gatherers.pa	9.262	-0.274 *	-7.735 *	-0.02	0.922 *	-0.004 (.)	0.34	0.56	antagonistic	synergistic
FR.filterers.pa	1.492	-0.023	-0.914	-0.005	0.099 (.)	0.001 (.)	0.13	0.28	antagonistic	antagonistic
FR.omnivorous.ab	4.476	-0.328 *	-5.028	-0.033	1.498 *	-0.003	0.33	0.64	antagonistic	single
FR.shredders.ab	2.097	-0.083 *	-0.171	-0.01	-	-	0.09	0.26	single	single
FR.predators.ab	5.261	-0.133 *	-3.665	0.004	0.471 *	-	0.2	0.39	antagonistic	single
FR.grazers.ab	5.307	-0.103	-1.879	-0.014	0.761 *	0.001	0.15	0.42	antagonistic	ns
FR.gatherers.ab	6.592	0.061	1.242	-0.016	0.292	-0.001	0.06	0.43	ns	ns
FR.filterers.ab	4.616	-0.069	-3.565	-0.044	0.307	0.009 *	0.15	0.19	ns	antagonistic
RD.ab	1.101	-0.002 *	-0.037 *	0	0.006 *	-0.00002	0.36	0.36	antagonistic	single
RD.omnivorous.ab	0.059	-0.003	-0.012	0	-	-	0.03	0.08	ns	ns
RD.shredders.ab	0.111	-0.008 *	-0.005	-0.002	-	0.0002 (.)	0.17	0.23	single	antagonistic
RD.predators.ab	0.465	-0.004	-0.043	0.001	-	-0.0004 *	0.33	0.33	ns	opposing
RD.grazers.ab	0.452	-0.007 *	-0.145	0	0.005	-	0.11	0.1	single	single
RD.gatherers.ab	0.156	-0.005 *	0.010	0	-	-	0.16	0.16	single	single
RD.filterers.ab	0.287	-0.016 *	-0.372	0.001	0.028	-	0.29	0.45	single	single
FRic	0.235	-0.011 *	-0.194	0	0.023 (.)	-	0.35	0.71	antagonistic	single

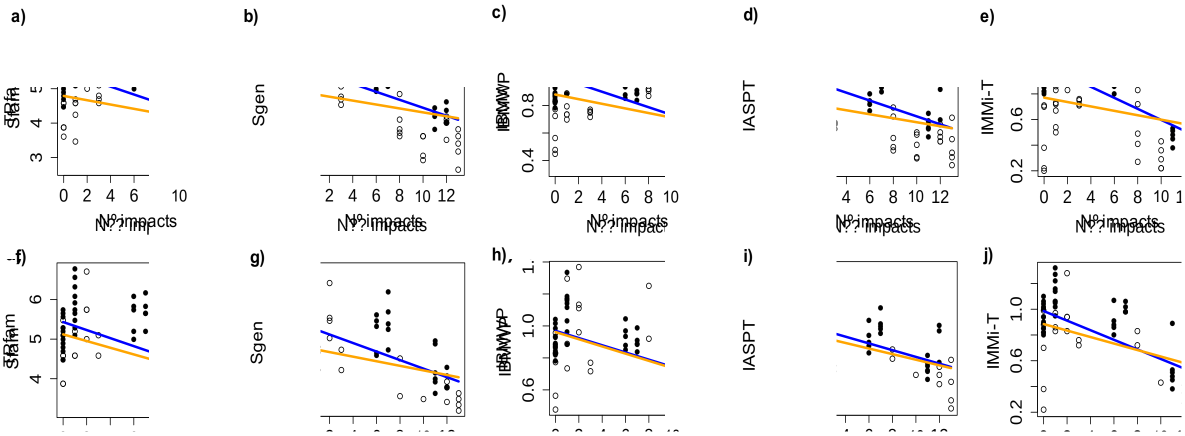


Figure 3. Plots showing the individual response of the five widely used metrics from the all aquatic-phases dataset (Sfam, Sgen, IBMWP, IASPT and IMMi-T; a to e, respectively; Table 1) and the flowing-phase dataset (f to j) along an anthropogenic impacts gradient (Nº impacts). Full circles represent perennial rivers and empty circles intermittent ones. Fitted values for LMEs models are represented as blue lines for perennial rivers and as orange lines for IRs. All responses were antagonistic except for h, for which a single effect was observed.

New functional metrics

The number of impacts explained >50% of the variance for most functional metrics but, in some cases, ZF_T, DP_i and their interactions with the number of impacts explained a similar percentage (Tables S4 and S5). A single effect of the number of impacts was observed for several FR and RD metrics (Tables 2 and 3): FR.ab, FR.shredders.ab, RD.grazers.ab, RD.gatherers.ab and RD.filterers. ab for all the aquatic phases dataset, and FR.ab, FR.shredders.pa, FR.filterers.pa, RD.shredders.ab, RD.grazers.ab, RD.gatherers.ab and RD.filterers.ab for the flowing phase dataset. Among them, the most responsive metrics (r^2m > 0.20) were FR.ab (r^2m = 0.23) and RD.filterers.ab (r^2m = 0.29) from all the aquatic phase dataset, and FR.filterers.pa (r^2m = 0.33) from the flowing phase dataset (Table 4). Following our criteria (Figure 1), FR.ab, FR.filterers.pa and RD.filterers.ab represent universal metrics (Table 4), with FR.ab and RD.filterers.ab reliable for samples collected in both flowing and disconnected pool phases, and FR.filterers.pa reliable only for flowing phase samples.

Table 3. Results of LMEs from the dataset including only the flowing phase. See Table 2 for further details.

Sfam	-0.104	-2.441	0.258 (.)	0.71	antagonistic
IMMiT	-0.039	-1.058 *	0.126 *	0.87	antagonistic
FR.shredders.pa	-0.043	-0.283	-	0.21	single
FR.omnivorous.ab	-0.346	-5.472	1.922 *	0.76	antagonistic
FR.gatherers.ab	0.072	1.519	-	0.53	ns
RD.shredders.ab	-0.009	0.016	-	0.18	single
FRic	-0.011	-0.197	0.027 (.)	0.63	antagonistic

For other functional metrics showing significant responses to predictors, the number of impacts and ZF_T resulted in interactive effects. For the aquatic phase dataset, nine metrics showed an antagonistic response and one synergistic (Table 2), whereas for the flowing phase dataset, all interactive metrics showed an antagonistic response (Table 3). We also observed interactions between the number of impacts and DP_i resulting in four antagonistic, one synergistic and one opposing effect on the aquatic phase metrics (Table 2). Among them, several functional metrics were identified as responsive metrics (r^2m > 0.20), with r^2m values ranging from 0.20 to 0.39 in the aquatic phases dataset, and from 0.24 to 0.45 in the flowing phase dataset (Table 4). According to our criteria (Figure 1), these metrics could be reliable in intermittent rivers after non-proportional calibration.

Table 4. Selection of the most responsive metrics (r^2m > 0.20) in detecting anthropogenic impacts in perennial and intermittent rivers. See Figure 1 for details of metric designation.

Universal (i.e. no calibration needed)	Functional	YES	b
	Widely used	NO, only valid during flowing phase	WP
proportional calibration; adapting reference conditions and response gradient to anthropogenic impacts)			hredders.pa
			redators.ab
	Widely used	YES	n
			i-T

Null models indicated that all predictor terms had non-random effects on FR.pa, FR.ab and FR.omnivorous.pa models including all aquatic phases (Table S6) and, thus, functional metric responses reflected anthropogenic impacts and/or flow intermittence, not taxonomic variation. For the flowing phase dataset, several metrics had non-random effects on all model terms (i.e. FR.ab, FR.omnivorous.pa, FR.predators.pa, FR.omnivorous.ab, FR.predators.ab and FRic models; Table S7), and null models indicated that the number of impacts term had non-random effects on all models except for FR.shredders.ab and FR.filterers.ab (Table S7).

DISCUSSION

Our results showed that natural disturbances (i.e. flow intermittence) could confound biological quality assessments by altering metric responses to anthropogenic impacts. Most of our widely used and new functional metrics decreased with increasing anthropogenic impacts, but showed an interactive antagonistic response with flow intermittence. Thus, most metrics would not accurately indicate the biological quality of intermittent rivers, and would require calibration (Fig. 1c). However, the widely used IBMWP index and few functional metrics could provide reliable biological assessments in intermittent rivers when applied during the flowing phase, and the functional redundancy based on the whole community abundance (FR.ab) remained effective even in disconnected pools.

Compared to perennial rivers, aquatic communities in intermittent rivers typically support fewer taxa and a higher proportion of generalists, due to environmental harshness (Bogan et al. 2017; Soria et al. 2017). As a result, the usefulness of many widely used biomonitoring metrics based on taxon diversity is limited, especially when using standard values obtained from perennial rivers (Prat et al. 2014; Chiu et al. 2017). Similar limitations of widely used metrics have been observed in other naturally disturbed ecosystems such as when using riparian plant communities as indicators in intermittent rivers (Bruno et al. 2016) or when using invertebrates in estuaries (Elliott and Quintino 2007) or saline rivers (Gutiérrez-Cánovas et al. 2019). Nonetheless, our results suggested that one widely used metric, the IBMWP index, could be applied in intermittent rivers during flowing phases. This aligns with other studies in Mediterranean-climate rivers (e.g. Munné and Prat 2011; Mazor et al. 2014; Prat et al. 2014), which suggest that widely used metrics may work at intermittent sites if flowing phases are sufficiently long and predictable (Gallart et al. 2012, 2017). For example, Munné and Prat (2011) found no differences for IBMWP between perennial and intermittent rivers during wet years, as flow permanence in intermittent rivers was high. However, during dry years, IBMWP values varied considerably even if samples were collected during flowing phases (Munné and Prat 2011). Thus, the wide spatial and temporal hydrological variability within intermittent rivers (e.g. different dry phase duration at different locations at different years) could produce misleading bioassessment results in most cases (Mazor et al. 2009; Chessman et al. 2010; Papastergiadou and Manolaki 2012), especially in less predictable, seasonal climate types (Tonkin et al. 2017). Hence, to avoid misleading biological quality assessments in intermittent rivers, either existing metrics need to be recalibrated (e.g. by incorporating long-term variability in these metrics) or new metrics, as those presented here, require development (Munné and Prat 2011; Stubbington et al. 2018).

Most of our new functional metrics responded differently at perennial and intermittent sites, as evidenced by antagonistic effects. Our results align with recent studies considering flow intermittence and salinity as natural disturbances combined with other anthropogenic impacts (Belmar et al. 2019; Gutiérrez-Cánovas et al, 2019). The fact that intermittent rivers often showed a weaker reduction in functional metrics may reflect strong trait filtering in naturally disturbed ecosystems (Mouillot et al. 2013). Moreover, traits enabling species' persistence in certain naturally disturbed environments may contribute to be co-tolerance of other disturbances (Vinebrooke et al. 2004). In intermittent rivers, resistance and resilience traits that enable species to persist in highly variable flow conditions might also enable them to persist under certain anthropogenic impacts (Bonada and Resh 2013; Belmar et al. 2019). For example, macroinvertebrates with mechanisms for tolerating low dissolved oxygen concentrations may in turn be indicative of either flow intermittence or organic pollution (Stubbington et al. 2017). Thus, metrics that indicate adaptations to flow intermittence could be used for biomonitoring anthropogenic impacts only if they are calibrated differently for perennial and intermittent rivers.

Our results also identified functional metrics with similar responses to anthropogenic impacts in perennial and intermittent rivers (i.e. single effect), indicating their ability to detect impacts regardless of flow intermittence. The most responsive metrics during flowing phases were functional redundancy based on the whole community abundance (FR.ab) and the filterers presence–absence (FR.filterers.pa), as well as abundance-weighted response diversity of filterers (RD.filterers.ab), with FR.ab also responsive in disconnected pools. Thus, for example, the decrease in RD.filterers.ab with increasing anthropogenic impacts indicates a reduction in resistance and/or resilience traits (i.e. response traits) within this functional trophic group. The decrease in FR.filterers.pa also evidenced taxonomic homogenization within this functional trophic group as the number of anthropogenic impacts increased (Laliberté et al. 2010; Gagic et al. 2015). For example, genera such as Chimarra or Ephemera were not observed when the number of impacts increased. Our results thus indicate that metrics derived from functional trophic groups that are not affected by natural disturbances, could act as universal metrics in naturally disturbed ecosystems such as intermittent rivers.

By using the response-effect trait approach, functional metrics may provide detailed information on environmental changes and their effects on ecosystem functioning (Suding et al., 2008; Laliberté et al. 2010; Mouillot et al. 2013). Response diversity (RD) metrics might help to differentiate community responses to both natural disturbances and anthropogenic impacts, whilst functional redundancy (FR) metrics based on effect traits might help to anticipate the effects of that change on ecosystem functioning (Suding et al. 2008). For example, the decrease in FR for filter feeder taxa

(FR.filterers.pa) might affect organic matter processing and thus change ecosystem functioning (Bogan et al. 2017). As a consequence, community structure might also be less resistant to environmental changes and therefore increase the vulnerability to future anthropogenic impacts (Gutiérrez-Cánovas et al. 2015; McLean et al. 2019). Similarly, the distinct decrease of FR and RD metrics in the predator functional trophic group (i.e. FR.predators.pa, FR.predators.ab and RD.predators.ab) in intermittent rivers could signal potential effects of anthropogenic impacts on predation rates, and inform about cascade effects stemming from reduced predator abundance (Hooper et al. 2012; Rodríguez-Lozano et al. 2015).

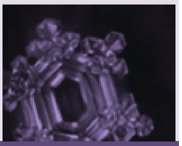
Given the different predictability, duration and spatial patterns of the aquatic phases in intermittent rivers (Bonada and Resh 2013; Leigh and Datry 2017), our proposed functional metrics could contribute to improved bioassessment of these rivers. As most of the widely used metrics were not reliable during flowing phases nor disconnected pools, calibration is needed considering their response gradient to anthropogenic impacts. Even though the widely used IBMWP index detected anthropogenic impacts in intermittent rivers during flowing phases, this needs to be considered with caution as its reliability may vary between wet and dry years (Munné and Prat 2011). In this case, information on the degree of flow intermittence, seasonal predictability and temporal patterns of flowing phases is required (Gallart et al. 2017). Compared to widely used metrics, the functional redundancy based on whole community abundance (FR.ab) could be even applied during disconnected pools. Besides, functional metrics are more accurate in detecting ecosystem degradation and may represent a step forward in the management of naturally disturbed ecosystems (e.g. Bruno et al. 2016; Belmar et al. 2019). These metrics might enable prediction of biological responses to intensifying anthropogenic impacts in a climate change context (Belmar et al. 2019). Therefore, water managers should start incorporating alternative functional metrics in the routine biomonitoring of naturally disturbed rivers. Regardless of the biomonitoring metrics used, distinguishing natural from human-induced flow intermittence and assessing the degree of hydrological alteration of a river is crucial (Gallart et al. 2017). Future research should test both widely used and new functional metrics in datasets encompassing multiyear time periods, across different climates, and for specific anthropogenic impacts, as well as on other taxonomic groups.

ACKNOWLEDGEMENTS

The study was supported by the LIFE+ TRivers (LIFE13 ENV/ES/000341) project. We acknowledge the contribution of FEHM lab members and students who participated in fieldwork. C.G.-C. was supported by a "Juan de la Cierva-Formación" research contract (MINECO, FJCI-2015-25785). We especially thank Rachel Stubbington for her supervision and useful suggestions that greatly improved the manuscript.

CHAPTER 4

Adapting participatory processes in river management: insights from temporary rivers



ABSTRACT

Participatory processes can help to promote a more sustainable and equitable management of water resources and equally engage citizens in management. In this sense, the European Water Framework Directive (WFD) mandates to incorporate the participation of stakeholders and the general public in the development and updating of the river basin management plans. Yet, the WFD implementation has been mainly focused on perennial rivers without considering temporary rivers properly, neither in biomonitoring programs nor participatory processes.

This paper aims at adapting participatory processes in river basin management to enhance the inclusion of ecosystems with poor or no social recognition such as temporary rivers.

To do so, we examined previous experiences of participatory processes conducted in the WFD and adapted them to propose and implement an approach for promoting stakeholders' engagement in temporary rivers. The approach is based on a collaborative leadership, includes multiple participatory engagement mechanisms, uses future global change scenarios and the concept of ecosystem services at different stages of the process, and aims at involving stakeholders not only in the proposal of measures stage but in the diagnosis of the ecological status. It also includes an evaluation of participants' satisfaction on the process. We tested our approach in temporary rivers from the Mediterranean region.

We found that the combination of environmental education and citizen science activities, together with the inclusion of the ecosystem services concept, was the most useful way to raise awareness on the biodiversity and ecological value of temporary rivers and to promote stakeholders' engagement. Workshops conducted during the diagnosis stage played an important role in both including stakeholders' suggestions and increasing their knowledge on temporary rivers. Further, envisaging climate-related future scenarios allowed participants to incorporate measures that could tackle new and emerging pressures on these ecosystems. As future environmental changes will increase the proportion of rivers with temporary flow regimes, our approach can contribute to adapt current participatory processes to future needs.

1. INTRODUCTION

Participatory processes are included in most international, regional and national environmental policies as a tool to engage society in decision–making (Aguirre-Muñoz et al. 2008; Razzaque 2009). Such engagement ensures the consideration of economic, political, ecological, cultural and social aspects, and is key for defining realistic environmental targets and increasing the success of management actions (Carayannis and Campbell 2010; Crowley at al. 2017). Participatory processes are usually built on comprehensive and holistic approaches in which all local community members and other interested parties are involved (Razzaque 2009; Carayannis and Campbell 2010), using a wide variety of engagement mechanisms (Reed 2008). The most commonly used participatory engagement mechanisms consist of surveys, interviews, workshops, scientific dissemination and environmental education activities (Reed 2008; Videira et al. 2006), which can be applied alone or in combination. Recently, few initiatives have also included citizen science projects as a tool to increase public engagement in environmental decision-making (When et al. 2015; Gray et al. 2017; Mukhtarov et al. 2018). Others have incorporated the ecosystem services concept (Jorda-Capdevila et al. 2016) or envisage future scenarios related to management actions to tackle new and emerging pressures on the environment (Kallis et al. 2006; Quevauviller 2011; Verkerk et al. 2017).

In the last decades, participatory processes have been incorporated in water–related policies to promote a more sustainable and equitable management of water resources and to freely and equally engage citizens in management (Carr 2015; Hand et al. 2018). For example, in Europe, the Water Framework Directive (WFD) explicitly requests every member state to conduct participatory processes when elaborating river basin management plans (EC 2000). Similarly, in the United States, the Environmental Protection Agency encourages public participation in different environmental and conservation management decisions, also including river basin management plans (RCRA 2016).

Despite participatory processes are a key aspect in river management, they have been mainly focused on perennial rivers. Temporary rivers, those that recurrently stop flowing and may dry out completely, represent nearly 50% of the current global river network and support several unique and endemic aquatic and terrestrial biota (Datry et al. 2017a,b). Beyond providing ecosystem services typical of perennial rivers, temporary rivers provide additional services such as unique genetic material from endemic species of these ecosystems among others (Datry et al. 2017b). However, these ecosystems are still rarely recognized and their management is still in its infancy compared to that in perennial rivers (Datry et al. 2017a,b). For example, temporary rivers are usually eluded by flow gauging networks (Gallart et al. 2016), not always incorporated in biomonitoring programs and their ecological quality is not fully assessed (Stubbington et al. 2018). Besides, their wide spatial and temporal hydrological variability can produce misleading bioassessment results (Soria et al. 2020). Moreover, in most cases, society seems to hold these rivers in low esteem and they are often associated to environmental degradation (Leigh et al. 2019a). In this context, participatory processes in temporary rivers management remain scarce (but see Conallin et al. 2018). Incorporating temporary rivers in participatory processes could contribute to improve their current management and to increase their social recognition. Considering that many perennial rivers are expected to change to temporary flow regimes as a result of global change and increased human demands for water resources (Döll and Schmied 2012; Datry et al. 2017b), developing participatory processes in temporary rivers may help adapting current river management practices to future environmental changes.

Here, we aim at adapting participatory processes in river basin management to enhance the inclusion of ecosystems with low social recognition, such as temporary rivers. We first examine previous experiences of participatory processes under the WFD by summarizing the main approaches and mechanisms used in the development of river basin management plans. Second, we propose an approach to be applied in temporary rivers based on information extracted from these experiences. Third, we apply our approach in Mediterranean-climate temporary rivers from Spain. Finally, we emphasize the main challenges encountered and highlight the insights gained from this experience.

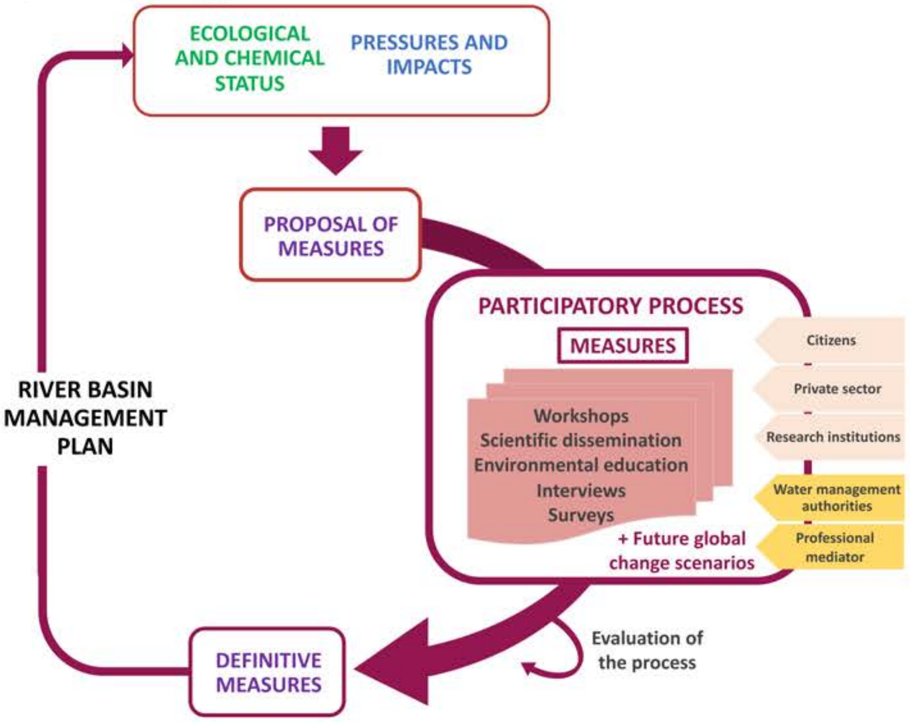
2. PARTICIPATORY PROCESSES UNDER THE WATER FRAMEWORK DIRECTIVE: APPROACHES, MECHANISMS AND INCLUSION OF TEMPORARY RIVERS

In the European Union, the WFD provides a common framework for the management and protection of surface and ground water bodies (EC 2000). It aims at achieving a ‘good status’ in water bodies, which is measured in terms of chemical and ecological status for surface waters, and chemical and quantitative status for groundwater (EC 2000). The WFD mandates member states to define river basin districts as a management framework; designate their water bodies as artificial, heavily modified or natural; and implement river basin management plans (RBMP) and programs of measures (PoMs) to achieve their ‘good status’ (EC 2000). The implementation proceeds in six-year cycles and requests the development and updating of both documents with the active involvement of stakeholders and the general public (EC 2000) (Fig. 1a).

Even though recommendations on how to conduct participatory processes under the WFD exist (ComEC 2003), there is still a lack of standardized methodology and information on the effectiveness of the different approaches and mechanisms (Newig and Koontz 2014; Kochskämper et al. 2016; Boeuf and Fritsch 2016). Notwithstanding, identifying the leadership of the process, the potential groups to be engaged (i.e. stakeholders), the timing for their incorporation and the mechanisms for their engagement are key aspects to be considered (Videira et al. 2006; De Stefano 2010; Porter and Birdi 2018). In addition, after conducting a participatory process, it is important to evaluate whether the process was perceived as satisfactory, and if there was a real influence on the planning process with tangible results (Videira et al. 2009; De Stefano 2010; Kochskämper et al. 2016). Here, we scrutinized peer review publications on official participatory processes conducted since 2003 for the development and implementation of RBMPs and PoMs, which resulted in 23 records from 12 countries (see Appendix 1 for more details). We checked for the type of leadership, type of stakeholders participating and if they were incorporated at early stages of the process, the mechanisms used to engage them, and the evaluation of the participatory process. Regarding the mechanisms and tools used to engage stakeholders, we assessed the use of surveys, interviews, workshops, scientific dissemination, environmental educational activities and citizen science. For the evaluation of participatory processes, we assessed the satisfaction of participants in terms of their perception on the use of engagement mechanisms and leadership, and the real influence of the process on the planning process. In addition, we found convenient assessing if the concept of ecosystem services and future global change scenarios were considered, as previous studies showed their relevance to increase public awareness on rivers' current and future environmental decision-making (Kallis et al. 2006; Jorda-Capdevila et al. 2016). We also checked if any of the scrutinized publications included temporary rivers or not to assess their level of exclusion in participatory processes conducted in Europe.

As summarized in Table 1, three main type of leadership have been implemented in participatory processes from Europe: (a) lead by water management authorities, (b) collaborative leadership between research institutions and water management authorities, and (c) a bottom-up initiative from stakeholder's groups with no formal lead (Pahl-Wostl 2006). Our synthesis on the participatory processes indicated that those lead by water management authorities or those with a collaborative leadership were the most common, while only one case included a bottom-up initiative. Regarding the engagement of stakeholders, the Guidance on Public Participation from the WFD (ComEC 2003) presents a list of potential groups, which include governmental administration (at European, national, regional and local levels), professionals in the public and private sector, non-governmental organizations (NGOs) and individual citizens. In Table 1, we divided stakeholders as citizens, the public administration, research institutions and the private sector. Citizens include both the general public and specific sectors, such as local associations, community groups and environmental NGOs.

a) Participatory process within the WFD context



b) Our proposal

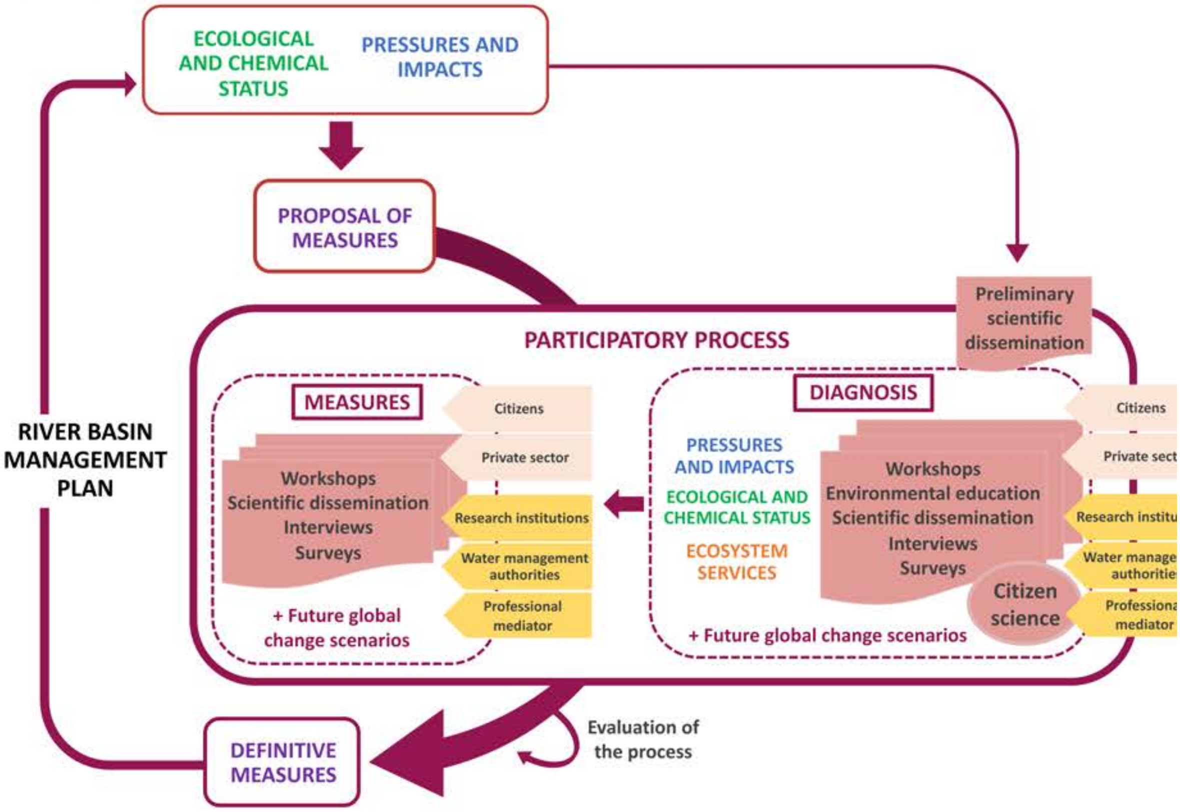


Figure 1. Diagram on the approach of a participatory process in river basin management plans within the current WFD context (a), and our proposal to enhance the inclusion of temporary rivers (b). The leadership is indicated in yellow. Dashed lines indicate the two stages proposed within a participatory process: diagnosis and measures.

Public administrations include those related to the implementation of water management measures, such as the public water agencies or government-owned water companies, but also other local municipalities such as town and regional councils. Universities and entities/institutes related to the process were included in Table 1 as research institutions. The private sector includes agri-food and stock sectors, as well as medium-small farmers, tourism sector, private water managers and other possible water-related industries. Most case studies included citizens and governmental administration as stakeholders, whereas research institutions and the private sector were not always present (Table 1). Regarding the timing of incorporation of stakeholders, all case studies included them at early stages of the process (Table 1). Among the different mechanisms to engage stakeholders, the most common were interviews, surveys, workshops and scientific dissemination, but very few studies used a combination of more than three of them (Table 1). Environmental education was only used in one case and citizen science was not included in any of the studies. Participatory processes were perceived as satisfactory in most cases, except for 2 studies out of 10, for which stakeholders suggested that there was not enough time for questions and meaningful discussion (Kochskämper et al. 2016) or that the government limited their involvement and fell back to the aims already contained in the old plans (Liefferink et al. 2011). Only 3 studies out of 10 showed that there was a real influence on the planning process (Table 1). For the rest, the process was not fair due to the lack of influence on the planning process (e.g. Belfast, Lough and Lagan basins in UK), or because the social context of the process ended up being just a first draft for further planning (e.g. Miera and Campiazo basins in Spain).

The ecosystem service concept was only included in one case with the objective of increasing public awareness on rivers (Table 1). Despite the WFD allows to incorporate climate-related water risks information when developing the RBMP (EC 2009; Quevauviller 2011), only two participatory processes envisaged clear future global change scenarios that could involve a deterioration (e.g. growth of mass tourism) or an improve of the status of water bodies (e.g. balanced development, emphasis on water conservation). Due to climate change is expected to reduce water availability, identifying future locally-relevant challenges for the management and adaptation of river basins is key (Verkerk et al. 2017). Finally, despite temporary rivers are common across the European river networks, especially in the Mediterranean Basin (Stubbington et al. 2018), none of the participatory processes included them (Table 1), evidencing the need to ensure their full consideration in RBMP.

Table 1. Participatory processes conducted in the context of the WFD linked to the development of official river basin management plans. They were classified by (a) type of leadership, (b) stakeholders' engagement, (c) timing of their involvement (i.e. whether stakeholders were included since the beginning of the process or not), (d) participatory engagement mechanisms used, (e) evaluation of the process, and by the consideration of (f) citizen science information, (g) future global change scenarios, (h) ecosystem services and (i) temporary rivers. na: data could not get from the article. See Appendix 1 for further details.

		Spain	**Greece**	**Portugal**	**Germany**	**Denmark**	**France**	**The Netherlands**	**Germany**	**Spain**	**United Kingdom**
		(Kallis et al., 2006)	*(Kallis et al., 2006)*	*(Videira et al. 2009)*	*(Moellenka et al. 2010)*	*(Lieffrink et al. 2011)*	*(Lieffrink et al. 2011)*	*(Lieffrink et al. 2011)*	*(Kochskämper et al. 2016)*	*(Kochskämper et al. 2016)*	*(Kochskämper et al. 2016)*
Type of leadership	**Water management authorities**	×	✓	×	×	✓	✓	×	✓	×	✓
	Collaborative	✓	×	✓	✓	×	×	×	×	✓	×
	Bottom-up initiative	×	×	×	×	×	×	✓	×	×	×
Type of stakeholders involved in the process	**Citizens**	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Public administration	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Research institutions	✓	×	✓	✓	×	×	✓	×	✓	×
	Private sector	✓	✓	✓	✓	×	✓	✓	×	×	×
Inclusion of stakeholders at early stages of the process		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Type of participatory engagement mechanisms	**Workshop**	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Interview	✓	✓	✓	×	na	na	✓	×	×	×
	Survey	✓	×	×	✓	na	na	×	×	×	✓
	Scientific dissemination	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Environmental education	×	×	✓	×	×	×	×	×	×	×
Evaluation items	**Satisfaction with the process**	✓	✓	✓	✓	×	✓	✓	✓	✓	×
	Real influence	×	×	×	×	×	✓	✓	✓	×	×
Inclusion of citizen science information		×	×	×	×	×	×	×	×	×	×
Inclusion of future global change scenarios		×	✓	✓	×	×	×	✓	×	×	×
Inclusion of ecosystem services		×	×	×	✓	×	×	×	×	×	×
Inclusion of temporary rivers		×	×	×	×	×	×	×	×	×	×

3. ADAPTING PARTICIPATORY PROCESSES TO INCLUDE TEMPORARY RIVERS

Temporary rivers are among the most underprotected and poorly managed of all freshwater ecosystems (Leigh et al. 2019a). Due to the high hydrological variability of these ecosystems and the lack of gauging data, obtaining information of their hydrological regime is way more complex. Integrating as many sources of information as possible is therefore key to improve its hydrological and ecological evaluation and, in turn, improve the measures to be implemented. In this sense, the involvement of both local citizens and stakeholders can result in a powerful tool for a complete understanding of the hydrological characteristics of temporary rivers. In addition to biomonitoring-related difficulties, the lack of management and protection of these ecosystems may be partly because society usually holds them in low esteem and as synonym of environmental degradation (Acuña et al. 2017; Leigh et al. 2019a). For instance, when analysing statements about rivers' aesthetic and recreational provision, more positive attitudes were observed towards perennial than temporary rivers (Leigh et al. 2019a). This can negatively affect participatory processes conducted in temporary rivers, as stakeholder engagement might be more difficult and require greater efforts compared to perennial rivers (Conallin et al. 2018; Leigh et al. 2019a). Here we propose an approach that could benefit temporary river management adapting previous experiences conducted in Europe (section 2). Our approach builds on the idea of raising awareness on the biodiversity value of these ecosystems (Leigh et al. 2019a) and on the ecosystem services they provide (Datry et al., 2017b), combined with a strategic design of the participatory process to potentially achieve better social and decision-making outcomes. We argue that the following elements will be key to engage stakeholders in temporary rivers: (1) establishing a collaborative leadership of the process and accurately analyse the potential stakeholders to be involved, (2) using multiple participatory engagement mechanisms and tools, (3) incorporating future global change scenarios, (4) considering the concept of ecosystem services at different stages of the process, (5) involving stakeholders not only in the proposal of measures but also in the diagnosis of ecological status, and (6) evaluating the outcomes of the process (Fig. 1b).

3.1. A collaborative leadership of the process and an accurate analysis of stakeholders

The success or failure of a participatory process can be determined by how stakeholders with different backgrounds tackle a problem, e.g. role of power, views of environment vulnerability and management style (Gray 2004; De Stefano 2010; Porter and Birdi 2018). In this sense, the collaboration between representatives from management, research and private consultants (i.e. professional mediators) in public participation can help approaching stakeholders’ perspectives and facilitate the resolution of potential conflicts (Moellenkamp et al. 2010; Porter and Birdi 2018). Thus, instead of a leadership conducted by water management authorities (Fig. 1a), we considered that a collaborative approach that includes other parties can offer a more adaptive water management (Fig. 1b). For example, water management authorities can bring existing networks of stakeholders, but they might lack procedural knowledge on how to design and conduct a participatory process (Kochskämper et al. 2016). Instead, research institutions can design and evaluate the participatory process from inception to end, and an external professional mediator (i.e. not related to any of the stakeholders) can help to align all the parties and coordinate all the activities (Moellenkamp et al. 2010; Kochskämper et al. 2016). Research institutions can also complement the evaluation conducted by water management authorities by providing information from other sources. This can be especially useful for processes involving temporary rivers, since in most cases they are excluded from the WFD biomonitoring (Stubbington et al. 2018). Finally, to optimize the inclusion of stakeholders, we also recommend a more specific stakeholder analysis to identify representatives of all groups, which can be done through a first round of surveys or interviews asking for their willingness to participate (Reed 2008; De Stefano 2010).

3.2. Using multiple participatory engagement mechanisms and tools

The use of combined participatory engagement mechanisms and tools contributes to increase public awareness and knowledge about values and benefits of rivers (Kallis et al. 2006; Mostert et al. 2007). Within all mechanisms, those that promote open and constructive dialogues between stakeholders can enhance individuals’ problem-solving and decision-making skills and, thus, benefit the outcomes of the process (Videira et al. 2006; Varner 2014; Mukhtarov et al. 2018). These mechanisms include workshops and environmental education activities (Fig. 1a,b). To maximize the exchange of information between participants, we consider that workshops should be the central participatory mechanism, complemented with other supporting mechanisms. Moreover, complementary participatory engagement mechanisms, such as scientific dissemination, surveys and interviews should be included (Fig. 1a,b), as well as other visual mechanisms such as video, photovoice or art-based, among others.

Scientific dissemination using information panels, leaflets, newspapers and online platforms can contribute to offer information on the status of water bodies and main pressures and impacts to the entire community, as well as increase public awareness and their interest in participating (Fig. 1b). This is especially relevant in the case of temporary rivers, as stakeholders involved in the participatory process might not be aware of the biodiversity and ecological value of these ecosystems nor of their current status. To include those stakeholders that cannot attend face-to-face workshops but may have relevant contributions to the participatory process, the use of an online survey can be useful. Indeed, the field of online public participation is in a growth phase with many emerging opportunities for all stakeholders, as it empowers and engages far more participants (Gray et al. 2017; Mukhtarov et al. 2018).

In addition, at present there are several citizen science projects that can provide tools to be used along a participatory process of rivers (Gray et al. 2017; Mukhtarov et al. 2018; Krabbenhoft and Kashian 2020). Some of them include features that can be especially useful to increase stakeholders' awareness and knowledge on temporary rivers, such as CrowdWater (CrowdWater website 2020), The Barrier Tracker (Portal Amber International website 2020), Stream Tracker (Stream Tracker website 2020) or RiuNet (RiuNet website 2020) mobile applications. Further, their use can also be useful to collect data of these ecosystems before the process starts and, thus, complement data provided by water management authorities or research institutions.

3.3. Incorporating future global change scenarios

Changes in biodiversity and ecosystem functioning caused by global change are affecting the ecological and chemical status of rivers and the ecosystem services they provide (MA, 2005; Jorda-Capdevila et al. 2016). In this context, river basin management practices should be adapted to future environmental changes such as the increase of temporary flow regimes as a result of more extreme droughts and increased human demands for water resources (Döll and Schmied 2012; Datry et al. 2017a). Thus, the incorporation of future global change scenarios is key to ensure a more adaptive and integrated management of rivers (Kallis et al. 2006; Quevauviller 2011). In fact, it is expected that member states implementing the WFD clearly demonstrate how global change projections have been considered in the pressures and impacts assessment, in the monitoring programmes, and in the PoMs (EC 2009). In addition, focusing on a future goal can also help to energize brainstorming in the participatory process (Kallis et al. 2006). In our approach, we suggest that stakeholders identify which factors could involve a deterioration of the temporary rivers ecological status in the future, and incorporate this information when developing the RBMP and PoMs (see section 3.5). To do so, we propose to include a medium-long term scenario (e.g. >20-30 years), which might vary depending on the characteristics of the river basin district and the member state (Kallis et al. 2006; Jager et al. 2016). Additionally, expected changes on the delivery of ecosystem services could also be incorporated (see section 3.4).

3.4. Incorporating the concept ecosystem services

Rivers provide essential ecosystem services, including provisioning, regulation and cultural services (MA, 2005). In the case of temporary rivers, even when the riverbed is completely dry, they can offer services such as walking trails, a source of medicinal plants or migration corridors for animals (Datry et al. 2017b). When developing the final PoMs, the prioritization of the measures usually consider the effects of management actions on the status of water bodies but not on the human well-being resulting from changes in the provision of ecosystem services (Terrado et al. 2016). The combination of both the status of water bodies and their ecosystem services conditions might help stakeholders to prioritize those optimal management actions according to the cost-effectiveness criteria required by the WFD and, thus, improve decision-making in selecting suitable measures and the implementation of RBMPs (Terrado et al. 2016). In addition, several studies have shown that incorporating the concept of ecosystem services in participatory processes of the WFD can contribute to increase public awareness on rivers' environmental and conservation issues, and to enhance participants' engagement (Jorda-Capdevila et al. 2016; Grizzetti et al. 2016). We therefore suggest incorporating the concept of ecosystem services during the participatory process and provide the necessary information for the participants to distinguish the most relevant ecosystem services provided by each water body, and link them with the management measures listed in the RBMP and PoMs (see section 3.5). We think that this step could strengthen participant's understanding of the impact of the proposed measures on the environment and, thus, represent a step forward for increasing social engagement in water-related decision making (Terrado et al. 2016). This might be especially relevant when incorporating temporary rivers due to the inherent social-ecological complexity of these ecosystems (Datry et al. 2017b; Leigh et al. 2019a). Cultural ecosystem services such as landscape aesthetics, cultural relevance, religion and spirituality, education and research, public use, way of transport and recreation seem to be easier to link with changes in the state of the environment by the general public and, thus, can better contribute to promoting awareness on these ecosystems (Jorda-Capdevila et al. *in revision*).

3.5. Involving stakeholders in the diagnosis before the proposal of measures

Effective decision-making in participatory processes requires access to relevant information but also the capacity to contribute with reliable information (Tippet et al. 2005; De Stefano 2010). To develop this capacity, all participants should have an adequate level of empowerment about the topic (Mostert et al. 2007; Moellenkamp et al. 2010; Porter and Birdi 2018). In addition, not only communication but active participation from all participants should be promoted since the beginning of the process, that is, knowledge of the topic should be transferred from water authorities to other stakeholders but also the other way around. Therefore, knowledge should be held to be the product of processes on which all participants collaborate closely (Pouliot 2009). In this sense, involving participants in the diagnosis and assessment of the target ecosystem could: (1) increment their knowledge before measures are proposed and discussed, (2) help to raise awareness on the biodiversity and ecological value of these ecosystems, and (3) provide complementary data to water management authorities. This becomes even more important when conducting a participatory process in ecosystems with poor or no social recognition such as temporary rivers which, in turn, may lack monitoring data due to the lack of gauging stations in most of these ecosystems (Gallart et al. 2016). Our approach proposes to incorporate a river diagnosis step prior to the proposal of measures resulting in a two-stage participatory process: (1) diagnosis and (2) measures (Fig 1b).

3.5.1. The diagnosis stage

The diagnosis stage aims at engaging stakeholders and gathering new information on the impacts and status of water bodies (i.e. hydrological, ecological and chemical status). To increment participants' knowledge and awareness on the water bodies to be worked on, we suggest to provide them all the available information on the status and impacts of these ecosystems (see section 3.2). Such information can be obtained from monitoring and/or research programs conducted by water management authorities and researchers, respectively, and, when available, from citizen science projects (Gray et al. 2017; Mukhtarov et al. 2018; Van Cauwenbergh et al. 2018). To gather new information of each water body from participants, they can contribute to their diagnosis by double-checking the information provided by the organizers and/or identifying new ones when necessary. In addition, an evaluation of ecosystem services (see section 3.4), together with an activity on future global change scenarios could be incorporated to complement the diagnosis (see section 3.3). We therefore suggest that participants identify which future factors could cause a deterioration of the status of water bodies and the ecosystem services they provide, as well as potential changes in the current pressures and impacts. As the use of multiple mechanisms is crucial to conduct a successful participatory process (see section 3.2), we also propose conducting an environmental education activity within the diagnosis workshop. One example could be organizing a short field trip to a temporary river nearby the workshop location using citizen science (see section 3.2). Including these complementary activities within the workshop could contribute to raise awareness on temporary river management, implement an adequate level of empowerment to all participants, and show them how they can contribute to the diagnosis in the future (Conallin et al. 2018).

3.5.2. The measures stage

The measures stage corresponds to the traditional participation process to review the PoMs before its implementation (EC 2009). Typically, water agencies conduct a workshop in which all stakeholders and a mediators are involved (Fig. 1a,1b). In this workshop, management measures are exposed by water agencies via scientific dissemination mechanisms (e.g. Lieffrink et al. 2011; Kochskämper et al. 2016). In turn, participants provide their contributions to obtain a final prioritization of measures (EC 2009). Compared to traditional workshops on measures, we suggest to incorporate the results gathered in the previous diagnosis workshop. To do so, participants can contribute by double-checking if impacts and pressures detected in the diagnosis workshop had measures from the RBMPs associated and/or by identifying new ones. Ideally, participants should be the same ones from the diagnosis workshop. To include ecosystem services (see section 3.4), we propose that the workshop includes activities where participants can link the proposed measures with their effects on the provision of selected ecosystem services. Future global-change scenarios identified in the diagnosis workshop can also be considered here. This can be done using different methods, such as reference ranking with criteria, relative preference ranking or pair-wise ranking (Anyaegbunam et al. 2004). This will give stakeholders the opportunity to identify which measures could contribute the most to improve the status of water bodies.

3.6. Evaluating the outcomes of the participatory process

The evaluation of the outcomes is required to increase social learning (i.e. learning from practice) on public participation in river management (Tippet et al. 2005; Mostert et al. 2007; Varner 2014). Lessons learned from participatory processes of the WFD have shown the benefits and challenges in involving stakeholders (e.g. Videira et al. 2006; Kochskämper et al. 2016), but little is known about its effectiveness when incorporating temporary rivers. In this sense, regardless of the ecosystem considered, participants can be asked to identify the factors fostering or hindering the outcomes of the process, e.g. the role of stakeholder involvement, politics and institutions, opportunities for interaction, openness and transparency (Mostert et al. 2007; Parés et al. 2015). Considering previous experiences in Europe (Table 1), we suggest that any evaluation process should ask participants to: (1) conduct a short survey to evaluate whether the process was satisfactory (e.g. activities, leadership, timing, stakeholder engagement), and (2) evaluate whether there was a real impact of the participants’ contributions to the RBMPs (e.g. which new measures were included). Finally, we suggest to share all the outcomes through both scientific literature and online databases (Varner 2014).

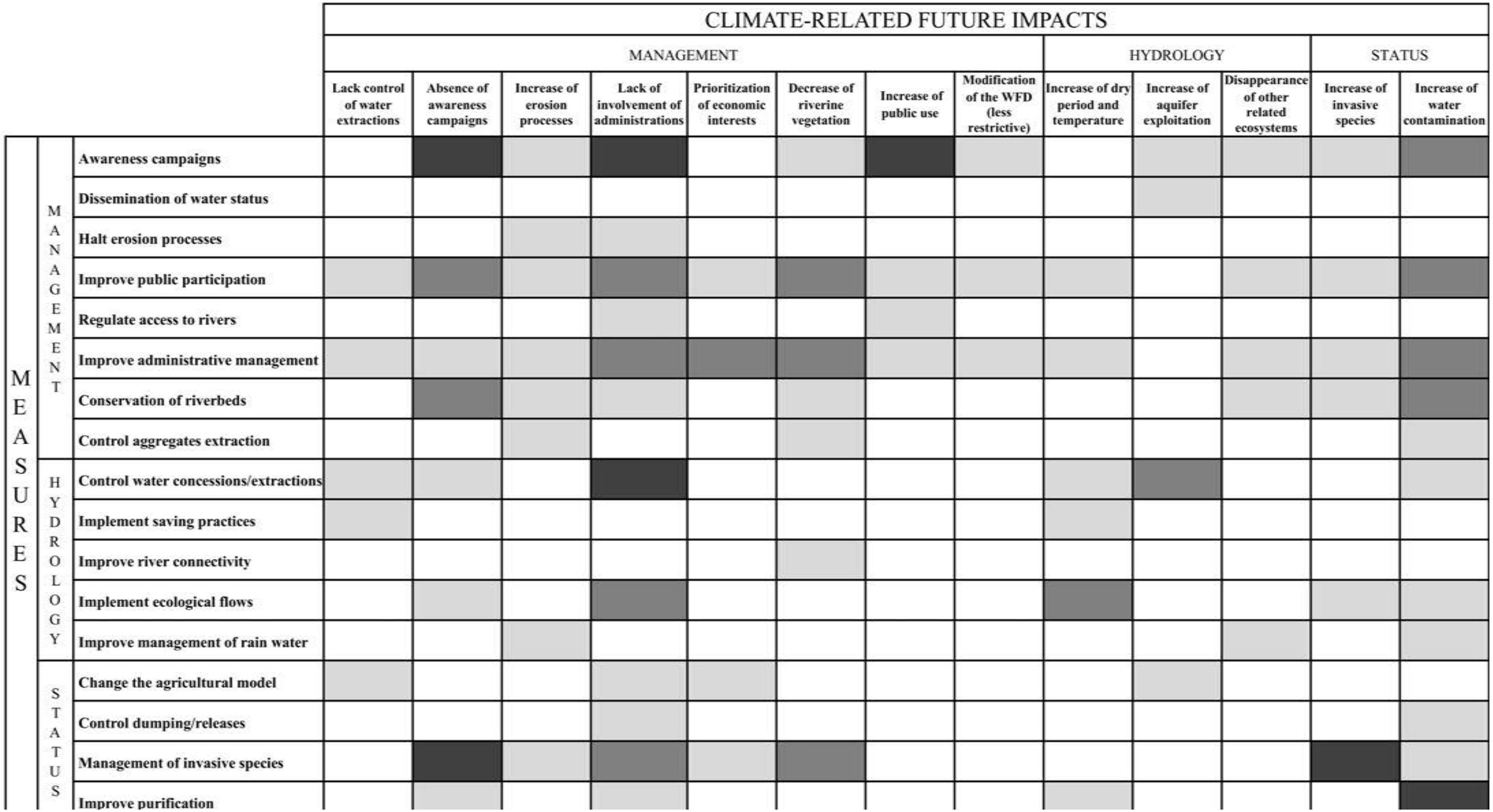
4. A CASE STUDY FROM MEDITERRANEAN-CLIMATE TEMPORARY RIVERS

Between June 2017 and May 2018 we conducted a participatory process and implemented the approach described in the previous section. Our process included Mediterranean-climate riverine water bodies belonging to 3 different river basin districts in Spain (Ebro, Júcar and the Catalan River Basin District). These water bodies were study sites of the project LIFE+ TRivers (http://www.lifetrivers.eu/), which aimed at developing operational methods for implementing the WFD in temporary rivers. Eleven perennial and eleven temporary water bodies were included (Fig. S1). These 22 water bodies were grouped in 5 areas of participation: Girona, East Tarragona, West Tarragona, South Tarragona and Castelló and Valencia (Fig. S1). Overall, our participatory process included several local users (e.g. citizens living nearby the water body), nine local environmental associations and NGOs, two private entities, five research institutions, six local municipalities (i.e. town and regional councils), and two water management authorities (Table S1). Our participatory process developed dissemination activities before the participation process and implemented a collaborative leadership between water management authorities, research institutions and a professional mediator (see details in Appendix 2).

The diagnosis and measures workshops were structured as explained in section 3.5, but few specific aspects need to be highlighted. For the diagnosis workshop, we included all stakeholders except citizens water management authorities' representatives to allow citizens and private sector stakeholders bring their opinions independently of the official constraints. In this workshop, researchers and the mediator exposed the four different main topics: management, hydrology, ecological status and ecosystem services (Fig. S2a,b). The concept of ecosystem services was explained to the participants focusing on cultural services. Then, the contributions on pressures and impacts of each water body from participants, as well as on cultural ecosystem services (see section 3.4), were conducted with a brainstorming dynamic (Anyaegbunam et al. 2004) (Fig. S2c,d). Participants also identified which future factors related to global change and other anthropogenic impacts could involve a deterioration of the status of water bodies in future-scenarios (see section 3.3). For the sake of simplicity and comparisons purpose between areas of participation, participants' contributions and factors related to global change were grouped by general themes and divided in three main topics: management, hydrology and ecological status. To conclude the diagnosis workshop, an environmental education activity was conducted using the citizen science app RiuNet (Fig. S2e,f). Activities conducted in the diagnosis workshop resulted in participants identifying several pressures and impacts for each water body of each area of participation (Table S2). Moreover, several interviews on the hydrological regime and alterations were conducted to citizens inhabiting the study sites.

Most common contributions related to the management of pressures and impacts identified by participants were an absence of awareness programs and environmental education, a lack of involvement of the competent administrations for the conservation of temporary rivers, and a non-existence of measures to manage forests in the river basin and the riparian zone. Among the pressures and impacts related to hydrology, contributions were about a lack of control to regulate water use, an uncontrolled dumping, and an increase of water extractions. Contributions related to the ecological status were mostly about the presence of invasive species and limitations of sewage treatment plants in improving ecological status. Participants also identified 13 factors related with future global change scenarios that could involve a deterioration of these water bodies (Table S2). The most frequently selected factors in each area of participation were related to an increase of: (i) public use, (ii) invasive species, (iii) water contamination, (iv) lack of involvement of the competent administrations, and (v) absence of awareness campaigns (Fig. 2). Among cultural ecosystem services, participants identified the landscape aesthetic values as the most important one (Table S3). Spirituality and fishing-hunting cultural ecosystem services were never selected by participants. Differences in ecosystem services obtained by area were mainly related with the singularities of each site. For example, bath was identified as an important ecosystem service in areas where most of rivers were perennial and swimming was frequent. In contrast, in areas where temporary rivers had a low frequency of flow periods (i.e. ephemeral or episodic flow regimes prevailed), bath was omitted and hiking in riverbeds was the most common ecosystem service selected.

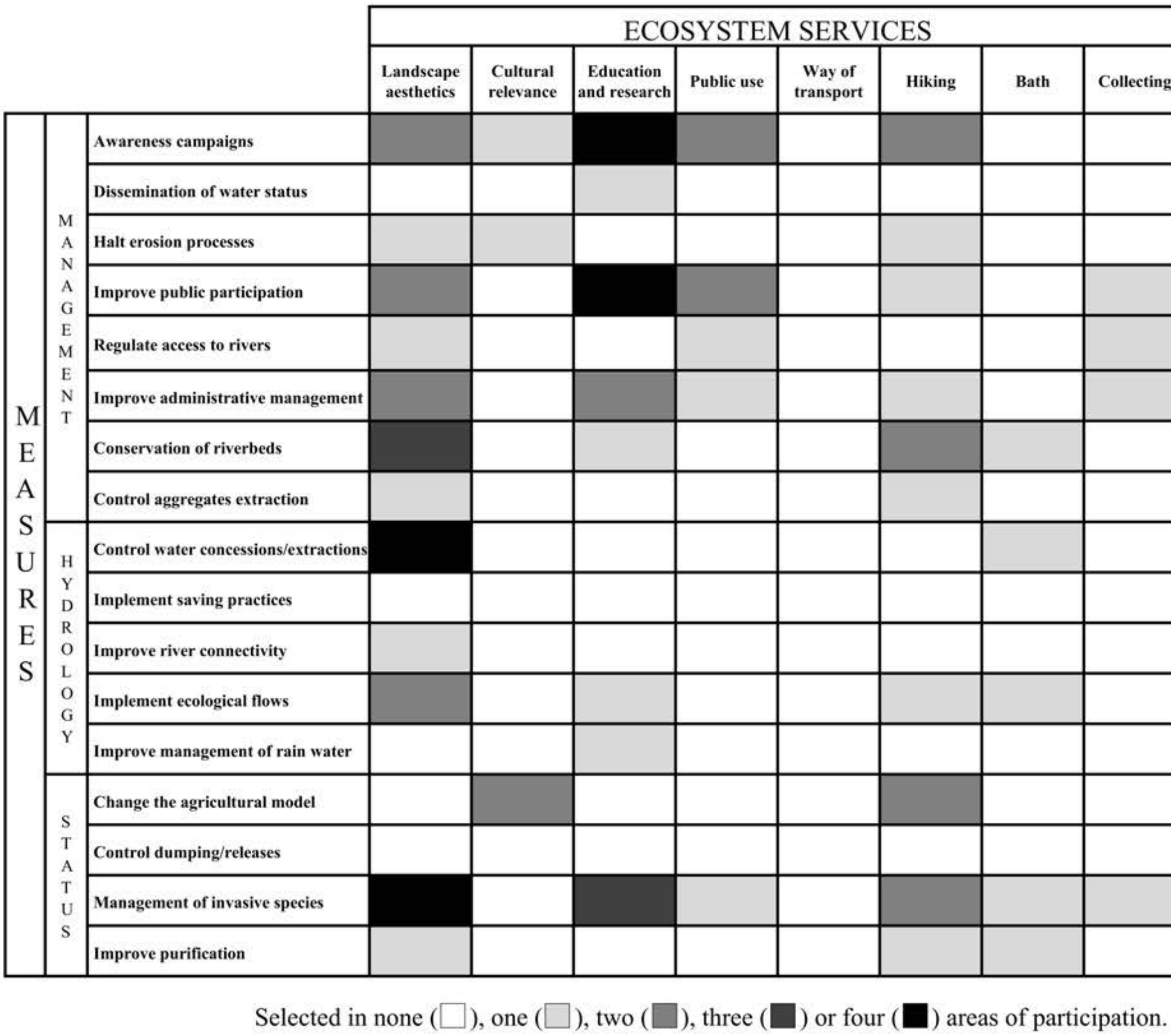
In the measures workshop participants contributed by double-checking whether impacts and pressures detected in the diagnosis workshop had associated measures and identified new ones when necessary (see section 3.5). Then, measures were prioritized according to which ones could help to mitigate climate-related future impacts on the ecosystems (Fig. S2g,h). To do so, participants assigned weights to measures (1= very effective, 2= effective). Among the measures identified by participants, eight were related to management, five to hydrology and four to the ecological status of water bodies (Table S2). The most frequently selected measures were: (i) promote social and institutional awareness campaigns; (ii) improve the control of water concessions and extractions; (iii) improve invasive species management, and (iv) improve purification (Fig. 2). Measures related to the maintenance of cultural ecosystem services were also identified and linked to the proposed measures. Among cultural ecosystem services, landscape aesthetics and education-research were the most frequently linked to the proposed measures by face-to-face participants (Fig. 3). Landscape aesthetics ecosystem service was mostly linked to measures such as establishing clear guidelines for the conservation of the riverbed and its riverside vegetation or controlling water extractions or improving management of invasive species. Regards to education-research one, it was mostly linked to measures related to social and institutional awareness campaigns or improve public participation, but also to the improvement of management of invasive species.



			CLIMATE-RELATED FUTURE IMPACTS											
			MANAGEMENT								HYDROLOGY			STATUS	
			Lack control of water extractions	Absence of awareness campaigns	Increase of erosion processes	Lack of involvement of administrations	Prioritization of economic interests	Decrease of riverine vegetation	Increase of public use	Modification of the WFD (less restrictive)	Increase of dry period and temperature	Increase of aquifer exploitation	Disappearance of other related ecosystems	Increase of invasive species	Increase of water contamination
MEASURES	MANAGEMENT	Awareness campaigns		▓	░	▓		░	▓	░		░	░	░	▒
		Dissemination of water status										░			
		Halt erosion processes			░	░									
		Improve public participation	░	▒	░	▒	░	▒	░	░	░		░	░	▒
		Regulate access to rivers				░			░						
		Improve administrative management	░	░	░	▒	▒	▒	░	░	░		░	░	▒
		Conservation of riverbeds		▒	░	░		░					░	░	▒
		Control aggregates extraction			░			░							░
	HYDROLOGY	Control water concessions/extractions	░	░		▓					░	▒			░
		Implement saving practices	░								░				
		Improve river connectivity						░							
		Implement ecological flows		░		▒					▒			░	░
		Improve management of rain water			░								░		░
	STATUS	Change the agricultural model	░			░	░					░			
		Control dumping/releases				░									░
		Management of invasive species		▓	░	▒	░	▒						▓	░
		Improve purification		░		░					░				▓

measure identified by face-to-face participants in workshops. Measures are divided by management, hydrology and ecological status of water body.

At the end of both workshops, a short survey was conducted to allow participants to evaluate the quality and learnings of the process (see section 3.6). According these surveys, participants were highly satisfied with the whole process and the associated activities (Table S5). For example, satisfaction with the time schedule and duration of the activities, the use of multiple mechanisms, and the opportunity of give their opinions freely were all scored high. In relation to the evaluation of the stakeholders' engagement, participants suggested that the inclusion of the environmental education activity conducted through the RiuNet citizen science project was the most successful format to learn the main topics of the process and provided a helpful experience. Participants also evaluated positively that their contributions to the RBMPs were directly linked to a formal decision-making process.



			ECOSYSTEM SERVICES							
			Landscape aesthetics	Cultural relevance	Education and research	Public use	Way of transport	Hiking	Bath	Collecting
MEASURES	MANAGEMENT	Awareness campaigns	▒	░	■	▒	□	▒	□	□
		Dissemination of water status	□	□	░	□	□	□	□	□
		Halt erosion processes	░	░	□	□	□	░	□	□
		Improve public participation	▒	□	■	▒	□	░	□	░
		Regulate access to rivers	░	□	□	░	□	□	□	░
		Improve administrative management	▒	□	▒	░	□	░	□	░
		Conservation of riverbeds	▓	□	░	□	□	▒	░	□
		Control aggregates extraction	░	□	□	□	□	░	□	□
	HYDROLOGY	Control water concessions/extractions	■	□	□	□	□	□	░	□
		Implement saving practices	□	□	□	□	□	□	□	□
		Improve river connectivity	░	□	□	□	□	□	□	□
		Implement ecological flows	▒	□	░	□	□	░	░	□
		Improve management of rain water	□	□	░	□	□	□	□	□
	STATUS	Change the agricultural model	□	▒	□	□	□	▒	□	□
		Control dumping/releases	□	□	□	□	□	□	□	□
		Management of invasive species	■	□	▓	░	□	▒	░	░
		Improve purification	░	□	□	□	□	░	░	□

Selected in none (□), one (░), two (▒), three (▓) or four (■) areas of participation.

ecological status of water body.

In parallel, an online survey was developed to include the inputs of those stakeholders that were not able to attend. The design, structure and questions of these surveys were divided in sections following the contents of the face-to-face diagnosis and measures workshops. As a result, the most common contributions to the diagnosis of water bodies identified through online participants were about uncontrolled dumping, insufficient sewage treatment, lack of information about temporary rivers, poor management of riverine vegetation, illegal water extractions, regulation infrastructures, and invasive species (Table S6). Consequently, several climate-related future impacts were identified by online participants, where the most recurrent were related to an increase of the dry period and temperature and aquifer exploitations, but also to a lack of involvement of the competent administrations and an absence of awareness campaigns (Table S6). Among cultural ecosystem services, online participants also identified the landscape aesthetic values as the most important one. Concerning the measures, the most frequently ones were related to promote social and institutional awareness campaigns and public participation, control water concessions and extractions and improve river connectivity (Table S6).

Once the measures proposed by both face-to-face and online participants were collected, the two water management authorities involved analysed them and assessed their feasibility in terms of implementation (Table S2). This resulted in measures that were already considered in the PoMs of the RBMPs (58%), new ones that could be accepted for the RBMPs of 2016-2021 (or will be accepted but are still studying how) (18%), those that are responsibility of other administrations (i.e. local authorities or national and regional administration) (20%), and those that should be rejected (4%) because they were not compliant with the planning purposes or because of technical, economic or timing reasons. Some examples of the most relevant measures that were incorporated in RBMPs were those related to the eradication of invasive species, the implementation of ecological flows, and the improvement of the river connectivity and the wastewater treatment systems (Table S4). Finally, both water management authorities committed to incorporate these temporary water bodies in the next RBMPs (i.e. 2022-2027).

5. LESSONS LEARNT AND KEY MESSAGES

Our approach seems to ensure a more adaptive and integrated management of rivers in general, but also of temporary rivers. Involving stakeholders not only in the proposal of measures stage but in the diagnosis of the ecological status has resulted key in our participatory process. Inputs from participants about the hydrological regime and alterations of temporary rivers were key to improve the diagnosis (Gallart et al. 2017) and, thus, to improve the related measures in the RBMPs. Indeed, interviews to the riverside inhabitants turned out to be a primary source of information, complementary to gauging records and aerial photographs (Gallart et al. 2017). Our results also suggested that using multiple mechanisms and the ecosystem service concept facilitated participatory decision-making process and increased inclusiveness. In fact, using environmental education and citizen science activities was the most useful way to raise awareness of temporary rivers. Simple monitoring methods linked to management thresholds such as the RiuNet app kept local community directly involved with the surrounding temporary rivers. Nevertheless, we observed that public knowledge and awareness towards these ecosystems varied among areas of participation due to the singularities of each site, as also suggested in Leigh et al. (2019a). This should be taken into account when promoting stakeholders' engagement with these ecosystems. For example, participants had a better understanding of temporary rivers in areas where these ecosystems were naturally ephemeral (or episodic) and they used to hike along their riverbeds. Thus, including the use of the cultural ecosystem services concept during the diagnosis stage of our process was key to increase public awareness on these ecosystems, especially in areas where they were undervalued (Jorda-Capdevila et al*. in revision*). Further, the use of the ecosystem services concept has increased since the second cycle of the RBMPs, but less evidence is available on their use in the development and updating of these RBMPs (Grizzetti et al. 2016). Despite water management authorities from several state members have high expectations for incorporating an ecosystem services approach in RMBPs, it is still in an explorative stage (Grizzetti et al. 2016).

Our approach has shown to be useful in participatory process including temporary rivers, but to promote its success it should always be adapted to the specific context of the region. For example, considering the institutional and political context, the pre-existing relationships between stakeholders, or the culture of national/local stakeholder involvement. In this sense, in some areas of participation we found a tense socio-political context due to the Catalan independence referendum that prevented some participants from attending. In other areas, difficulties were simply related to low population density. Furthermore, we observed that in areas of participation where there were not many local organizations nor NGOs, participation was lower compared to areas with strong associative network. Thus, we adapted the way of carrying out the activities according to the different characteristics of these areas of participation. In this sense, professional neutral mediators were key (Moellenkamp et al. 2010; Kochskämper et al. 2016). Another limitation observed in our participatory process was the low assistance of the private sector. For instance, agri-food and stock sectors (e.g. trade union, big industries, medium farmers) or the tourism sector did not attend. Thus, efforts to engage the private sector should be increased to obtain the engagement of 'all interested parties' equally, as promoted by the WFD (EC 2009).

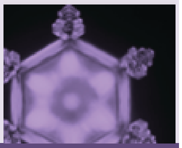
The WFD also expects member states to clearly demonstrate how global change projections have been considered in the pressures and impacts assessment in the RBMPs (EC 2009), but does not include temporary rivers in the RBMPs. Given that temporary flow regimes are increasing as a result of global change and increased human demands for water resources, river basin management practices also should be adapted to these future environmental changes (Döll and Schmied 2012; Datry et al. 2017a). In this sense, the cyclical nature of the WFD implementation brings the opportunity for incorporating new experiences in European water governance. So, why are water management authorities still not incorporating temporary rivers properly neither in the RBMPs nor in its participatory processes? Perhaps the simplest explanation is that this issue is a matter of time. Considering the on-going climate-related factors, it is clear that it will be necessary to incorporate them in the near future. In this sense, adaptive management approaches, such as ours, have the potential to aid in providing the framework to consider the complexities of temporary river systems and improve the management of these systems. Nevertheless, further research is required to increase social learning on public participation of temporary rivers.

To conclude, we consider that our approach could be applied not only in temporary rivers but also in other ecosystems with poor or no social recognition, such as urban rivers, wetlands or peatlands. In addition, these ecosystems are usually underprotected and/or not always included in biomonitoring programs, so less data is available. In this sense, incorporating knowledge from participants, as well as information from citizen science projects, can be key. Despite some participatory processes have been conducted in temporary rivers (Conallin et al. 2018), urban rivers (Moran et al. 2019), wetlands (Smrekar et al. 2020) or peatlands (Heli et al. 2019), processes in ecosystems such as perennial rivers, lakes or forests still predominate. Over the decades, these poorly recognised ecosystems have been degraded due to over exploitation of their resources and improper development activities. Since global change will further affect these vulnerable ecosystems, efforts to better consider them in management and conservation programs need to account for participatory processes too.

ACKNOWLEDGEMENTS

The study was supported by the LIFE+ TRivers [LIFE13 ENV/ES/000341] project. DJ-C was supported by a Juan de la Cierva contract (FJCI-2017-34977) and the CLIMALERT project (PCIN-2017-068) of the Spanish Ministry of Science and Innovation. We acknowledge all the participants in our workshops: citizens, local environmental associations (i.e. SITRA, Salvem Gaià, Associació medioambiental La Sénia, Associació Hàbitats, Plataforma pel riu Siurana, Plataforma Sierra de Chiva, AEMS ríos con vida, Connecta Natura and Acció Ecologista-Agró), research institutions (i.e. UAB, IRTA and CIEF), private sector (i.e. Corriols i Riberes SL, Crearqció and Fundación Natural Life) and local municipalities (i.e. La Bisbal, Alcover, La Sénia and Cheste town councils, as well as Consorci de les Gavarres and Parc Natural Tinença Benifassà).

GENERAL DISCUSSION



GENERAL DISCUSSION

This thesis provided an overview on how anthropogenic impacts might affect aquatic biodiversity in TRs (**Chapters 1 and 2**), and on how complementary approaches are required for understanding biodiversity patterns in TRs and for improving their management (**Chapters 2, 3 and 4**). This includes new perspectives on the measurement of TRs biodiversity to better target conservation efforts (**Chapter 2**), the development of new bioassessment methods able to detect anthropogenic impacts in TRs (**Chapter 3**) and the properly incorporation of TRs in the participatory processes of the River Basin Management Plans (RBMPs) (**Chapter 4**).

The thesis was mainly focused on Mediterranean-climate rivers but also provide general insights that could be considered in TRs of other climatic regions. In the following sections, we discuss the main results obtained from this thesis, provide information on novel approaches that are currently being developed, and present some future perspectives for improving the management and conservation of TRs.

TOWARDS A BETTER UNDERSTANDING OF TRs' BIODIVERSITY PATTERNS

Globally, TRs hold highly dynamic communities that typically change among flowing, disconnected pools and dry phases over space and time. Therefore, including both spatial and temporal biodiversity patterns are key to capture the full variation in their community composition (Ruhí et al. 2017; Stubbington et al. 2019a,b). Evidence shows that considering only species richness and community composition, even over time, might not be sufficient to protect the processes that maintain their ecosystem functioning (Crabot et al. 2019; Leigh et al. 2019b). To better manage and preserve aquatic biodiversity under future global change scenarios and to avoid potential ecosystem consequences of biodiversity loss, conservation efforts should be targeted towards both spatiotemporal taxonomic and functional diversity patterns. To be able to incorporate all this relevant information on community composition in conservation, however, a better understanding of TRs' biodiversity patterns is required.

The expected increase in the prevalence of TRs worldwide due to global change could result in a decrease in freshwater biodiversity

As a result of a meta-analysis on 44 published studies of perennial rivers and TRs biodiversity, we found a significantly higher biodiversity in perennial than in TRs (**Chapter 1**). Here, we focused on α diversity and, specifically, we extracted taxonomic richness from these 44 published studies. Among the taxonomic groups considered (i.e. macroinvertebrates, fish, diatoms and macrophytes), our findings suggested that biodiversity losses may be more relevant for macroinvertebrates. Moreover, our results also showed significant differences in studies conducted within arid and temperate climates, dry and wet sampling seasons, headwaters and regions subject to different levels of anthropogenic impacts. Therefore, our results provide new information on how these impacts could threaten aquatic biodiversity and how conservation efforts may best be directed.

Nevertheless, to really analyse these global trends, future research should compare perennial and TRs biodiversity in regions beyond those included here (e.g. Africa, Asia or South America) and across a wider variety of taxonomic groups (e.g. microbes). Since analysing taxonomic diversity alone might provide limited insight into the impacts of disturbance on ecosystem functioning, further studies incorporating functional (Villéger et al. 2013, 2015) and genetic diversity (e.g. Múrria et al. 2017) among perennial rivers and TRs could expand our findings.

From this thesis and other studies we can also conclude that TRs are highly dynamic in space and time, and so are their biological communities. Thus, further global studies comparing biodiversity measures such as β diversity that are able to capture such dynamism in TRs could contribute to better understand TRs' biodiversity patterns (e.g. Tonkin et al, 2017; Van der Vorste et al. *under review*).

Contribution of TRs to β diversity can inform freshwater conservation in the Mediterranean region

Our results showed that, overall, both taxonomic and functional richness were significantly higher in perennial rivers than in TRs, while local site contributions to taxonomic and functional β diversity (LCBD) were higher in TRs (**Chapter 2**). Higher LCBD values observed in TRs indicated a higher degree of ecological uniqueness of these ecosystems in terms of both species and traits composition. When comparing perennial rivers and TRs over time, there was a decrease of taxonomic and functional richness in TRs with the loss of surface flow at the beginning of summer. During the same period, however, there was an increase of taxonomic and functional LCBD in TRs. Moreover, when comparing perennial rivers and TRs over time, perennial rivers also showed certain variability over time. Compared to rivers from other climatic regions, Mediterranean-climate rivers are characterised by being highly predictable in terms of seasonality, resulting in community shifts even in perennial rivers (Bonada and Resh 2013). Nevertheless, TRs are characterized by a higher gain/loss of species and traits throughout the year (Tornés and Ruhí 2013; Leigh et al. 2019b). In addition, in our study, higher values of taxonomic and functional LCBD over time corresponded mostly to TRs during the disconnected pools phase. From a conservation point of view, our results highlight the importance of TRs to biodiversity conservation of mediterranean rivers, especially during the disconnected pool phase, suggesting that these ecosystems cannot be ignored in conservation planning strategies. This is even more relevant with the predictions of TRs increasing worldwide because of global change (Döll and Schmied 2012), which, in turn, might also increase the frequency of disconnected pools (Gallart et al. 2017; Bonada et al. 2020). Moreover, considering Mediterranean-climate TRs high spatiotemporal hydrological variability and that using taxonomic measures alone to protect biodiversity might provide limited insight into the impacts of disturbance on ecosystem functioning (**Chapter 2**), freshwater conservation planning should consider monitoring the spatiotemporal variability of both taxonomic and functional biodiversity in these ecosystems. Quantifying functional β diversity can provide valuable insights into how biodiversity loss affects ecosystem functioning and, thus, be more accurate in detecting ecosystem degradation, representing a step forward in the management of these ecosystems (Crabot et al. 2019; Leigh et al. 2019b; Sánchez-Montoya et al. 2020). In this regard, despite there has been an increase of research on spatiotemporal taxonomic β diversity in TRs (e.g. Ruhí et al. 2017; Rogosch and Olden 2019; Stubbington et al. 2019b; Sánchez-Montoya et al. 2020), our study is one of the few that also includes spatiotemporal functional β diversity patterns (but see also Crabot et al. 2019 and Leigh et al. 2019b).

Despite the strengths of our study, future research should test both taxonomic and functional spatiotemporal patterns of β diversity encompassing larger time periods to analyse both inter and intrannual flow variability (e.g. Rogosh and Olden 2019). In addition, considering that climate change can be a driver of biotic homogenization in freshwater ecosystems (White et al. 2018), further steps after this thesis would be to examine metacommunity ecology research in TRs (Cañedo-Argüelles et al. 2015; Datry et al. 2017b; Cid et al. 2020). To be able to apply these approaches in our study, however, it would be necessary to increase also the number of sampling sites along the studied rivers, and/or within each of our three river basins. Usually, biotic homogenization is evaluated by comparing spatial turnover of species between time periods (Olden et al. 2004; White et al. 2018) and there are several approaches, such as partitioning the LCBD into turnover and nestedness components (i.e. replacement and richness LCBD; Legendre 2014). For instance, in studies conducted in TRs with macroinvertebrates or fish using the

LCBD approach (e.g. Ruhí et al. 2017 and Rogosh and Olden 2019; respectively), they observed that species replacement (turnover) contributed more than differences in species richness (nestedness) to the total β diversity. Analysing these components, therefore, may provide insights into conservation strategies, as an increase in turnover through time implies that conservation must target numerous sites to maintain γ diversity, whereas an increase in nestedness suggests a few key sites for protection (Socolar et al. 2016). Moreover, since biotic homogenization might be either referring to genetic, taxonomic or functional homogenization, future research should also enquire into all three types of homogenization (Villéger et al. 2017; Múrria et al. 2017).

Finally, from a conservation point of view, current approaches on systematic conservation planning (Hermoso et al. 2013) should be applied to TRs, considering all biodiversity components and dimensions for different biological groups and other relevant conservation targets, such as natural hydrological connectivity in these TRs and the importance of maintaining disconnected pools.

DISTINGUISHING NATURAL FROM HUMAN-INDUCED FLOW INTERMITTENCE IN TRs

To conduct a correct evaluation of TRs' ecological status, the prerequisite should be the correct characterization of its hydrological regime (Gallart et al. 2017). Due to the high hydrological variability of TRs and their lack of gauging data, however, classifying the hydrological regime and assessing the degree of hydrological alteration of these ecosystems is way more complicated than in perennial rivers (Datry et al. 2017b; Gallart et al. 2017). Moreover, the detection of anthropogenic impacts at TRs is challenging because the reliability of standard biomonitoring metrics is generally uncertain for such naturally disturbed systems (Chiu et al. 2017; Cid et al. 2017). Therefore, new methods for TRs bioassessment must be able to disentangle natural disturbances from anthropogenic impacts (Prat et al. 2004, Leigh et al. 2013a,b). In addition, since disconnected pools in TRs are transitional habitats of major ecological relevance in freshwater ecosystems (**Chapter 2**; Bonada et al. 2020) having tools to assess both hydrological and ecological characteristics that can be applied either during flowing or disconnected pools phases would greatly facilitate its management and conservation.

Classifying the hydrological regime and assessing the degree of hydrological alteration of a river

Recently, several methods have been developed for the correct characterization of TRs hydrological regime, such as wet-dry mapping, remote sensing (e.g. satellite images, fixed cameras), field sensors (e.g. conductivity, temperature, level and/or presence-absence of water), hydrological metrics (e.g. zero flow days), models (e.g. IHACRES or SWAT) or data from citizen science (Turner and Richter 2011; Costigan et al. 2017). Regarding the assessment of the hydrological alteration, there are also several tools that conduct the evaluation by comparing impacted hydrographs with reference ones corresponding to natural hydrological regime, which is not always available in TRs (Gallart et al. 2016). Some examples of these tools are IHA (Indicators of Hydrologic Alteration; Richter et al. 1996), ELOHA (Ecological Limits Of Hydrologic Alteration; Poff et al. 2010), IHARIS (Indicators of Hydrologic Alteration in RIverS; Martínez Santa-María and Fernández Yuste 2010) or DRIFT (Downstream Response to Imposed Flow Transformations; Brown et al. 2013) indicators. Despite its strengths, these tools present some limitations since (1) require long series of flow rates data from before and after water extractions or the construction of flow regulation structures such as dams, (2) hydrological alterations that occur on short time scales are not evaluated, and (3) groundwater alterations are not included (Gallart et al. 2012).

In this sense, in **chapters 2, 3 and 4**, we used the TREHS software tool (Temporary Rivers Ecological and Hydrological Status; see Gallart et al. 2017) to incorporate other sources of information and thus compensate for these limitations, such as: observations in situ (i.e. monitoring sampling), gauging stations (when available), satellite images (e.g. Google street view or orthophotos from the Cartographic and Geological Institute of Catalonia), and interviews to citizens inhabiting the study sites (**Chapter 4**). Moreover, to obtain information on TRs' temporal hydrological variability between flowing, disconnected pools and dry phases, in this thesis we also used temperature data loggers (UA-002 HOBO). Unlike other methods, TREHS software and temperature data loggers consider the permanence of disconnected pools phase of TRs. Since disconnected pools are key to maintain local and regional aquatic biodiversity, such methods are a step forward to better predict the temporal and spatial occurrence of disconnected pools across TRs networks (Gallart et al. 2017; Bonada et al. 2020; **chapter 2**). Future research should be focused on developing simple methods to assess hydrological metrics in disconnected pools. A possibility, for example, should be to collect water samples from disconnected pools and to assess time since disconnection using isotopic analysis (Bonada et al. 2020).

Incorporating alternative metrics in the routine biomonitoring of TRs

As observed in our results from **chapter 3**, natural disturbances (i.e. flow intermittence) could confound biological quality assessments by altering metric responses to anthropogenic impacts. Most of the widely used metrics based on macroinvertebrates showed a different response depending on whether sites were subjected to natural flow intermittence or not, evidenced by antagonistic effects. Thus, these metrics might not be reliable for assessing both perennial and TRs and would require calibration. Hence, to avoid misleading biological quality assessments in intermittent rivers, either existing metrics need to be recalibrated (e.g. by incorporating long-term variability in these metrics) or new metrics, as those presented here, require development.

In this sense, **chapter 3** provided several functional metrics that were able to detect anthropogenic impacts regardless of natural flow intermittence. These functional metrics included functional redundancy (i.e. the number of taxa contributing similarly to an ecosystem function, here a trophic function) and response diversity (i.e. how functionally similar taxa respond to natural disturbance and anthropogenic impacts). Of these metrics, functional redundancy of the whole community would be reliable even when applied during disconnected pools. Results from chapter 3 can therefore help to improve conservation and management of TRs, as these metrics could be used for biomonitoring either perennial or TRs (i.e. either during flowing or disconnected pools phases) and provide a more holistic approach to understand the response of biological communities to environmental changes.

Nonetheless, metrics proposed by this study were a first step to test which type of biomonitoring tools could work in these rivers and, thus, further research should be conducted. Ideally, relationships between functional redundancy/diversity metrics and anthropogenic impacts would be consistent across different climate and biogeographic influences (Stubbington et al. *in prep*), or at least vary along natural gradients in a systematic way that can be explicitly represented in statistical models. However, intercorrelations between traits and large-scale environmental filtering for certain sets of traits (e.g. desiccation-resistant forms in drier climates such as Mediterranean ones) are likely to preclude the establishment of a universal model of responses to anthropogenic stressors in TRs (Magand et al. 2020). This is because traits are linked in trait syndromes due to ecological and evolutionary processes, so that each trait is not free to independently respond to multifarious environmental changes (Wilkes et al. *in prep*). In fact, early indications are that the reliability of functional metrics might depend strongly on the choice of traits used to calculate them (Wilkes et al. *in prep*; Múrria et al. 2020). Future research towards functional metrics should also explore other biological groups (e.g. diatoms, fish). For instance, we are currently analysing whether widely used indices and functional metrics of diatom communities can detect anthropogenic impacts in TRs (Burfeid-Castellanos et al. *in prep*).

In addition to functional approaches, other existing alternatives to improve TRs' biomonitoring could be also implemented in future studies, such as molecular techniques or additional bioindicators. Widely used metrics based on macroinvertebrates might still not work correctly when applied in TRs due to the taxonomic resolution used (i.e. family level) unable to capture the species-specific environmental tolerances. An identification at species taxonomic level would thus allow working with metrics that could be more sensitive to both natural flow intermittence and anthropogenic impacts (Bonada et al. 2006a; Macher et al. 2016). When species level identification is not possible, the use of a DNA-based taxonomy method can provide solutions (Pawlowski et al. 2018; Serrana et al. 2019). In addition, the application of metabarcoding techniques on water and sediment samples (i.e. environmental DNA; eDNA) could be highly relevant in TRs and especially during the disconnected pools phase (Harper et al. 2019; Bonada et al. 2020). In this regard, it would be interesting that future research use metabarcoding techniques based on eDNA to establish a protocol to determine TRs' biological quality during the disconnected pools phase. The main limitation of these metabarcoding techniques, however, is the lack of a sufficiently extensive and representative reference library, with a specific genetic barcode associated to each specie. For this reason, to better validate metabarcoding when applied in TRs, and especially during their disconnected pools phase, the use of eDNA data should be validated with the biological samples collected using standard protocols and identified using traditional taxonomic approaches (i.e. morphology). Regarding bioindicators, some of them are currently being evaluated using terrestrial and semi-aquatic macroinvertebrates (Leigh et al. 2016b, Sánchez-Montoya et al. 2016; Stubbington et al. 2019a), microbial communities (i.e. through microbial source tracking or MST methods; Wilkes et al. 2013) and hyporheic macroinvertebrates (Leigh et al. 2013a,b). Nevertheless, more studies investigating how terrestrial and semi-aquatic macroinvertebrates respond to anthropogenic impacts would be necessary (Datry et al. 2017a).

INCORPORATING TRs PROPERLY IN THE RBMPS AND ITS PARTICIPATORY PROCESSES

The adaptive management approach proposed in this thesis (**chapter 4**) has the potential to consider the complexities of TRs and improve their management considering future needs. Several key findings were obtained from the experience in TRs participatory process conducted in this thesis. Our study showed that to promote the links between science, policy and society not only communication but active participation from all stakeholders should be promoted since the beginning of the process. This becomes even more important when conducting a participatory process in ecosystems with poor or no social recognition such as TRs which, in turn, may lack monitoring data due to the lack of gauging stations in most of these ecosystems (Gallart et al. 2016; 2017).

In our study, inputs from participants about the hydrological regime and alterations of TRs were key to improve the diagnosis and, thus, to improve the information required to propose management measures in the RBMPs. In this sense, the consideration of citizen science projects can be really useful when few or no data is available, as in TRs or other ecosystems with low social recognition. In addition to be useful for collecting new data, citizen science, together with environmental activities, proved to be positive to raise awareness on the biodiversity and ecological value of TRs and to engage local stakeholders and the general public. This might be especially relevant when incorporating TRs due to the inherent social-ecological complexity of these ecosystems (Datry et al. 2017b; Leigh et al. 2019a).

Considering that the success of most river management actions, including conservation and/or restoration, might depend on the social recognition of the target ecosystem, future initiatives aiming at protecting TRs biodiversity should join efforts to improve people's perceptions of these ecosystems (Rodriguez-Lozano et al. 2020). A possible way of improving this situation in TRs could be using the concept of ecosystem services (Datry et al. 2017b; Jorda-Capdevila et al. *under review*). In our approach, distinguishing the most relevant ecosystem services provided by each water body and linking them with the management measures listed in the RBMP and PoMs strengthened participant's understanding of the impact of the proposed measures on the selected TRs. Even though the incorporation of ecosystem services in the RBMP and PoMs would represent a step forward for increasing social engagement in water-related decision making (Terrado et al. 2016), it is still in an explorative stage (Grizzetti et al. 2016).

In a context of global change, studies assessing and mapping ecosystem services at the river basin level could be especially relevant to develop effective mitigation management actions to cope with future environmental changes (Jorda-Capdevila et al. 2019). In this sense, future perspectives should consider how such environmental changes might affect the ecosystem services provision in TRs by developing scenarios. In our approach, stakeholders identified which factors could involve a deterioration of the TRs ecological status in the future, and incorporate this information when developing the RBMP and PoMs. Since global change will further affect TRs but also other vulnerable and poorly recognised ecosystems such as urban rivers (Moran et al. 2019), wetlands (Smrekar et al. 2020) or peatlands (Heli et al. 2019), efforts to better consider them in management and conservation programs need to account for participatory processes too. In this regard, our experience in this thesis might also be useful to be applied in these ecosystems since, as with TRs, they are usually underprotected, not always included in biomonitoring programs and therefore, less data might be available.

CONCLUSIONS

The main conclusions of this PhD thesis are the following:

- The meta-analysis conducted in **chapter 1** show that, overall, biodiversity was significantly higher in perennial than in TRs. Moreover, our findings suggest that biodiversity loss may be specially relevant for macroinvertebrates and under particular environmental conditions, such as in arid and temperate climates, dry and wet sampling seasons, headwaters, and regions subject to different levels of anthropogenic disturbance.

- Our results in **chapter 2** highlight the importance of TRs to freshwater biodiversity conservation in Mediterranean-climate regions, especially during the disconnected pools phase, suggesting that these ecosystems, cannot be ignored in conservation planning strategies. To better manage and preserve aquatic biodiversity under future global change scenarios and to avoid potential ecosystem consequences of biodiversity loss, conservation efforts should be targeted towards both spatiotemporal taxonomic and functional diversity patterns.

- Our results in **chapter 3** show that natural flow intermittence can confound river bioassessment results using current methods, and that a set of new functional metrics could be used as effective alternatives to standard metrics in naturally disturbed intermittent rivers. Functional redundancy of the entire community could be used for TRs' biomonitoring even during the disconnected pools phase.

- Our experience in including TRs in participatory processes in **chapter 4**, shows the potential of adapting previous approaches to consider the complexities of TRs in management and conservation programs considering future needs and environmental changes. Involving stakeholders in early steps of the participatory process was key to obtain a more detailed information for TRs' diagnosis and for the management measures to be applied. Environmental education and citizen science activities, together with the inclusion of the ecosystem services concept, was the most useful way to raise awareness on the biodiversity and ecological value of TRs and to promote stakeholders' engagement.

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Zuur, A.F. et al. (2010). A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1: 3-14. Doi: 10.1111/j.2041-210X.2009.00001.x

SUPPLEMENTARY MATERIAL

SUPPLEMENTARY MATERIAL FROM CHAPTER 1:

Biodiversity in perennial and intermittent rivers: a meta-analysis

Appendix 1. Codes used in the forest plot to identify each replicated study and their corresponding full references.

Artemiadou2	Artemiadou V., Statiri X., Brouziotis T. & Lazaridou M. (2008) Ecological quality of smal mountainous Mediterranean streams (river type R-M4) and performance of the Europea intercalibration metrics. Hydrobiologia, 605, 75-88.
Banks2007	Banks J.L., Li J. & Herlihy A.T. (2007) Influence of clearcut logging, flow duration, an season on emergent aquatic insects in headwater streams of the Central Oregon Coas Range. Journal of the North American Benthological Society, 26, 620-632.
Beche2007	Bêche L.A. & Resh V.H. (2007) Short-term climatic trends affect the temporal variability o macroinvertebrates in California 'Mediterranean' streams. Freshwater Biology, 52, 2317 2339.
Beugly2010	Beugly J. & Pyron M. (2010) Variation in Fish and Macroinvertebrate Assemblages Amon Seasonal and Perennial Headwater Streams. American Midland Naturalist, 163, 2-13.
Blanchette20	Blanchette M.L. & Pearson R.G. (2012) Macroinvertebrate assemblages in rivers of th Australian dry tropics are highly variable. Freshwater Science, 31, 865-881.
Bonada2006	Bonada N., Rieradevall M., Prat N. & Resh V.H. (2006) Benthic macroinvertebrat assemblages and macrohabitat connectivity in Mediterranean-climate streams o northern California. Journal of the North American Benthological Society, 25, 32-43.
Bonada2007	Bonada N., Doledec S. & Statzner B. (2007) Taxonomic and biological trait differences o stream macroinvertebrate communities between mediterranean and temperate regions implications for future climatic scenarios. Global Change Biology, 13, 1658-1671.
Bonada2008_	Bonada N., Rieradevall M., Dallas H., Davis J., Day J., Figueroa R., et al. (2008) Multi-scal assessment of macroinvertebrate richness and composition in Mediterranean-climat rivers. Freshwater Biology, 53, 772–788.
Chadwick201	Chadwick M., Thiele J., Huryn A., Benke A. & Dobberfuhl D. (2012) Effects of urbanizatio on macroinvertebrates in tributaries of the St. Johns River, Florida, USA. Urba Ecosystems, 15, 347-365.

DeJong2013	De Jong G.D., Smith E.R. & Conklin D.J. (2013) Riffle beetle communities of perennial an intermittents streams in Nothern Nevada, USA, with a new state record for Optioservu Castaneipennis (fall) (COLEOPTERA: ELMIDAE). Coleopterists Bulletin, 67, 293-301.
Garcia2011	García-Roger E., Del Mar Sánchez-Montoya M., Gómez R., Suárez M., Vidal-Abarca M. Latron J., et al. (2011) Do seasonal changes in habitat features influence aquati macroinvertebrate assemblages in perennial versus temporary Mediterranean streams Aquatic Sciences, 73, 567-579.
Graca2004	Graça M.A., Pinto P., Cortes R., Coimbra N., Oliveira S., Morais M., et al. (2004) Factor Affecting Macroinvertebrate Richness and Diversity in Portuguese Streams: a Two-Scal Analysis. International Review of Hydrobiology, 89, 151-164.
Leigh2013	Leigh C. (2013) Dry season changes in macroinvertebrate assemblages of highly seasona rivers: responses to low flow, no flow and antecedent hydrology. Hydrobiologia, 703, 95 112.
Mackie2013	Mackie J.K., Chester E.T., Matthews T.G. & Robson B.J. (2013) Macroinvertebrate respons to environmental flows in headwater streams in western Victoria, Australia. Ecologica Engineering, 53, 100-105.
Monaghan20	Monaghan K.A. & Soares A.M. (2010) The bioassessment of fish and macroinvertebrate in a Mediterranean–Atlantic climate: Habitat assessment and concordance betwee contrasting ecological samples. Ecological Indicators, 10, 184-191.
Novais2014	Novais M.H., Morais M.M., Rosado J., Dias L.S., Hoffmann L. & Ector L. (2014) Diatoms o temporary and permanent watercourses in Southern Europe (Portugal). River Researc and Applications, 30, 1216–1232.
Perez2011	Pérez-Quintero J.C. (2011) Freshwater mollusc biodiversity and conservation in tw stressed Mediterranean basins. Limnologica - Ecology and Management of Inland Waters 41, 201-212.
Prenda1999	Prenda J. & Gallardo-Mayenco A. (1999) Distribution patterns, species assemblages an habitat selection of the stoneflies (Plecoptera) from two Mediterranean river basins i southern Spain. International Review of Hydrobiology, 84, 595-608.
Price2003	Price K., Suski A., Mcgarvie J., Beasley B. & Richardson J.S. (2003) Communities of aquati insects of old-growth and clearcut coastal headwater streams of varying flow persistence Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 33 1416-1432.
Rabeni1998	Rabeni C.F. & Wallace G.S. (1998) The influence of flow variation on the ability to evaluat the biological health of headwater streams. IAHS PUBL, 411-417.

Roux2008	Roux D.J., Nel J.L., Ashton P.J., Deacon A.R., De Moor F.C., Hardwick D., et al. (2008 Designing protected areas to conserve riverine biodiversity: Lessons from a hypothetica redesign of the Kruger National Park. Biological Conservation, 141, 100-117.
Ruiz2006	Ruiz García A., Herrera Grao A.F. & Ferreras-Romero M. (2006) Distribution of Trichopter communities in the Hozgargantacatchment (Los Alcornocales Natural Park, SW Spain) International Review of Hydrobiology, 91, 71-85.
Santos2011	Santos A.N. & Stevenson R.D. (2011) Comparison of Macroinvertebrate Diversity an Community Structure among Perennial and Non-Perennial Headwater Streams Northeastern Naturalist, 18, 7-26.
Skoulikidis20	Skoulikidis N., Lampou A., Karaouzas I., Gritzalis K., Lazaridou M. & Zogaris S. (2014) Strea ecological assessment on an Aegean island: insights from an exploratory application o Samothraki (Greece). Fresenius Environmental Bulletin, 23, 1173-1182.
Zbinden2008	Zbinden M., Hieber M., Robinson C.T. & Uehlinger U. (2008) Short-term colonizatio patterns of macro invertebrates in alpine streams. Fundamental and Applied Limnology 171, 75-86.

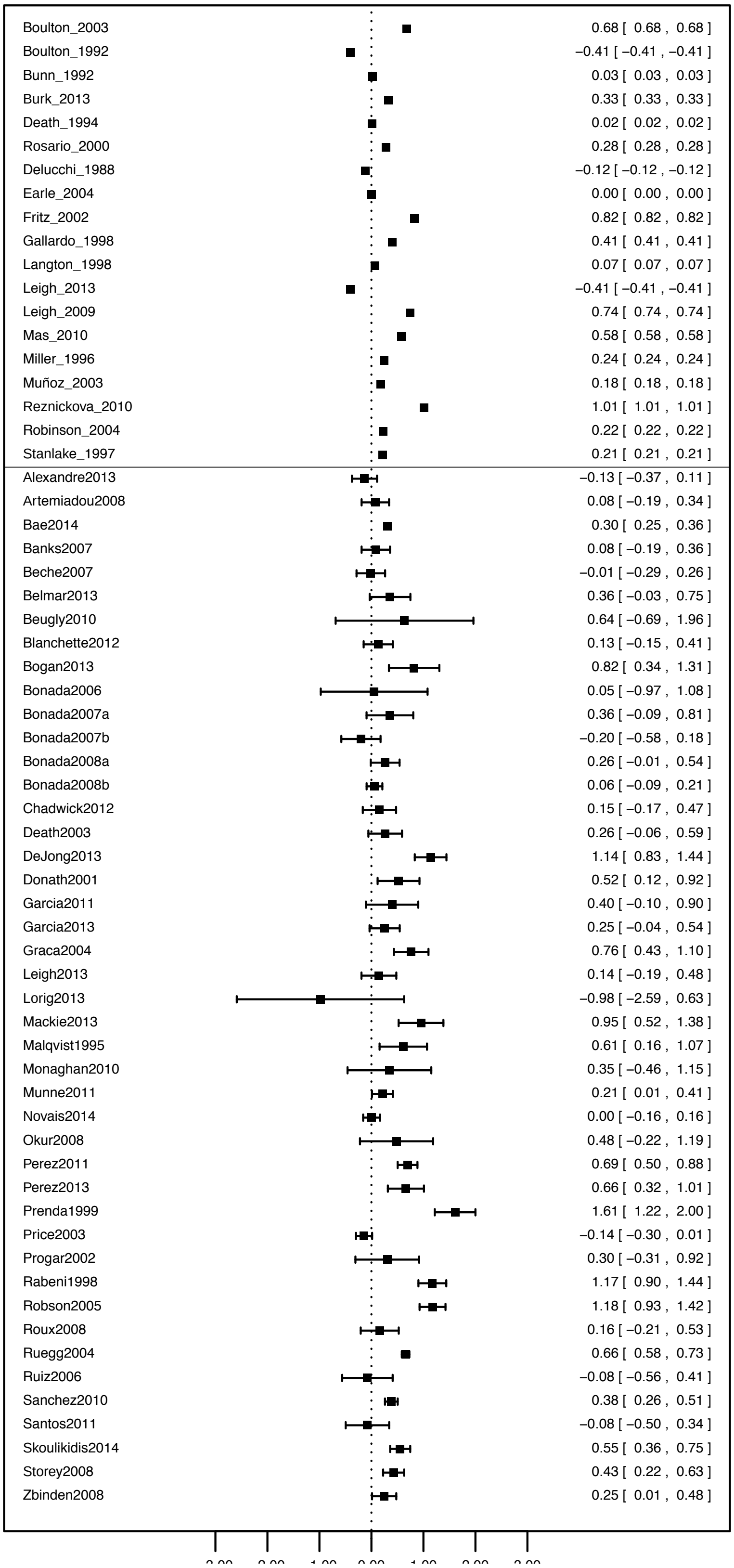
Appendix 2. Codes used in the forest plot to identify each non-replicated study and their corresponding full references.

Boulton_1992	on A.J., Valett H.M. & Fisher S.G. (1992) Spatial distribution and taxonomi osition of the hyporheos of several Sonoran Desert streams. Archiv fü biologie, 125, 37-61.
Burk_2013	R.A. & Kennedy J.H. (2013) Invertebrate communities of groundwater-dependen a with varying hydrology and riparian cover during a supraseasonal drough al of Freshwater Ecology, 1-20.
Death_1994	R.G. & Winterbourn M.J. (1994) Environmental Stability and Communit tence: A Multivariate Perspective. Journal of the North American Benthologica y, 13, 125-139.
Delucchi_1988	chi C.M. (1988) Comparison of community structure among streams with differen oral flow regimes. Canadian Journal of Zoology, 66, 579-586.
Fritz_2002	K.M. & Dodds W.K. (2002) Macroinvertebrate assemblage structure across ss prairie stream landscape. Archiv für Hydrobiologie, 154, 79-102.
Gallardo_1998	do-Mayenco A., Prenda J. & Toja J. (1998) Spatio-Temporal Distribution an gical Preferences of Coexisting Hydropsychid Species (Trichoptera) in Tw erranean River Basins (S Spain). International Review of Hydrobiology, 83, 12
Langton_1998	on P.H. & Casas J. (1998) Changes in chironomid assemblage composition in tw erranean mountain streams over a period of extreme hydrological conditions biologia, 390, 37-49.
Leigh_2009	C. & Sheldon F. (2009) Hydrological connectivity drives patterns o oinvertebrate biodiversity in floodplain rivers of the Australian wet/dry tropics water Biology, 54, 549-571.
Mas_2010	Marti E., Garcia-Berthou E., Sabater S., Tomanova S. & Munoz I. (2010) Comparin ssemblages and trophic ecology of permanent and intermittent reaches in erranean stream. Hydrobiologia, 657, 167-180.
Reznickova_2010	ckova P., Soldan T., Paril P. & Zahradkova S. (2010) Comparison of mayfl meroptera) taxocenes of permanent and intermittent Central European sma ns via species traits. Biologia, 65, 720-729.
Robinson_2004	son C.T., Tockner K. & Burgherr P. (2004) Drift benthos relationships in th nal colonization dynamics of alpine streams. Archiv für Hydrobiologie, 160, 44

Appendix 3. Information of 44 replicated studies (see Appendix 1 for the complete reference) on levels of the 6 factors (see Table 1). Studies are alphabetized by first author name. Macro = macroinvertebrate, Algae/Mac = algae/macrophytes, Multihab = multihabitat, Mult = multiple and NA = no data.

Artemiadou2008	Macro	Small	C	Medium-high
Beugly2010	Fish	Small	D	Medium-high
Bonada2007a	Macro	Mult	Mult	Low
Chadwick2012	Macro	Small	C	Medium-high
Garcia2013	Macro	Small	C	Low
Mackie2013	Macro	Small	C	Low
Novais2014	Algae/Mac	Mult	C	Low
Price2003	Macro	Small	C	Medium-high
Roux2008	Fish	Mult	C	Low
Santos2011	Macro	Small	D	NA

Appendix 4. Forest plot for the overall design of the original model (without trim-and-fill method) with all studies (replicated and non-replicated) using the response ratio as measure of effect size. Non-replicated studies are listed at the top and replicated studies are listed below, separated by a line. Studies within replicated/non-replicated are alphabetized. Each study is indicated in the left column with the first author and the year of publication (see Appendix 1 and 2 for the complete reference). Estimated values of each study (using the response ratio) with their corresponding confidence intervals are displayed in the centre of the plot with the exact values on the right.



SUPPLEMENTARY MATERIAL FROM CHAPTER 2:

Contribution of intermittent rivers to beta diversity can inform freshwater conservation in the Mediterranean region

Figure S1. Boxplots showing taxonomic and functional local richness (a and b, respectively) and LCBD (c and d, respectively) considering all sampled times. Full boxes represent perennial rivers (PRs) and empty ones IRs. P values are displayed for significant differences between PRs and IRs.

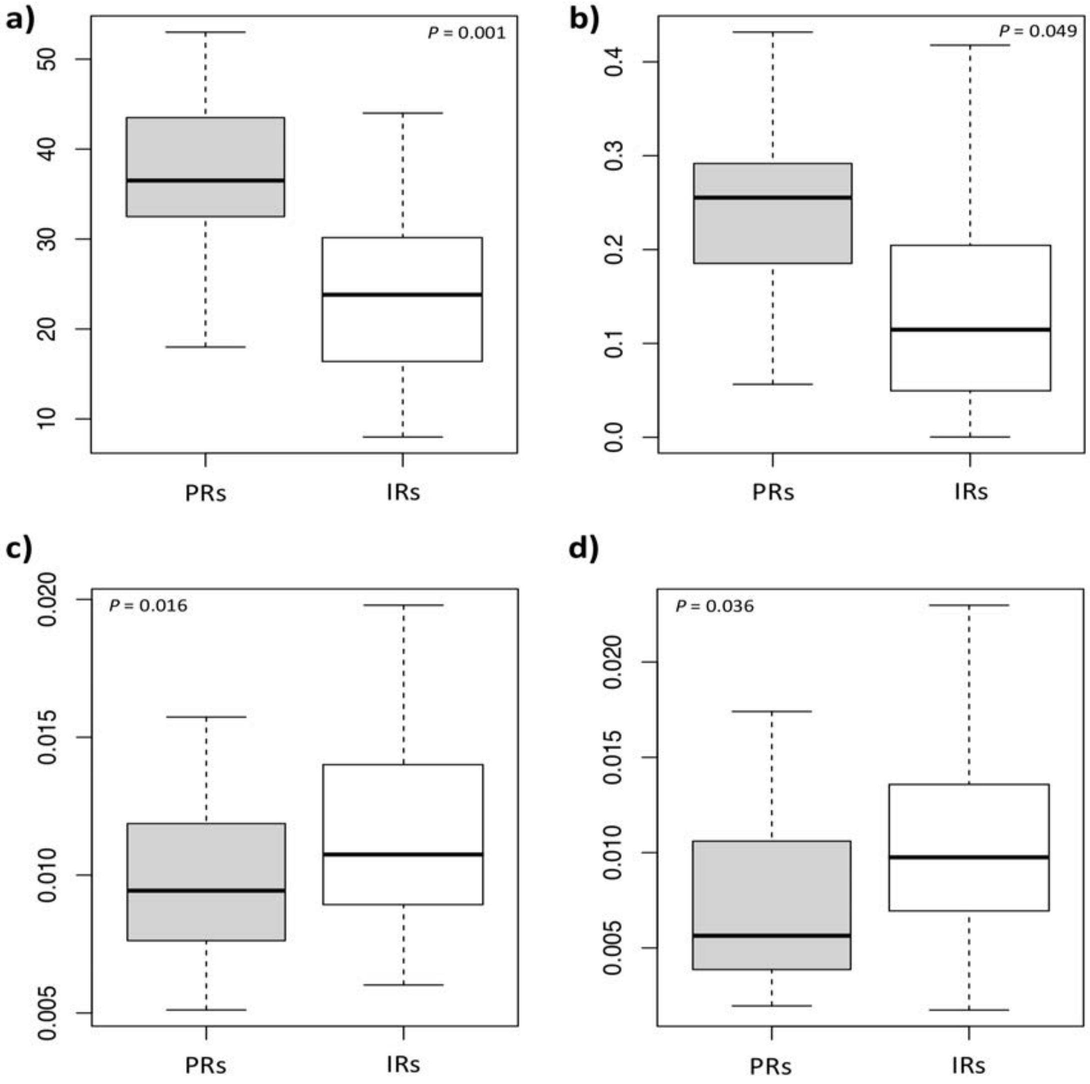


Figure S2. Plots showing the response of T-LCBD and F-LCBD best LME models for the hydrological predictor of ZF_a (a and d, respectively). The number of impacts was also selected in both best models (b and e, respectively), and the EH was also selected for the T-LCBD best model (c). Full circles represent perennial rivers and empty circles IRs. Fitted values for LMEs models are represented as blue lines for perennial rivers and as orange lines for IRs.

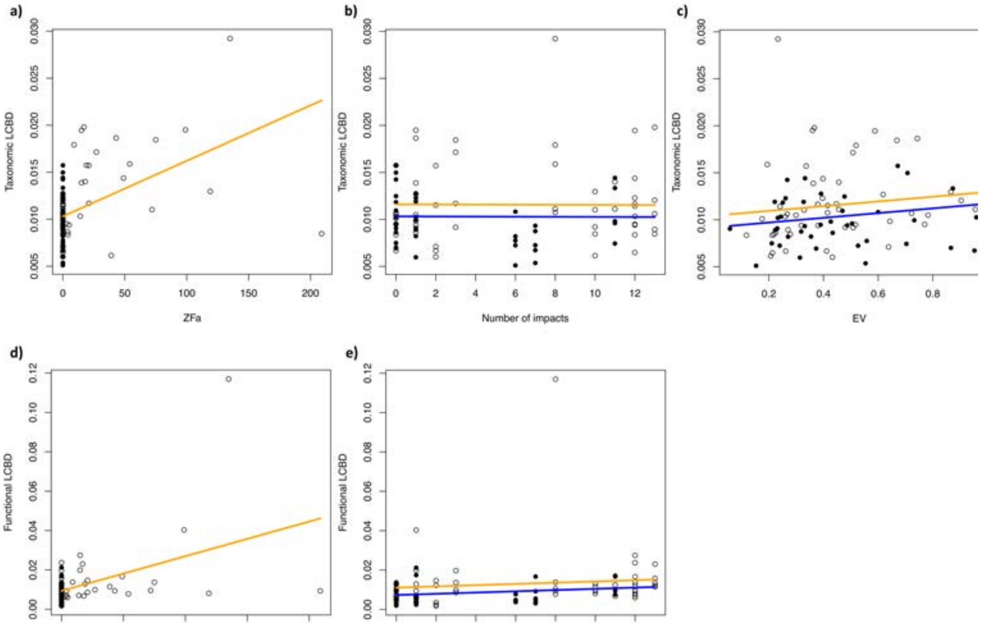


Figure S3. Plots showing the response of T-LCBD and F-LCBD best LME models for the hydrological predictor of DP_a (a and d, respectively). The number of impacts was selected in both best models (b and e, respectively), and the EH was also selected for the T-LCBD best model (c). Full circles represent IRs during the flowing phase and empty circles IRs during the disconnected pool phase. Fitted values for LMEs models are represented as purple lines for IRs during the flowing phase, and as brown dashed lines during the disconnected pool phase.

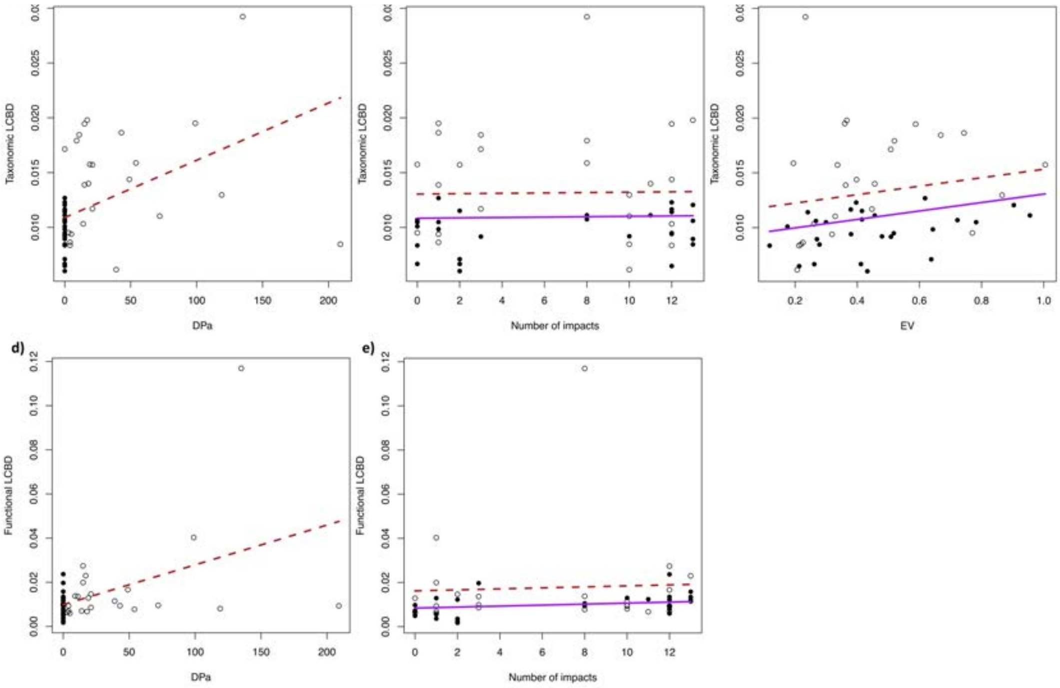


Table S1. The two main tested models with different combinations of the hydrological predictor, which resulted in 4 sub-models. Models differ between the accumulated zero flow days (ZF_a) and the accumulated number of days with disconnected pools (DP_a) since the last flow resumption occurred. EH: environmental heterogeneity.

	umber of impac	**EH**	**DP_a**
M2b	x	x	x

Table S2. Taxonomic and functional LCBD response variables (T-LCBD and F-LCBD, respectively) used in LME models showing: AIC values, ΔAIC and multicollinearity (i.e. variance inflation factor or VIF test). Here models with ΔAIC < 2 from each response variables are indicated in bold. Models differ between the accumulated zero flow days (ZF_a) and the accumulated number of days with disconnected pools (DP_a) since the last flow resumption occurred. EH: environmental heterogeneity. Nº impacts: number of impacts.

LCBD	**Model**	**ΔAIC**	**º impacts**	**ZF_T**	**DP_a**
	2a	1.39	1.03		
	2b	1.51	1.05		1.02

Table S3. Results of a post-hoc pairwise comparisons among perennial and IRs in each sampled time using a Tukey's HSD test. Significant comparisons (P < 0.05) are indicated in bold.

	nomic richness	**Functional richness**	**F-LCB**
P3-I3	0.273	0.947	0.57
P4-I4	0.708	0.996	0.12

Table S4. Results of beta regression analysis when T-LCBD and F-LCBD response variables were explained by community richness metrics (i.e. taxonomic and functional richness, respectively).

Taxonomic richness	-0.008	-2.878	**0.004**

Table S5. Taxonomic and functional LCBD (T-LCBD and F-LCBD, respectively) values of each perennial (PRs) and IRs site for each time (t1-t5) and considering all sampling times (i.e. spatiotemporal). Significant values (P < 0.05) are indicated in bold. The highest T-LCBD and F-LCBD values over time (i.e. above the community average; T-LCBD > 0.043 and F-LCBD > 0.034) are underlined. Both natural (NHR) and observed hydrological regimes (OHR) of each river were calculated by TREHS software (Gallart et al., 2017), and * indicates a hydrological impact (see Soria et al. 2020 for further details). T-LCBD and F-LCBD values were separated according to two levels of anthropogenic impacts: least impacted (Least Imp; number of impacts among 0 and 5) and impacted (Imp; number of impacts ≥ 6).

			t1-spring		t2-spring		t3-summer		t4-summer		t5-autumn		ɔpatiotemporal (t1-t5)	
NHR		Level of impa	T-LCBD	-	T-LCBD	-	T-LCBD	F-LCBD	-	F-LCBD	-	F-LCBD	-	F-LCBD
PR	PR	Least Imp	0.009		0.007		0.009	0.002		0.004		0.004		0.018
PR	PR	Least Imp	0.01		0.007		0.01	0.004		0.01		0.012		0.043
PR	PR	Least Imp	0.009		0.007		0.011	0.003		0.007		0.004		0.018
PR	PR	Least Imp	0.009		0.008		0.009	0.007	0.01	0.009	0.01	0.003		0.031
PR	PR	Least Imp	0.012		0.013		0.012	0.008		0.003		0.003		0.042
PR		Imp	0.005		0.007		0.009	0.005		0.002		0.029		0.046
PR		Imp	0.008		0.005		0.007	0.003		0.004		0.004		0.023
PR		Imp	0.01		0.007		0.013	0.021		0.007	0.01	0.007		0.057
IR	IR	Least Imp	0.008		0.007		-	-	-	-		0.007		0.018
IR	IR	Least Imp	0.01		0.01		0.016	0.015	-	-	0.01	0.007		0.042
IR	IR	Least Imp	0.01		0.014		-	-	-	-		0.004		0.007
IR	IR	Least Imp	0.013		0.009		**0.019**	0.01	**0.02**	**0.033**	0.01	0.006		0.035
IR		Least Imp	0.007		0.007		0.016	0.016		0.015		0.004		0.039
IR	IR	Least Imp	0.009		0.012		-	-		0.006		0.012		0.026
IR		Imp	0.011		0.011		0.018	0.014		0.008		**0.133**		0.046
IR		Imp	0.009	0.01	0.006		0.011	0.012		0.009		0.008		0.052
PR		Imp	0.011		0.014		-	-	-	-	-	-		0.026
PR		Imp	0.006		0.012		**0.019**	**0.012**		0.012		0.011		0.036
IR		Imp	0.011		0.008		0.01	0.006		0.015		0.004		0.035

SUPPLEMENTARY MATERIAL FROM CHAPTER 3:

Natural disturbances can produce misleading bioassessment results: Identifying metrics to detect anthropogenic impacts in intermittent rivers

Figure S1. Distribution of the 20 sampling sites in northeast of the Iberian Peninsula along Catalan internal basins, Ebro basins and Júcar River Basins.

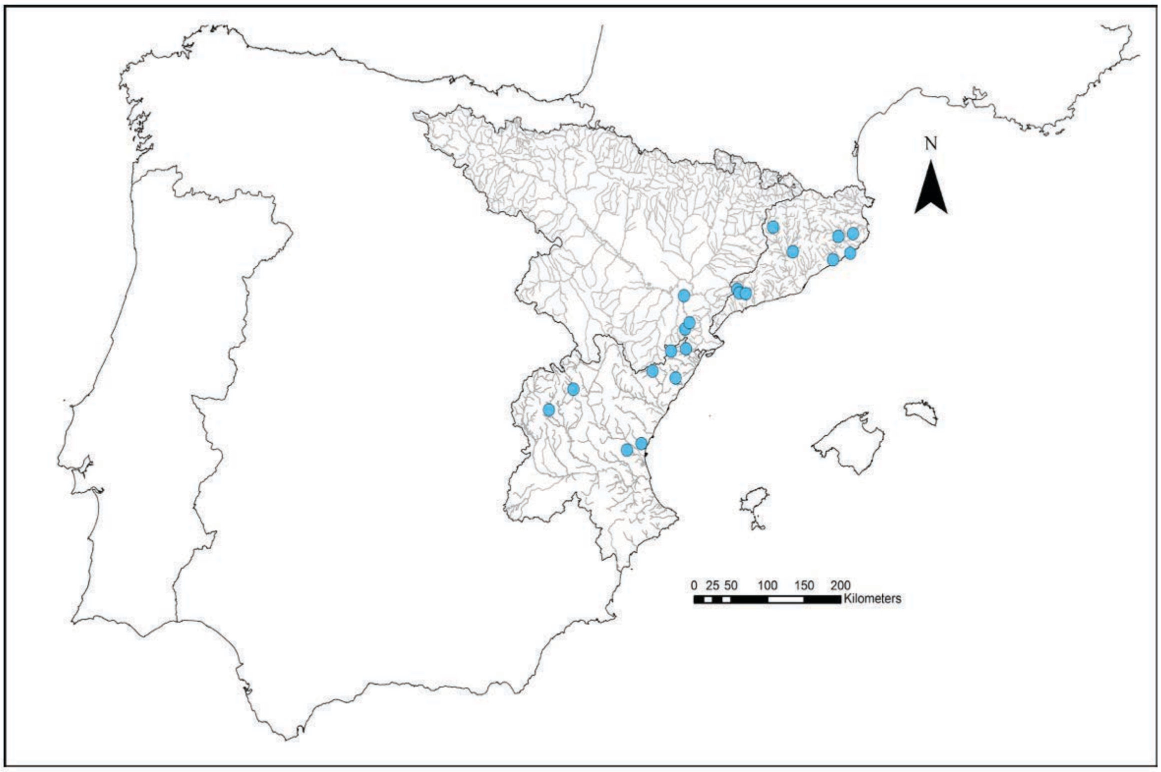


Table S1. Categories of biological 1 traits used as response traits grouped by resistance and resilience traits, and the rationale of the response obtained from Lytle and Poff 2004; Bogan et al. 2017; Stubbington et al. 2017. Selected categories of traits were: asexual reproduction, with resistance forms (i.e. diapause or dormancy, cocoons), aerial respiration (i.e. spiracle, hydrostatic vesicle), flier and burrower (i.e. epibenthic) or interstitial (i.e. endobenthic) locomotion and substrate relation, less than a year life cycle duration, more than one reproduction cycles per year, aerial active and aquatic passive (i.e. drift) dissemination.

Resistance trait	Resistance forms	resistance s (i.e. diapause rmancy.	When flow is disconnected increased resistance against droughts may be favoured.
	Respiration	l (i.e. spiracle, ostatic vesicle)	Increased oxygen deficit may favour air breathers.
		ower enthic) and stitial obenthic)	Drying promotes movement into the hyporheic zone or other refuges (e.g. moist sediment under rocks, detritus patches, shallow depressions beneath woody debris).
	Potential number of reproduction cycles per year	cles	Adult females more likely to survive long enough to lay eggs when flow resumes.
	Dispersal	l active	Flow cessation favours flying. For adults, it facilities recolonization over larger areas and from distant perennial refuges (pools). Especially for intermittent rivers with natural long dry periods
		tic passive)	It is the primary source of invertebrate colonization when flow resumes. Drift is also known to increase with chemical disturbances.

Table S2. Both natural and observed hydrological regimes (HR) of each river were calculated by TREHS software (Gallart et al., 2017), and * indicates a hydrological impact. Physicochemical parameters (dissolved O_2, conductivity, Tª, PO4, NO3, Chl-a) of each river indicating the maximum and minimum values and their standard deviation. Rivers are listed from 1 to 20: Aigua d'Ora (1), Algars (2), Brugent (3), Cabriel (4), Canaletes (5), Carraixet (6), Cèrvol (7), Daró (8), Glorieta (9), Guadazaón (10), Matarranya (11), Monlleó (12), Onyar (13), Pineda (14), Poyo (15), San Miguel (16), Sènia (17), Torrent del Puig (18), Talamanca (19) and Tossa (20).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
HR	PR	PR	PR	PR	PR	IR	IR	IR	IR	PR	PR	IR	PR	IR	IR	IR	PR	PR	IR
	PR	PR	PR	PR	PR	IR*	IR	IR	IR*	IR*	IR*	IR	PR*	IR	IR*	IR*	PR*	PR*	IR
O_2 (mg/l)	12		10	18.2	11.6	11	11.1	10.9	11.3	9.8	11.9	10.8	9.2	9.5	6.5	10.1	11.2	10	8.6
	6.2	6.4	7.4	7.6	6.5	7.2	8.7	2.4	3.7	2.6	4	1.7	4.3	3	1.8	1	5.2	3.3	4.5
	2.2	1.5	1.3	4.1	2.1	1.6	1.3	4.1	3.2	5.1	3.1	4.3	2	4.6	1.9	3.7	2.7	2.4	2.1
Cond (µS/cm)	523	598	665		471	2152		635			1437		552	613		943	503	1063	1034
	293.8	374	404.3			1488		251.1	556	420	595		386	554		688		478.1	
	87	83	112	66	62	241	54	154	331	55.4	309	50	63	42	320	98	42	251	326
Tª (ºC)	23.7		20.3	20.8	19.9	34.7	29.1	26.2	21.5	16.5	29.1	21.7	23.7		26.2	25.6	20.6	21.3	18.6
	4.7	8.5	10.9	3.2	7.3	15.5	7.9	7.5	7.8	15.5	9	7.2	6.7	12	11.3	12.7	12.9	12.9	8.8
	7	6	4	7	5	7	11	7	5	0.7	8	6	6	1	6	5	3	3	5
PO_4 (mg/l)	1.4	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0	0.1	0.1	0.1	0.1	2.6	5.4	0.1	1.5	0.1
	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	0.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0.8	2	0	0.4	0
NO_3 (mg/l)	2.5	2.5	2.5	2.5	2.5	73.4	5.3	2.5	2.5	7.5	20	2.5	10.9	5.8	51.4	60.6	17.9	38.9	9.2
	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5
	0	0	0	0	0	23	2	0	0	3.5	7	0	3	2	19	26	8	13	4
Chl-a	18.1		19.3	40.3	58.9	106.7	3.8	16.2	30.9	11.7	110.4	6.3	25.4	7	185	51.8	53.1	44.6	45.6
mg/l)	0.1	0.9	2.7	7.5	3	28.7	0.1	3	15.4	5	3.2	1.2	2.6	1.6	26.7	13.2	2.9	10.8	5
	7	7	6	13	23	29	2	5	6	4.7	46	3	9	4	59	17	25	14	21

Table S3. The degree of anthropogenic impacts of each site was measured considering the number of impacts occurring at each river location through the Mediterranean reference criteria (MRC) (Sánchez-Montoya et al., 2009). The MRC index includes information on several types of impacts, such as invasive species, diffuse sources of pollution, land use intensity, riparian vegetation, the morphology of the river and their habitat conditions, and their hydrological alterations and regulations (Sánchez-Montoya et al., 2009). The information for each site was obtained from the list of pressures and impacts of the three different River Basin water authorities included in our study combined with field observations (e.g. detection of invasive species) and, in the case of hydrological alterations, from the TREHS software (see Table S2). Rivers are listed from 1 to 20: Aigua d'Ora (1), Algars (2), Brugent (3), Cabriel (4), Canaletes (5), Carraixet (6), Cèrvol (7), Daró (8), Glorieta (9), Guadazaón (10), Matarranya (11), Monlleó (12), Onyar (13), Pineda (14), Poyo (15), San Miguel (16), Sènia (17), Torrent del Puig (18), Talamanca (19) and Tossa (20).

Riparian getation zone	1) Cover and composition appropriate for the type and geographical ocation of the river	1	0	0	0
	2) Lateral connectivity between river and riparian corridor is maintained .e. no cultivation and significant impervious area in riparian zone)	1	0	0	0
Introducced sp, lution	1) No significant impairment by exotic plant or animal species on utochthonous species	1	0	0	0
	2) No dumping of urban effluents	1	0	0	0
	3) No dumping of industrial effluents	1	1	0	1
	4) No irrigation return channel for floodwater farming	1	0	1	1
Diffuse sources of lution and land es	1) Dry land farming < 20% of drainage area (i.e. cereal, vineyard and tree rops as olive) and not connected to riparian vegetation zone	1	0	0	1
	2) Intensive irrigated farming < 3% in drainage area (i.e. rice field, rigated vineyard and others irrigated fruit tress) and not connected to iparian vegetation zone	1	1	1	1
	3) Urban use < 0.7% in drained area	1	1	0	0
	4) Burnt vegetation < 7% in drainage area at least seven years ago and not onnected to riparian vegetation zone	1	1	1	1
	5) No evidence of intensive use of grazing	1	1	1	1
	6) Natural land uses > 80% in drainage area	1	0	0	0
River morphology d habitat nditions	1) Representative diversity of substrate materials appropriate for the type	1	1	0	1
	2) No canalisation (i.e. stream bottoms and stream margins must not be xed)	1	1	1	1
	3) No transversal structures "dams" (i.e. no retention of sediments)	1	0	0	1
	4) No sand or gravel extraction	1	1	1	1
Hydrological eration and ulation	1) No water diversion for irrigation or other purpose	1	0	0	0
	2) No alterations of the natural hydrograph and discharge regime (e.g. eservoirs, hydroelectric)	1	0	0	0
	3) No effect of inter-basin water transfer	1	1	1	1
	4) Near natural level of groundwater (i.e. aquifer not affected by over-xploitation)	1	0	0	1
al MRC		20	9	7	12
al number of impacts (calculated as the inverse of MRC)		**0**	**11**	**13**	**8**

Table S4. Percentage of the variance explained by Nº impacts, DP_i and ZF_T and by their interactions for each metric using the dataset including all aquatic-phases. Nº impacts: number of impacts. DP_i: the number of days in the disconnected pool phase since last sample was taken. ZF_T: total number of zero flow days.

Response	º impacts	DPi	mpacts ZF_T	pacts DPi	Resid	R^2m
IASPT	49	11	11	2	0.2	0.44
FR.omnivorous.pa	56	6	25	1	0.3	0.32
FR.gatherers.pa	49	9	26	3	0.4	0.34
FR.predators.ab	53	0	29	2	0.5	0.2
RD.ab	69	6	22	3	0.6	0.36
RD.grazers.ab	54	7	7	7	0.8	0.11

Table S5. Percentage of the variance explained by Nº impacts and ZF_T, and by their interactions metric using the flowing-phase dataset. Nº impacts: number of impacts. ZF_T: total number of zero flow days.

fam	69	23	8	0.26
MMiT	74	11	15	0.12
R.shredders.pa	97	3	0	0.69
R.filterers.pa	47	50	3	0.65
R.grazers.ab	29	10	61	0.69
D.omnivorous.	100	0	0	0.93
D.gatherers.ab	92	0	8	0.71

Table S6. Null model results showing z-score values for each functional metric from the dataset including all aquatic-phases. Significant p-values (< 0.05) are indicated in bold. Nº impacts: number of impacts. DP_i: the number of days in the disconnected pool phase since last sample was taken. ZF_T: total number of zero flow days.

	Nº impacts	**ZF_T**	**Nº impacts x ZF_T**	**Nº impacts x DPi**
redders.pa	-	-1.59	-	-1.77
erers.pa	-	0.86	0.88	-
azers.ab	-0.66	0.74	-	0.74
nnivorous.ab	-0.27	0.47	0.35	-0.34
therers.ab	-0.08	-	-0.26	-0.20

Table S7. Null model results showing z-score values for each functional metric from the flowing-phase dataset. Significant p-values (< 0.05) are indicated in bold. Nº impacts: number of impacts. ZF_T: total number of zero flow days.

FR.pa	**-2.99**	**-3.19**
FR.predators.pa	**-10.55**	**7.56**
FR.omnivorous.ab	**-4.08**	**5.73**
FR.gatherers.ab	**1.85**	-0.23
RD.shredders.ab	**-3.13**	-0.38
RD.filterers.ab	**-2.89**	0.97

Appendix 1. Details on functional metrics estimation:

To quantify functional redundancy metrics (FR), a Gower effect trait taxon-by-taxon dissimilarity matrix was derived from the original taxon-by-effect-trait matrix to produce a classification dendrogram for macroinvertebrates, based on Ward's clustering method (e.g. Laliberté et al. 2010; Bruno et al. 2016a). After visual inspection of the dendrogram and assessing groups' coherence, six functional trophic groups representing different trophic roles were defined: omnivorous, shredders, predators, grazers, gatherers and filter feeders. Omnivorous had mixed feeding habits, including a variety of shredding, grazing and gathering affinities. FR for each sampling site was calculated as the average abundance (ab) or traits richness (i.e. presence-absence; pa) for each functional trophic group as well as for the entire community (i.e. total abundance or richness divided by the number of occurring functional trophic groups) (Laliberté et al. 2010) (Table 1). To obtain response diversity metrics (RD), a second Gower taxon-by-taxon dissimilarity matrix based on response traits was calculated to build a functional response space through a Principal Coordinate Analysis (PCoA). The five most explanatory response trait axes (explained variance= 56.4 %; mean squared deviation=0.005) were retained, according to the method proposed in Maire et al. (2015). As a measure of Functional Richness of the response traits (FRic, Villéger et al. 2008), the ratio between the hyper volume filled by each community in the functional response space and that filled by all the taxa occurring within the study area was estimated, ranging 0 to 1. Also, the functional dispersion of the entire community (FDis, Laliberté and Legendre 2010) was estimated, which accounted for the mean distance of each taxon to the mean weighted centroid in the functional effect space (i.e. unweighted, presenceabsence as RD.pa, and abundance-weighted as RD.ab). Similarly, RD for each of the six functional trophic groups was quantified considering only the taxa from each group present at each community. In the latter case, only the abundance weighted index was used (e.g. RD.shredders.ab, RD.filterers.ab; see Table 1).

Appendix S2. Data analysis methods:

A multi-model inference approach to quantify predictor's standardised effect sizes and significance was adopted. This statistical technique ranks all the models generated using all the possible combination of predictors using Akaike's Information Criterion (AIC). Top models differing in no more than two AIC units (ΔAIC ≤ 2) from the model ranked first (i.e. with minimum AIC) were selected. To conduct the model averaging a natural average method was adopted. For each LME model, two measures of goodness-of-fit were estimated: marginal goodness-of-fit (r^2m) indicates the variance explained only by the fixed factors, while conditional goodness-of-fit (r^2c) shows the variance accounted by both fixed and random terms. All models were validated by visually checking their residuals for normality and homocedasticity. When heteroscedasticity was observed, a model term was added to LME to account for residual heterogeneity. This occurred for FR.shredders.pa, RD.shredders.ab and RD.filterers.ab metrics from both datasets, for FR.omniv.pa from the all aquatic-phases, and for FR.grazers.pa, FR.filterers.pa and FR.omnivorous.ab from the flowing-phase dataset.

SUPPLEMENTARY MATERIAL FROM CHAPTER 4:

Adapting participatory processes in river management: insights from temporary rivers

Figure S1. Distribution of the 22 water bodies grouped in 5 areas of participation which include several sites: Girona (A1; pink); East Tarragona (A2; purple); West Tarragona (A3; red); South Tarragona and Castelló (A4; blue), and Valencia (A5; yellow). Black sites were included in the LIFE+ TRivers project but not in the participatory process. A1 and A2 correspond to the Catalan River Basin District. A3 correspond to the Ebro River Basin. A4 and A5 correspond to the Júcar River Basin.

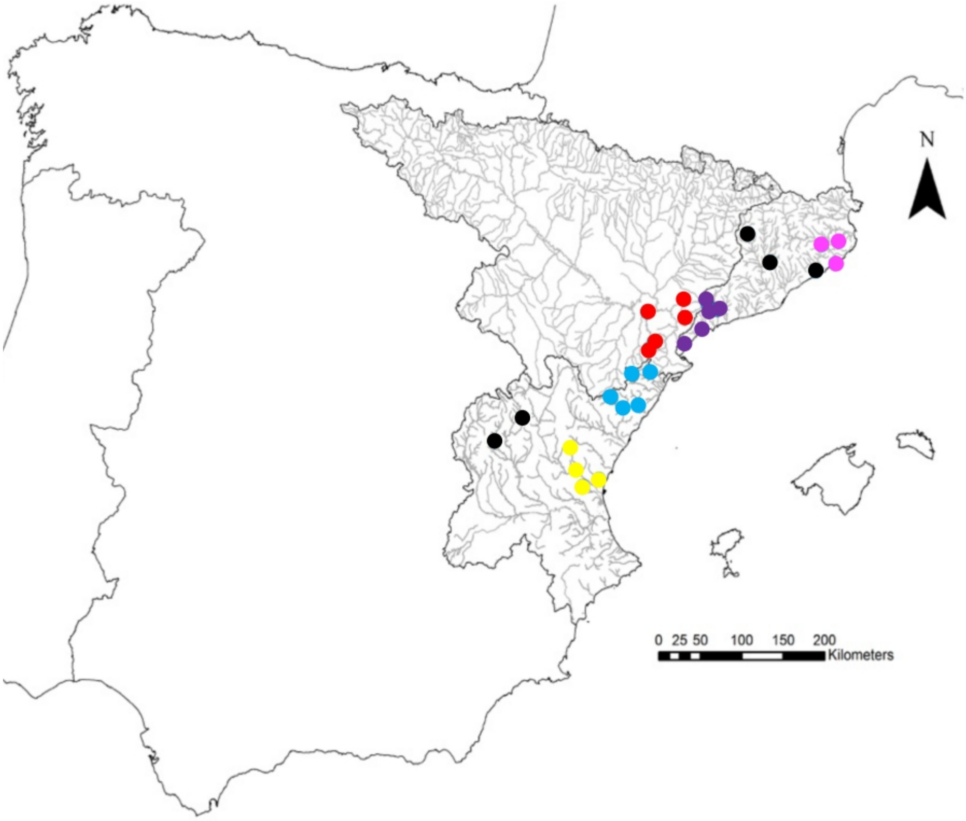


Figure S2. Pictures of our participatory process showing: (a,b) FEHM research group exposing the main topics; (c,d) dynamics to promote participants' contributions to the diagnosis of each water body; (e,f) field trip activity using the RiuNet app, and (g,h) prioritization dynamics conducted in the measures workshop.

Table S1. Summary of the face-to-face participants from both diagnosis and measures workshops.

	Local environmental associations and non-governmental organizations	RA
		taforma pel riu Siurana
RESEARCH INSTITUTIONS	Universities	HM research group (University of Barcelona)
		F
		ar River Basin District Water Agency
		este town council

Table S2. Summary of the climate-related future impacts and measures identified by the participants from the face-to-face workshops. Status: ecological status. For further details, see the LIFE+ TRivers website (http://www.lifetrivers.eu/actions).

	Climate-related future impacts	Measures
HYDROLOGY	An increase of erosion and sedimenta processes	Developing studies to halt erosion proces
	Prioritization of economic (e.g. tourism environmental interests	Regulation of the access to temporary riv
	An increase of the public use of rivers (bath)	Establish clear guidelines for conservation of the riverbed and its rivers vegetation
	An increase of the dry period temperature due to global change	Revision and control of water concessi and extractions
		Implement (or accomplish) ecological flo
	An increase of water contamination (e.g phytosanitary or illegal dumping)	Control of dumping/releases (fertiliz livestock farms)
		Improve purification (e.g modernization collectors, wastewater treatment system housing areas)

Table S3. Ecosystem services identified by face-to-face participants during the diagnosis workshop at the different areas of participation. See Figure S1 for the identification of the participation areas.

ıltural relevance	✓
ay of transport	
ıllecting	✓

Table S4. Examples of some of the most relevant measures that could be aligned with measures already included in the River Basin Management Plans (2016-2021) after the participatory process. Here only one measure from each participation area is shown. For identifying the participation areas (A1:A5) see Fig. S1. ACA: Catalan Water Agency (public water authority). CHJ: Júcar River Basin (public water authority). For further details, see the LIFE+ TRivers website (http://www.lifetrivers.eu/actions).

Eradicate invasive species. General measure.	ͻnty measures on this topic and a total 1,64M€ of investment w ι.
Improve river connectivity. General measure.	eral measures incorporated, including the need for building nectors in those structures impeding fish movement and migrati ͻore the river in case these strictures are not in use (measu ͻ10). Related with these measures, three additional measures tribute to the river connectivity: measure nº A2.007, dedicate rove the information on fluvial connectivity, measure nº A2.0C nitor actions, and measure nº A2.008 dedicated to disseminati activities. Costs associated to these measures are only include ısure nº A2.006 in the management plan 2016-2021, with a cc ,000.
flows (e- flows).	ɅI1166 "Application of ecological flows in all water bodies of the eral studies are planned for the Sénia river under the specific mea ɅI1149 "Study of the relation river-groundwater and sub super es in the river Sénia and implementation of e- flows". Only g get provided by CHJ. 258,05 million euro to reduce water abstra ssures. 6,20 million euro to reduce other hydrological pressures
Improve wastewater treatment systems. Improve the current treatment plant at Rambla del Poyo (Cheste- Chiva, El Oliveral).	ısure nº 08M0038. Basic actions in wastewater treatments in Cl Chiva. Only global budget provided by CHJ: 357,58 million eur roving point-source pollution.

Table S5. Evaluation of the satisfaction (%) of the participatory process by face-to-face and online participants of both diagnosis and measures workshops. Ranging from very low to very high. For further details, see the LIFE+ TRivers website (http://www.lifetrivers.eu/actions).

Topics evaluated	**Low**	**Indifferent**	**Very high**
Place where the process was held (ubication, installations)	4	5	53
Collaborative leadership (organization and logistics)	-	6	64
Clarity of working papers	-	18	50
Personal satisfaction in terms of real contributions in the diagnosis and measures stages	1	15	44
Diversity of stakeholders participating	5	17	41

Table S6. Results from online surveys conducted during the participatory process (% participants) showing the most common impacts identified in the water bodies, their climate-related future impacts and the management measures that could improve ecological status.

		icipants wers (%)
ures and impa nosis)	Lack of information about temporary rivers	16
	Invasive species	20
	Lack of involvement of the competent administrations	21
	Increase of aquifer exploitation	17
	Promote and improve public participation	16
	Improve river connectivity	18

Appendix 1. Methodologies about the selections of the studies from Table 1

We identified only published studies from an ISI Web of Knowledge (<www.accesowok.fecyt.es/>) literature search that recorded participatory processes under the WFD context and that were related to the development of the river basin management plan (RBMPs) and the proposal of measures (PoMs) (i.e. not only to specific measures). Member states were required to have produced the first RBMPs and PoMs by 2009 (EC, 2009) and, thus, we considered a time span from the 2003s (i.e. 2003-2009 six-year cycle) to the 8th of March 2020. A comprehensive search string of multiple terms for participatory process has been used, which resulted in 23 records. These 23 studies were from 12 different countries and different river basins: Ribble, Ythan, Dearne, Derwent, Belfast, Dee, Lough and Lagan (United Kingdom), Rhone (Switzerland), Muga, Guadiana, Ebro, Western Costa del Sol, Miera and Campiazo (Spain), Meuse (The Netherlands), Flemish (Belgium), Dordogne and several other river basins (France), Danube (Hungary), Bacchiglione (Italy), Guadiana and Alentejo region (Portugal), Evinos and Naxos (Greece), Dhuenn and Elbe-Lübeck (Germany) and several river basins from Denmark. We manually re-screened each of the 23 publications to select those relevant for our study according to the following criteria: the publication had to discuss or provide direct insights into the leadership of participatory process, the potential groups (i.e. stakeholders) that could be engage in a participatory process, which types of mechanisms were used to their engagement, which type of rivers were included (i.e. perennial or temporal rivers) and whether they included citizen science information, future scenarios and the concept of ecosystem services. This selection resulted in a total of 5 publications including 10 study cases.

Appendix 2. Further details on the type of stakeholders, leadership and dissemination activities of our study case

There was a collaborative leadership between the two water management authorities (i.e. Catalan River Basin District and Júcar River Basin District), two research institutions (i.e. the University of Barcelona and the IDAEA-CSIC, with members belonging to the FEHM research group; www.ub.edu/fem), and one professional independent mediator with experience in participatory processes. The two water management authorities and the two research institutions were partners of the LIFE+ TRivers project. Dissemination activities announcing the process were developed through the TRivers website (www.lifetrivers.eu/actions) social networks (i.e. Twitter and Facebook) and eBando (i.e. mobile application that share local events and announcements in municipalities). Besides, preliminary scientific dissemination on the diagnosis of each target water body was conducted one month before the start of the workshops (Fig. 1b). Information panels and leaflets were placed in strategic buildings of municipalities (e.g. city halls) and protected areas (e.g. natural park offices) close to the sampled water bodies during the project. Once stakeholders were identified, they were also contacted by e-mailing and ®WhatsApp. To facilitate the participation of stakeholders, both diagnosis and measures workshops were held in the most central village in each of the 5 area groups (Fig. S1). Participatory workshops took place between October and December of 2017, and the duration of each workshop was about 3-4 hours.

PUBLISHED ARTICLES

Oikos 126: 1078–1089, 2017
doi: 10.1111/oik.04118

Subject Editor: Florian Altermatt. Editor-in-Chief: Dries Bonte. Accepted 14 March 2017

Biodiversity in perennial and intermittent rivers: a meta-analysis

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Comprehensive knowledge of the effects of disturbances on biodiversity is crucial for conservation and management, not least because ecosystems with low biodiversity may be the most vulnerable. In rivers, the role of disturbance in shaping aquatic biodiversity has mainly focused on floods. Perennial rivers (PRs) often flood, whereas intermittent rivers (IRs) flood, stop flowing and dry. Despite the recent and significant increase in research on IRs, controversy remains about whether they are more or less biodiverse than PRs. Our aim was to determine (Q1) if PRs and IRs differ in biodiversity and (Q2) if the direction and magnitude of the differences (effect sizes) are related to environmental (climate, season, habitat, longitudinal zonation and anthropogenic disturbance) and/or biological factors (taxonomic group). We conducted a meta-analysis on 44 published studies of PR and IR biodiversity that had replicated data. We applied random effects models to the data to obtain weighted mean effect sizes for differences between PRs and IRs, and their confidence intervals, by first considering all studies and then by splitting studies into groups on the basis of the above factors. We found that biodiversity was significantly higher in PRs than in IRs (Q1). We also detected significant differences (PRs > IRs) in studies of macroinvertebrates, in those conducted within arid and temperate climates, dry and wet sampling seasons, headwaters, and regions subject to different levels of anthropogenic disturbance (Q2). Our meta-analysis suggests that the expected increase in the prevalence of IRs in certain regions of the world due to global change could result in a decrease in freshwater biodiversity. To better manage and preserve aquatic biodiversity under future global change scenarios and to avoid potential ecosystem consequences of biodiversity loss, conservation efforts should be targeted towards those environmental conditions or taxonomic groups with significant differences (PRs > IRs).

Synthesis

We conducted a meta-analysis of studies comparing biodiversity between perennial and intermittent rivers. We show that, in general, biodiversity was significantly higher in perennial than in intermittent rivers. Moreover, our findings suggest that biodiversity losses may be relevant for certain taxonomic groups and under particular environmental conditions. Considering that many perennial rivers are expected to become intermittent due to global change and increased human demand for freshwater, our results offer a glimpse of how these impacts could threaten aquatic biodiversity and how conservation efforts may best be directed.

Understanding how disturbance influences biodiversity is a recurrent topic in community ecology (Pianka 1966, Huston 1979, Hughes et al. 2007). Disturbance includes a wide variety of phenomena acting at multiple temporal (e.g. from days to eons) and spatial (e.g. from local to biogeographical) scales, with multiple potential consequences for populations, communities and ecosystems (Dornelas 2010). Ecologists hypothesised many years ago that disturbance decreased biodiversity and favoured ecological succession (Clements 1916) and that intermediate levels of disturbance enhanced biodiversity (Connell 1978, but see Fox 2013). Effects of disturbance on biodiversity have been studied in many ecosystems and across multiple taxonomic groups (Horner-Devine et al. 2004, Graham et al. 2009, Barlow et al. 2016). Most studies highlight the negative effects of disturbance on biodiversity (Loreau et al. 2001, Wardle et al. 2011, Hooper et al. 2012), while only few show the contrary pattern (Thom and Seidl 2015, Brunbjerg et al. 2015). Understanding and predicting when and how biodiversity might change following disturbance is crucial for effective conservation and management (Dornelas 2010).

The role of disturbance in shaping aquatic biodiversity has focused mainly on flood and drying events (Resh et al. 1988, Giller 1996). Flood events are pulse disturbances that occur relatively quickly (Junk et al. 1989, Ward and Stanford 1995), disrupting habitat conditions and eliminating individuals (Poff et al. 1997, Lake et al. 2000). In contrast, drying events are ramp disturbances that reduce aquatic habitat and eventually result in flow cessation and/or complete loss of surface water from the streambed, and can reduce aquatic biodiversity drastically (Williams 1996, Lake et al. 2000). Floods enhance connectivity among aquatic habitats, whereas drying fragments them (Stanley et al. 1997, Boulton 2003). Although it is widely known that floods and drying events affect the structure and function of rivers (Bonada et al. 2007a, Reich and Lake 2015) and that research on drying events has significantly increased during the last decade (Leigh et al. 2016a), the effects of floods have been more frequently reported that those of drying events (Datry et al. 2007, Lake et al. 2007). This may be because floods occur in all river types, whereas drying events are particular to intermittent rivers (IRs), in which surface flow ceases at some point in time and space (Acuña et al. 2014, Datry et al. 2014a, Leigh et al. 2016a). In contrast, perennial rivers (PRs) are characterized by continuous flow.

IRs are probably the most common fluvial ecosystems in the world (Datry et al. 2016a), and therefore drying events are probably more ubiquitous than previously thought. In addition, many PRs are expected to transition to IRs in the near future as a result of global change and increased human demand for fresh water (Palmer et al. 2008, Döll and Schmied 2012), increasing the importance and relative contribution of IR ecosystems to global aquatic biodiversity. However, although research on IRs is in what has been described as a boom phase (Datry et al. 2011, Leigh et al. 2016a), debate remains over whether IRs are more or less biodiverse than PRs. Some studies find that IRs are less biodiverse (Del Rosario and Resh 2000, Storey and Quinn 2008, Bogan et al. 2013), whereas others find the opposite (Dieterich and Anderson 2000), or no difference between IR and PR biodiversity (Miller and Golladay 1996, Casas and Langton 2008, Santos and Stevenson 2011). Clearly, a more thorough understanding and test of the biodiversity difference between PRs and IRs is required.

Biodiversity between PRs and IRs might differ depending on several factors. First, biodiversity in IRs can depend on how flow regime characteristics, which change among climatic zones, forge adaptations to drying (Boulton 2003, Lytle and Poff 2004). For example, the higher number of unique taxa in IRs than PRs in Mediterranean climates has been related to their predictable flow regimes (Bêche et al. 2006, Munné and Prat 2011). Second, biodiversity between PRs and IRs can vary seasonally. During the wet season, when both PRs and IRs flow, their biodiversity is more likely to be similar (Delucchi 1988, García-Roger et al. 2011), whereas during the dry season, IRs will likely have lower aquatic habitat availability than PRs, and thus lower aquatic biodiversity. Third, as biodiversity varies among habitats in PRs and IRs (García-Roger et al. 2013), habitat type is another relevant factor to consider. Riffles in IRs might host a lower biodiversity than in PRs because this habitat is the first to disappear during drying (Bonada et al. 2006a), whereas pools might show the contrary pattern if isolated pools remain in IRs during drying (Bonada et al. 2006a, Leigh and Sheldon 2009, Boersma et al. 2014). Fourth, biodiversity differences between PRs and IRs may vary with longitudinal zonation. IR headwaters might have lower biodiversity than PR headwaters because their greater isolation might hamper recolonization after drying (Finn et al. 2011, Datry et al. 2016b, c), whereas no significant landscape barriers would affect recolonization of middle reaches (of free-flowing rivers, at least). However, and fifthly, anthropogenic disturbance may dampen differences in biodiversity between PRs and IRs by homogenizing and simplifying communities (Rahel 2002) regardless of flow regime, climate, habitat, season, or the taxonomic group considered. Finally, the magnitude of change between biodiversity in PRs and IRs may vary depending on the taxonomic group considered (i.e. macroinvertebrates, fish, algae or macrophytes) because despite some taxa within all groups having traits of resistance and/or resilience to drying (Bonada and Resh 2013), their evolutionary history, species biodiversity and ecological tolerance varies. For example, although algae and macrophyte species are much more widespread than other freshwater groups, they have a limited set of biological adaptations to flow variation (e.g. see Lange et al. 2016 for algae in comparison to Tachet et al. 2002 for macroinvertebrates).

Here, we investigated the above hypotheses by comparing biodiversity in PRs and IRs using a meta-analytic approach. Specifically, we sought to determine (Q1) whether PR and IR biodiversity differ and (Q2) whether the direction and magnitude of any difference is related to the environmental (i.e. climate, season, habitat, longitudinal zonation, anthropogenic disturbance) or biological factors (i.e. taxonomic group) hypothesised to affect biodiversity patterns in river ecosystems. For our main question (Q1), we hypothesized that biodiversity should be lower in IRs than in PRs (Fritz and Dodds 2002, Storey and Quinn 2008, Bogan et al. 2013) because IRs are subject to drying events that act primarily as a disturbance decreasing aquatic biodiversity (Leigh and Datry 2016). However, if this loss of taxa in IRs is compensated by taxa with resistance and resilience traits to cope with drying (Bonada et al. 2007b, Grubbs 2011, Vander Vorste et al. 2016), biodiversity in PRs and IRs may be similar or IR biodiversity may be higher. Assessing the differences in biodiversity between PRs and IRs and understanding the conditions under which those differences differ is increasingly important for predicting aquatic biodiversity changes in the face of global change.

Methods

Data selection

We identified published studies that recorded biodiversity of PRs and IRs from an ISI Web of Knowledge (<www.accesowok.fecyt.es/>) literature search considering a time span from the 1900s to the 21 of August 2014 (Leigh et al. 2016a). Leigh et al (2016a) used a comprehensive search string of multiple terms for IRs which resulted in 10 800 records and then filtered these publications using further search terms associated with key topics of research on IR ecology and management: invertebrate ecology, fish ecology, biogeochemistry and ecological and hydrological assessment. They then screened the resultant groups of records manually to ensure relevancy to the topics and IR research more generally (e.g. removing studies in the medical field), obtaining 1237 publications (see Table S2 in Leigh et al. 2016a for full details of search parameters and screening criteria).

For this study, we re-screened each of the 1237 publications to select those relevant for the meta-analysis according to the following criteria: the publication had to discuss or provide direct insight into the ecology and/or management of PRs and IRs, the sampling design had to include sites which were not located along the same river (i.e. sites must be hydrologically independent), and the publication had to include means and standard deviations (SDs) of biodiversity measures (e.g. taxonomic richness, Shannon–Wiener diversity index) for each river type (PRs and IRs) or enough information to calculate these values. This selection resulted in a total of 63 publications, 44 with replicated data (i.e. studies with more than one PR and IR each from which the means and SDs were obtained) and 19 with non-replicated data (i.e. only one PR or IR from which biodiversity data was obtained) (see Supplementary material Appendix 1 and 2 for the full reference details of these publications). Most studies were conducted in North America, Europe and Australia. Very few studies were from Africa and Asia, and none were from South America (Fig. 1). For studies investigating biodiversity in more than one distinct region (e.g. South Africa and Australia) we derived biodiversity data separately for each region, whereas for studies which investigated multiple groups of organisms (e.g. fish, invertebrates, diatoms), we randomly chose one group only. Each of these individual investigations are referred to and counted as one study for simplicity.

We most commonly extracted means, SDs, and number of sites (n) directly, computed them from text and/or tables in the studies (27 studies), or obtained them directly from authors (26 studies). For the remaining 10 studies, we extracted data from figures using Plot Digitiser (<www.plotdigitizer.sourceforge.net/>). Where multiple measures of biodiversity (e.g. taxonomic richness, evenness, Shannon–Wiener diversity index) were available, we preferentially extracted richness data due to it being the most commonly reported measure across all studies. Only one study reported the Shannon–Wiener diversity index alone. We included both these measures (i.e. richness and the Shannon–Wiener diversity index) together in our analysis because our aim was to provide a general summary of the difference in biodiversity among groups (i.e. PRs and IRs) (Scheiner and Gurevitch 2001). Then, for each individual publication, we obtained information on site or sampling characteristics. In particular, we considered the following six factors, each with several levels within: climate, sampling season, habitat, longitudinal zonation, level of anthropogenic disturbance, and taxonomic group (Table 1, Supplementary material Appendix 3). We created different subsets of data using the levels of these factors and analysed them separately.

Effect size estimate

For replicated studies (with $n > 1$ PRs and $n > 1$ IRs, n_{PR} and n_{IR}, respectively), we obtained effect sizes using Hedge's g, which corresponds to the difference between the means of biodiversity in PRs and IRs $(\overline{PR} - \overline{IR})$ divided by the pooled standard deviation (S_{within}) and with a correction for small sample bias (J) (Rosenberg et al. 2000, Borenstein et al. 2009):

$$g = \frac{\overline{PR} - \overline{IR}}{S_{within}} J,\ S_{within} = \sqrt{\frac{(n_{PR} - 1)SD^2_{PR} + (n_{IR} - 1)SD^2_{IR}}{n_{PR} + n_{IR} - 2}},$$

$$J = 1 - \frac{3}{4(n_{PR} + n_{IR} - 2) - 1}$$

Figure 1. Distribution of publications, identified from an ISI Web of Knowledge literature search by Leigh et al. (2016a), that examined biodiversity in hydrologically independent perennial and intermittent rivers (PRs and IRs, respectively). White stars refer to studies with non-replicated data for PRs and/or IRs (n = 19), whereas black stars refer to studies with replicated data for PRs and IRs (n = 44).

Table 1. Description of the environmental and biological factors and levels within each factor, identified from individual publications and used in our meta-analysis with replicated data.

Environmental/biological factors	Levels	Observations
Climate	B, C, D, E, multiple	Dominant climate of each system was determined according to the Köppen classification of Peel et al. (2007), which considers five general climates: tropical (A), arid (B), temperate (C), cold (D), and polar (E). No studies were carried out in the tropical (A) climate and thus it is not included here. Multiple includes a combination of these climates.
Sampling season	dry, wet, multiple	Multiple refers to studies that sampled in both dry and wet seasons, or at multiple times of year in regions that cannot be described simply in terms of dry–wet seasonality
Habitat	riffles, pools, stones, multihabitat	Multihabitat includes riffles and pools. Stones refer to rock fragments of more than 25 cm.
Longitudinal zonation	headwaters, middle, multiple	Headwater reaches refer to a catchment area $<$ 100 km^2, or a stream order equal to or less than 3. Middle refers to reaches with a catchment area between 100 and 1000 km^2 or a stream order of 4–6. Large refers to a catchment area $>$ 1000 km^2. Multiple includes headwaters, middle and large reaches.
Anthropogenic disturbance	low, medium–high	This factor was considered very general and did not distinguishspecific types of disturbance (e.g. hydrological versus morphological). Low levels were distinguished from medium–high levels on the basis of information available in the published studies (e.g. low levels were assigned to sites within reserves; medium–high to sites in urban areas). Medium and high levels of disturbance were difficult to differentiate based on information provided in studies and were thus combined.
Taxonomic group	macroinvertebrates, fish, algae/macrophytes	

The variance of g was given by:

$$V_g = \left[\frac{n_{PR} + n_{IR}}{n_{PR} n_{IR}} + \frac{\left[\dfrac{\overline{PR} - \overline{IR}}{S_{within}} \right]^2}{2\left(n_{PR} + n_{IR}\right)} \right] J^2$$

For non-replicated studies, where means and standard deviations were not available, we obtained effect sizes using log(PR/IR), known as the response ratio. Following Hedges et al. (1999; see also Eq. 4.30 and 4.31 in Borenstein et al. 2009), we also computed the response ratio for replicated studies for comparison with the non-replicated studies, but we did not include it in the estimation of weighted effect sizes.

Weighted mean effect size

We used random effects models in all cases because we assumed that the true effect sizes vary among studies (Borenstein et al. 2009). This assumption is justifiable as our meta-analysis included a wide variety of studies that, for example, investigated different organisms or were conducted using different sampling methods. Statistically, this choice of meta-analytic model consists in estimating 1) the between-studies variance (T^2; see Eq. 12.2, 12.3, 12.4 and 12.5 in Borenstein et al. 2009) and 2) the total variance ($V_i = V_g + T^2$) to 3) assign the weight of each study ($W_i = 1/V_i$). Model outputs included the weighted mean effect size (wES) and its confidence interval, and a test of the hypothesis that the true wES is zero, following standard methods described in Borenstein et al. (2009). We estimated wES for the entire dataset (e.g. considering all replicated data in the one random effects model) and for each of the subsets of data separated by the six factors listed above (Table 1). For these subset analyses, the models were estimated without the intercept (Viechtbauer 2010). With this parameterization, a pooled value of T^2 was used, a procedure recommended by Borenstein et al. (2009) to increase the accuracy of the estimate of the between-studies variance.

We used a forest plot to illustrate the results of the meta-analysis. This plot shows the effect sizes and confidence intervals of each study and the wES (Gates 2002). A significant model (or a wES whose confidence interval does not include zero) indicates a significant difference between PR and IR biodiversity. The magnitude of the wES indicates the amount of difference between the two river types. Here, a positive wES indicates that biodiversity in PRs is higher than in IRs.

Publication bias

First, we visually assessed publication bias in the replicated studies using a funnel plot of effect size against a measure of study size or precision (e.g. the standard error of the effect size) (Sterne et al. 2011). Visually asymmetrical funnel plots usually indicate publication bias, whereas symmetrical ones indicate negligible publication bias. Second, we calculated the fail-safe number according to Orwin's equation (Orwin 1983), which gives the number of studies needed to reduce the average effect size to a pre-specified value, which is considered unimportant. We tested a range of values (with steps of 0.2) from 0.2 to 0.8 (corresponding, approximately, to half of the unweighted mean effect size). Third, we calculated the fail-safe number according to Rosenthal's approach ('file drawer analysis'). This indicates the number of missing studies (i.e. those unpublished or available but not captured by the literature search and selection process) needed to be retrieved and incorporated in the analysis to eliminate bias (Borenstein et al. 2009). A high value indicates that a meta-analysis (i.e. estimated effect size) is robust to publication bias, given that we would need a large number of studies to nullify the effect size. Finally, as a sensitivity analysis, we applied the trim-and-fill method (Duval and Tweedie 2000a, b). This method estimates and adjusts meta-analysis results for the numbers and outcomes of missing studies.

We checked our meta-analysis against the quality criteria provided by Koricheva et al. (2013). We fulfilled all applicable criteria. We computed all statistics using the R ver. 3.3.1 (<www.r-project.org>) and the libraries metafor (Viechtbauer 2010) and rmeta (Lumley 2012).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.559cs> (Soria et al. 2017).

Results

Overall differences between IRs and PRs

The overall meta-analysis revealed a statistically significant difference in PR and IR biodiversity (considering all replicate studies together), with a positive overall effect size (wES = 0.879, Table 2), thus indicating a significantly higher biodiversity in PRs than in IRs (Fig. 2). Positive effect sizes for the individual studies ranged from 0.01 to 7.95; negative effect sizes were smaller, ranging from –1.10 to –0.04 (Fig. 2). Accordingly, heterogeneity among studies was highly significant ($Q = 89.317$, $df = 43$, $p < 0.0001$).

Log response ratios estimated for replicated (weighted mean effect size [log(PR/IR)] = 0.38 ± 0.05 SE) and non-replicated (unweighted mean effect size [log(PR/IR)] = 0.25 ± 0.08 SE) studies were also positive (Supplementary material Appendix 4). The majority of non-replicated studies had effect sizes located in the positive side of the forest plot (Supplementary material Appendix 4), again indicating that biodiversity in PRs was, in most cases, higher than in IRs.

Specific differences in biodiversity between IRs and PRs

For most levels of the six factors, wES was significantly positive (Table 2), indicating higher biodiversity in PRs than IRs. We detected differences between PR and IR biodiversity for studies conducted within arid (B), temperate (C), cold (D) or multiple climate zones; within studies that considered dry, wet, or multiple seasons; a multi-habitat sampling regime; samples from headwaters or multiple longitudinal zones; sites subject to low and medium-high levels of anthropogenic disturbance; and that included macroinvertebrates (Table 2). We found non-significant results for polar climates (E); riffle, pool, and stone habitats; middle reaches; fish, algae and macrophytes (Table 2).

Publication bias

Although the funnel plot visually approached asymmetry (Fig. 3a), fail-safe numbers and the sensitivity analysis indicated minimal bias. According to Orwin's method, even if

Table 2. Results of the random effects models for the overall design (with and without trim-and-fill) and for the levels of the six factors. Bold typeface indicates $p < 0.005$. n = number of studies considered in each level; wES = weighted mean effect size; SE = standard error of the estimates; ci.lb and ci.ub = confidence interval (lower and upper limits, respectively). See Table 1 for a description of the factors and levels.

			Model results				
		n	wES	SE	p-value	ci.lb	ci.ub
Overall design		44	0.879	0.169	**<0.0001**	0.549	1.209
Climate	**B**	6	0.946	0.454	**0.0373**	0.056	1.836
	C	28	0.735	0.203	**0.0003**	0.336	1.133
	D	4	1.766	0.726	**0.0150**	0.343	3.188
	E	3	1.369	1.204	0.2556	–0.991	3.729
	multiple	3	1.244	0.556	**0.0254**	0.153	2.334
Sampling season	**dry**	10	1.304	0.387	**0.0007**	0.546	2.061
	wet	7	0.964	0.400	**0.0159**	0.180	1.748
	multiple	27	0.719	0.222	**0.0012**	0.283	1.155
Habitat	riffles	4	0.754	0.600	0.2089	–0.422	1.929
	pools	2	0.734	1.123	0.5132	–1.467	2.935
	stones	1	0.009	0.777	0.9912	–1.515	1.532
	multihabitat	32	0.994	0.194	**<0.0001**	0.613	1.375
Longitudinal zonation	**headwaters**	24	0.988	0.263	**0.0002**	0.472	1.504
	middle	1	–0.588	1.390	0.6723	–3.312	2.137
	multiple	11	1.028	0.295	**0.0005**	0.451	1.605
Anthropogenic disturbance	**low**	27	0.783	0.210	**0.0002**	0.372	1.195
	medium–high	14	1.016	0.293	**0.0005**	0.443	1.590
Taxonomic group	**macroinvertebrate**	36	1.059	0.181	**<0.0001**	0.704	1.413
	fish	6	0.446	0.411	0.2783	–0.360	1.252
	algae/macrophytes	2	0.024	0.509	0.9619	–0.974	1.022

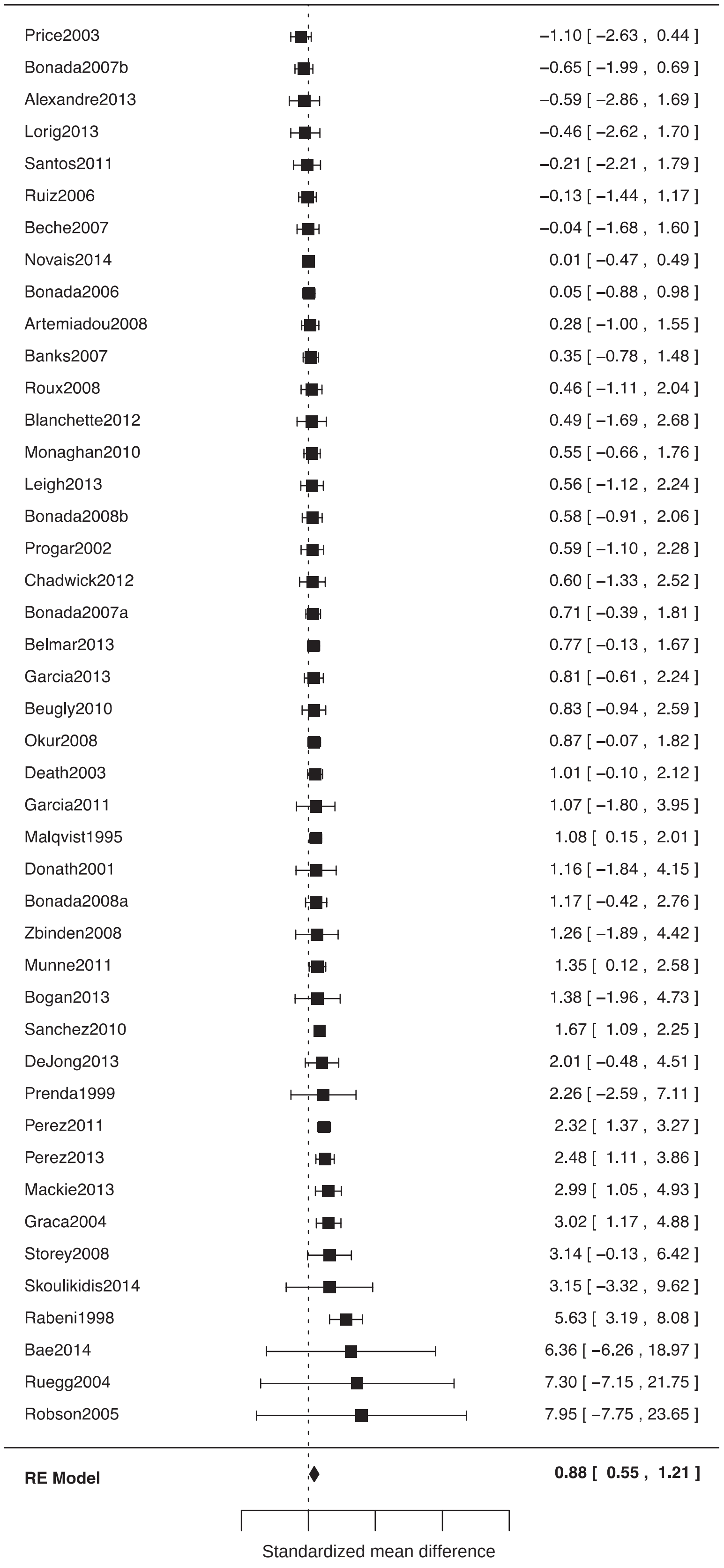

Figure 2. Forest plot for the overall design of the original model (without trim-and-fill) considering the 44 replicated studies ordered by increasing effect size from the top to the bottom. Each study is indicated in the left column with the first author and the year of publication (see Supplementary material Appendix 1 for the complete reference). Effect sizes of each study (using the standardized mean difference) with their corresponding confidence intervals are displayed in the centre of the plot with the exact values on the right. The filled diamond at the bottom shows the weighted mean effect size (wES) estimated by the model with the edges of the diamond showing the corresponding confidence interval.

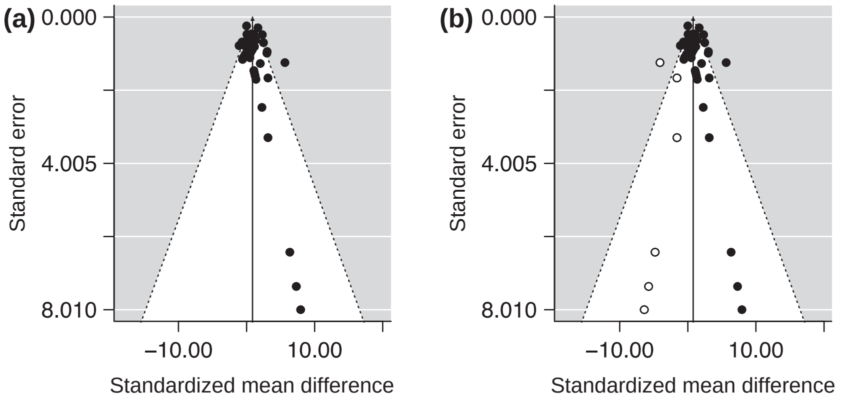

Figure 3. Funnel plots for the overall design using replicated studies without and with trim-and-fill, (a) and (b) panels, respectively. Filled circles represent the individual replicated studies, whereas open circles represent the missing studies required to produce a symmetrical plot.

a substantial effect size (0.8) is conservatively assumed as unimportant, a large number of unpublished studies would still be needed (Orwin's fail safe N = 38 studies) with no differences between the types of rivers for the estimated effect size to be reduced to an 'unimportant' value. As expected, this number increases substantially when lower effect sizes (i.e. 0.6, 0.4 and 0.2) are used in Orwin's equation (Orwin's fail safe N = 67, 124 and 295, respectively). According to Rosenthal's approach, the fail-safe number was 1352, suggesting that a large number of studies with non-significant differences between types of rivers would be needed to reverse the conclusion that PRs were more biodiverse than IRs. According to the trim and fill approach, only six studies were potentially missing from our analysis that if present would produce a symmetrical funnel plot (Fig. 3b). The wES estimated by this method was similar to the one reported above (trim and fill wES = 0.776 ± 0.178; 95% CI = 0.427 to 1.125).

Discussion

The studies analysed here compared biodiversity in PRs and IRs across a wide range of environmental conditions. We found a significantly higher biodiversity in PRs than in IRs, which confirmed our primary hypothesis. This finding agrees with individual studies showing that PRs are more species-rich than IRs and that flow intermittence is a disturbance that constrains a aquatic biodiversity (Del Rosario and Resh 2000, Storey and Quinn 2008, Bogan et al. 2013). However, several individual studies included in our meta-analysis found similar values of biodiversity in PRs and IRs; in these cases, the characteristic taxa found in IRs during the dry period compensated for the loss of taxa present during flow (Miller and Golladay 1996, Casas and Langton 2008, Santos and Stevenson 2011). Few of the studies analysed here had higher biodiversity in IRs than in PRs (Price et al. 2003, Bonada et al. 2007a, Alexandre et al. 2013). The persistence of isolated pools during the dry season in IRs, which favours the presence of a wide variety of species found exclusively in lentic waters and/or that prefer such habitat, may have increased IR biodiversity in these cases (Bonada et al. 2006a).

Although we found overall support for the hypothesis that PR biodiversity is higher than IR biodiversity, IRs occur throughout the globe, including many in regions in Africa, Asia or South America not covered by our meta-analysis (Datry et al. 2016a, Leigh et al. 2016a). In addition, most of the papers analysed here consider the most commonly studied taxonomic groups in river ecology (i.e. macroinvertebrates, fish, algae and macrophytes); no papers examining other highly diverse groups such as microbes (Palmer et al. 2000) fulfilled our selection criteria. To increase the robustness of our meta-analysis, there is a need for future research on studies comparing PRs and IRs biodiversity in regions beyond those included here and across a wider variety of taxonomic groups. This would provide a more comprehensive view of the effects of flow intermittence on aquatic biodiversity and the potential effects of current and future global change.

Our finding that PR biodiversity was higher than IR biodiversity within cold, arid and temperate (which includes Mediterranean) climates agrees with several studies from arid (Beugly and Pyron 2010, Leigh 2013, De Jong et al. 2013) and Mediterranean-temperate regions (Progar and Moldenke 2002, Roux et al. 2008, Storey and Quinn 2008). Flow predictability, which is related to climate predictability, plays an important role in shaping species adaptations and thus biodiversity (Lytle and Poff 2004); highly predictable environments (e.g. in predictably seasonal Mediterranean-climate regions) are considered to support higher biodiversity than less predictable ones. However, despite dry riverbeds providing habitat and refuge for terrestrial organisms (Steward et al. 2012, Corti et al. 2013, Corti and Datry 2016) and their disconnected pools acting as refuges for aquatic organisms (Bonada et al. 2007a, b, Sheldon et al. 2010, Datry et al. 2014a), flow intermittence is a strong disturbance even in predictable climates (Datry et al. 2014b, Leigh and Datry 2016). Indeed, although some aquatic organisms have traits to cope with flow intermittence (Bêche et al. 2006, Bonada et al. 2008, Blanchette and Pearson 2012), resistance traits acquired through evolution as a response to drying are much less frequent than resilience traits in IRs (Datry et al. 2014b, Leigh et al. 2016a, Vander Vorste et al. 2016), which would explain our overall result. Of particular concern is our finding of comparatively low biodiversity in arid-zone IRs given aridity is projected to increase in several regions of the world (e.g. the already arid southwest region of USA; Seager et al. 2013).

Our results do not support the view that differences in biodiversity between PRs and IRs are negligible during the wet season. However, despite the low number of studies considered, we did find support for the hypothesis that biodiversity in PRs is higher than in IRs during the dry season. In this latter case, the low habitat availability in IRs compared to PRs will reduce biodiversity unless isolated pools remain for long periods allowing many species to colonize and increase community variability among pools within reaches (Bonada et al. 2006a, Leigh and Sheldon 2009). By contrast, during the wet season, despite IRs having similar habitat availability as PRs, some studies have also shown that biodiversity may remain relatively low in IRs because fewer species may be available and able to colonize these habitats and/or because of alterations to food web structure and dimensions (Datry 2012, McHugh et al. 2015).

Aquatic organisms (i.e. macroinvertebrate, fish, algae and macrophytes) have adaptations to particular instream habitats, from riffles to pools (Bonada et al. 2006a, 2008, Dallas 2007). Most likely due to the small number of studies in the subsets, our hypothesis regarding habitat (i.e. biodiversity in PR riffles may be higher than in IR riffles, whereas the opposite pattern may be observed in pools) was not supported. However, studies sampling multiple habitats showed a higher biodiversity in PRs than in IRs, which agrees with findings from Graça et al. (2004), Belmar et al. (2013) and Leigh et al. (2013a). Multi-habitat sampling may be a better method to account for biodiversity of rivers (Leitão et al. 2014) because species characteristic of individual habitats may not occur across all habitat types (Bonada et al. 2006b, Cid et al. 2016).

The aquatic biodiversity of a particular reach not only depends on instream habitat characteristics, but also on the regional biodiversity and the balance between dispersal and abiotic/biotic factors. The river network structure plays an essential role for the dispersion of aquatic organisms and thus helps determine aquatic biodiversity patterns (Altermatt 2013). In PRs, biodiversity in lowland reaches is driven by mass effects whereas abiotic/biotic factors are considered more important in their headwaters (Brown and Swan 2010). In IRs, the relative role of dispersal versus abiotic/biotic factors depends not only on the hydrological phase of the reach (i.e. flowing, non-flowing, dry) but also on where the drying event occurs along the river network (Datry et al. 2014b, 2016c, d). We were unable to test how different configurations of drying events affect a aquatic biodiversity but, although more studies are needed for middle reaches, our results on longitudinal zonation agreed with our initial hypothesis. Flow and river characteristics change with longitudinal zonation and, according to the River continuum concept, alpha-diversity is expected to peak at middle reaches (Vannote et al. 1980, Finn et al. 2011). Indeed, the low alpha biodiversity in headwaters and their high isolation make them highly vulnerable to biodiversity loss by flow intermittence and hampers recolonization after flow resumption unless communities in IR headwaters are dominated by resistance strategies to drying (Datry et al. 2014b, 2016a). In contrast, middle reaches have higher alpha biodiversity and less isolation (Finn et al. 2011), resulting in no differences between PRs and IRs. On the other hand, headwaters make up a large proportion of all river networks (Naiman 1983, Benda et al. 2005) and the studies included in our analyses that were conducted in multiple reaches also included a higher proportion of headwater sites, supporting the hypothesis that PRs have a higher biodiversity than IRs when examined across multiple reaches (i.e. at large spatial scales). We suggest, however, that these interpretations should be viewed with caution due to the small number of studies in middle reaches.

Anthropogenic disturbances often decrease biodiversity by homogenising communities (Rahel 2002). Despite this, we found higher biodiversity in PRs than in IRs regardless of the level of anthropogenic disturbance (i.e. low or medium-high). We acknowledge, however, that our categorization of anthropogenic disturbances was coarse and more studies comparing biodiversity in PRs and IRs under more explicit and different disturbance categories are needed. The effect of anthropogenic disturbances on IRs is a relatively novel topic that is being considered in terms of management and conservation of river ecosystems (Skoulikidis et al. 2017). Current bioassessment methods are designed to detect the impacts of anthropogenic disturbances (Bonada et al. 2006b) but typically fail when applied to IRs. This means that the lower biodiversity of IRs compared to PRs cannot simply be interpreted as indicative of anthropogenic impairment. New methods for IR bioassessment must be designed that can disentangle natural from anthropogenic disturbances (Prat et al. 2004, Leigh et al. 2013b).

Biodiversity has been related to ecosystem resilience (defined by Holling 1973, "as the magnitude of disturbance that a system can experience before it shifts into a different state"), however, there is uncertainty about how ecosystem resilience will respond to increases in levels of anthropogenic disturbance and consequent impacts on biodiversity (Steffen et al. 2004). Walker and Meyers (2004) suggested that ecosystems might respond gradually to biodiversity loss, whereas Gunderson and Pritchard (2002) suggested that ecosystems will respond strongly, because crossing the threshold of biodiversity loss will produce sudden and dramatic changes in the responding state factors. Indeed, higher numbers of species are expected to increase the ability to recover from disturbances (Holling 1978, Folke et al. 2004). If IRs have significantly lower biodiversity than PRs, as found by us, ecosystem resilience could be affected. However, IR taxa have particular adaptations for surviving and recovering from drying (Lake 2011, Blanchette and Pearson 2012, Leigh et al. 2016b), which may help to mitigate the effects of future co-occurring disturbances (Mori et al. 2013, Vander Vorste et al. 2016). Although a growing number of studies on IRs consider ecosystem resilience (e.g. using functional characteristics of species; Bruno et al. 2016, Vander Vorste et al. 2016), the ecosystem effects of biodiversity loss in these systems needs to be investigated.

As a result of global change, extreme climatic events are expected to increase in frequency and intensity, with an increase in drying frequency, duration, and/or intensity in many regions (Beniston et al. 2007, Palmer et al. 2008, Döll and Schmied 2012). Some regions will experience shifts from PRs to IRs, whereas other regions will show the contrary pattern (Döll and Schmied 2012). If these hydrological regime shifts occur faster than the evolutionary scale at which species acquire adaptive traits (Filipe et al. 2013), dramatic effects on aquatic biodiversity and ecosystem processes and services will result (Datry et al. 2014a, IPCC 2014, Ledger and Milner 2015). In regions where PRs will shift to IRs, loss of species poorly adapted to dry conditions can be expected (Phillipsen and Lytle 2013, Jaeger et al. 2014). Our findings suggest such losses may be particularly relevant for certain taxonomic groups (i.e. macroinvertebrates) and under particular environmental conditions or in certain regions (e.g. in arid and temperate climate zones, and in headwaters). However, IRs communities of species with strong dispersal capacity and high fecundity may be minimally affected and able to colonize these novel IRs (Arscott et al. 2010, Datry et al. 2014a, b). In regions where IRs will shift to PRs, the expected increase in biodiversity in these novel PRs will ultimately depend on the connectivity to other PRs. PRs highly connected to novel PRs might maintain biodiversity, whereas the biodiversity in of highly isolated PRs may decline. As highly dynamic metacommunities are expected to dominate in this future scenario of IRs shifting to PRs and vice versa (Datry et al. 2016b), conservation efforts to reduce the risk of undesired hydrological regime shifts should be prioritized to avoid effects on ecosystem resilience (Folke et al. 2004) and could be targeted towards those environmental conditions or taxonomic groups with significant differences between PR and IR biodiversity.

Acknowledgements – We thank all authors that provided original data: Antoni Munné, María del Mar Sánchez, Esther Mas-Martí and Oscar Belmar.
Funding – This work is one aspect of the international research project "Intermittent River Biodiversity Analysis and Synthesis" (IRBAS, irbas.cesab.org). The IRBAS research project is supported by the Center for Synthesis and Analysis of Biodiversity (CESAB), which is funded jointly by the French Foundation for Research on Biodiversity (FRB) and the French National Agency for Water and Aquatic Environments (ONEMA). Financial support was received from the Centre for Synthesis and Analysis of Biodiversity (CESAB) and the Intermittent River Biodiversity Analysis and Synthesis working group (IRBAS).

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Supplementary material (available online as Appendix oik-04118 at <www.oikosjournal.org/appendix/oik-04118>). Appendix 1–4.

Received: 26 July 2019 | Accepted: 21 October 2019

DOI: 10.1111/1365-2664.13538

RESEARCH ARTICLE

Journal of Applied Ecology
BRITISH ECOLOGICAL SOCIETY

Natural disturbances can produce misleading bioassessment results: Identifying metrics to detect anthropogenic impacts in intermittent rivers

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Funding information
LIFE+ TRivers, Grant/Award Number: LIFE13 ENV/ES/000341; Juan de la Cierva-Formación, Grant/Award Number: FJCI-2015-25785

Handling Editor: Robert Arlinghaus

Abstract

1. Ecosystems experience natural disturbances and anthropogenic impacts that affect biological communities and ecological processes. When natural disturbance modifies anthropogenic impacts, current widely used bioassessment metrics can prevent accurate assessment of biological quality.
2. Our aim was to assess the ability of biomonitoring metrics to detect anthropogenic impacts at both perennial and intermittent sites, and in the latter including both flowing and disconnected pool aquatic phases. Specifically, aquatic macroinvertebrates from 20 rivers were sampled along gradients of natural flow intermittence (natural disturbance) and anthropogenic impacts to investigate their combined effects on widely used river biomonitoring metrics (i.e. taxonomic richness and standard biological indices) and novel functional metrics, including functional redundancy (i.e. the number of taxa contributing similarly to an ecosystem function, here a trophic function) and response diversity (i.e. how functionally similar taxa respond to natural disturbance and anthropogenic impacts).
3. Only the widely used IBMWP index (Iberian Biological Monitoring Working Party) was able to detect anthropogenic impacts in intermittent rivers when used during flowing phases. Several functional metrics also detected anthropogenic impacts regardless of flow intermittence. Besides, functional redundancy of the entire community remained effective even in disconnected pools.
4. *Synthesis and applications*. Our results show that natural flow intermittence can confound river bioassessment, and that a set of new functional metrics could be used as effective alternatives to standard metrics in naturally disturbed intermittent rivers. Our findings suggest that water managers should incorporate alternative functional metrics in the routine biomonitoring of naturally disturbed rivers.

KEYWORDS

bioassessment, functional diversity, intermittent rivers, intermittent streams, macroinvertebrates, multiple stressors, natural stress, temporary rivers

1 | INTRODUCTION

Ecosystems experience natural disturbances and anthropogenic impacts that affect biological communities and ecological processes (Dornelas, 2010; Turner, Webb, Bowers, & Hastings, 2003). Natural disturbances (e.g. droughts, floods, wildfires) have acted through evolutionary time and have resulted in species adapted to such abiotic stress (Bowman et al., 2009; Lytle & Poff, 2004). In contrast, anthropogenic impacts (e.g. pollution, land-use changes, biological invasions, and recently, climate change) are relatively new (<10,000 year), and may represent novel conditions for biota, impacting both biodiversity and ecosystem functioning (Hooper et al., 2012; Olden, Poff, Douglas, Douglas, & Fausch, 2004). Given the predicted consequences of global change, both natural disturbances and anthropogenic impacts may increase in many regions worldwide (Olden et al., 2004). Urgent action is thus needed to develop suitable assessment methods and management practices that consider the interaction of both type of impacts (Elliott & Quintino, 2007; Ghazoul, Burivalova, Garcia-Ulloa, & Vigo, 2015).

Biomonitoring methods detect anthropogenic impacts using metrics based on aspects of ecosystem structure and function (Bonada, Prat, Resh, & Statzner, 2006; Pereira et al., 2013). These metrics underpin biomonitoring programmes that aim to halt and reverse biodiversity loss, to maintain and enhance the quality of ecosystems, and to assess the effectiveness of conservation and restoration measures, such as the Water Framework Directive (WFD; European Commission, 2000), the Convention on Biological Diversity (CBD, 2010) or the International Union for Conservation of Nature (IUCN, 2016). Problematically, few current metrics integrate the effects of natural disturbances, which can confound the assessment of anthropogenic impacts and thus lead to inappropriate management actions (Gutiérrez-Cánovas et al., 2019; Pitacco et al., 2019; Tockner, Pusch, Borchard, & Lorang, 2010).

Functional metrics based on biological traits have shown to be promising tools for detecting anthropogenic impacts in different types of ecosystems (Laliberté et al., 2010; Mouillot, Graham, Villéger, Mason, & Bellwood, 2013; Statzner & Beche, 2010), and to be more accurate for the biomonitoring of naturally disturbed systems (Belmar et al., 2019; Bruno, Gutiérrez-Cánovas, Velasco, & Sánchez-Fernández, 2016). However, studies assessing the combined effects of natural disturbances and anthropogenic impacts on the functional composition of biological communities remain limited (e.g. Bruno, Gutiérrez-Cánovas, Sánchez-Fernández, Velasco, & Nilsson, 2016; Elliott & Quintino, 2007; Mouillot et al., 2013). Additionally, the response of functional metrics might improve when incorporating traits responding to environmental changes (i.e. response traits), and to the effect of such changes on ecosystem functioning (i.e. effect traits; Laliberté et al., 2010; Suding et al., 2008). Consequently, approaches that more directly link community dynamics to ecosystem functioning are emerging.

Nearly 50% of the current global river network has intermittent flow (Datry et al., 2014). Intermittent rivers, also known as temporary rivers in a broad sense, are dynamic systems that typically shift between flowing, disconnected-pools and dry periods, named hereafter as aquatic phases (Gallart et al., 2012, 2017). Repeated shifts between aquatic phases reorganize biological communities and, therefore, flow intermittence represents a natural disturbance (Lake, 2000; Leigh & Datry, 2017). Intermittent rivers also experience anthropogenic impacts, such as hydrological alterations (flow regulation, surface and/or groundwater extractions), geomorphological impacts (e.g. sediment extraction and physical habitat modifications), pollutants (e.g. heavy metals and nutrient additions) and biological invasions (Chiu, Leigh, Mazor, Cid, & Resh, 2017). Detection of these impacts at intermittent rivers is challenging because the reliability of standard biomonitoring metrics is generally uncertain for such naturally disturbed systems (Chiu et al., 2017; Cid et al., 2017). As the global extent of intermittent rivers increases due to climate change and water resource pressures (Döll & Schmied, 2012), understanding the combined effects of natural flow intermittence and anthropogenic impacts on widely used and novel river biomonitoring metrics is needed to underpin reliable biological quality assessments.

Our aim was to assess the ability of biomonitoring metrics to detect anthropogenic impacts at both perennial and intermittent sites, and in the latter including both flowing and disconnected pool aquatic phases. Specifically, aquatic macroinvertebrates from 20 rivers were sampled along gradients of natural flow intermittence (natural disturbance) and anthropogenic impacts to investigate their combined effects on widely used river biomonitoring metrics (i.e. taxonomic richness and standard biological indices) and novel functional metrics based on biological traits. Different types of responses to natural and anthropogenic gradients were used to assess the reliability and calibration requirements of potential metrics to both perennial and intermittent rivers (Figure 1). A single response effect occurs when a metric respond to anthropogenic impacts but not to natural flow intermittence (Figure 1a), indicating high reliability without calibration. An additive effect occurs when the effects of natural flow intermittence add to those of anthropogenic impacts but effects do not interact (Figure 1b), indicating that this metric could be reliable after proportional calibration with a constant term (i.e. adapting reference conditions). Finally, interactive responses occur when the effects of natural flow intermittence reduce, enhance or oppose those of anthropogenic impacts, and leads to antagonistic (Figure 1c), synergistic (Figure 1d) or opposing (Figure 1e) interactions, respectively (Feld, Segurado, & Gutiérrez-Cánovas, 2016). Metrics with these interactive responses could be reliable only after non-proportional calibration (i.e. adapting reference conditions and response gradient to anthropogenic impacts).

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in 20 river sites in the north-eastern Iberian Peninsula (Figure S1). The area has a Mediterranean climate (i.e. Csa and Csb; Kottek, Grieser, Beck, Rudolf, & Rubel,

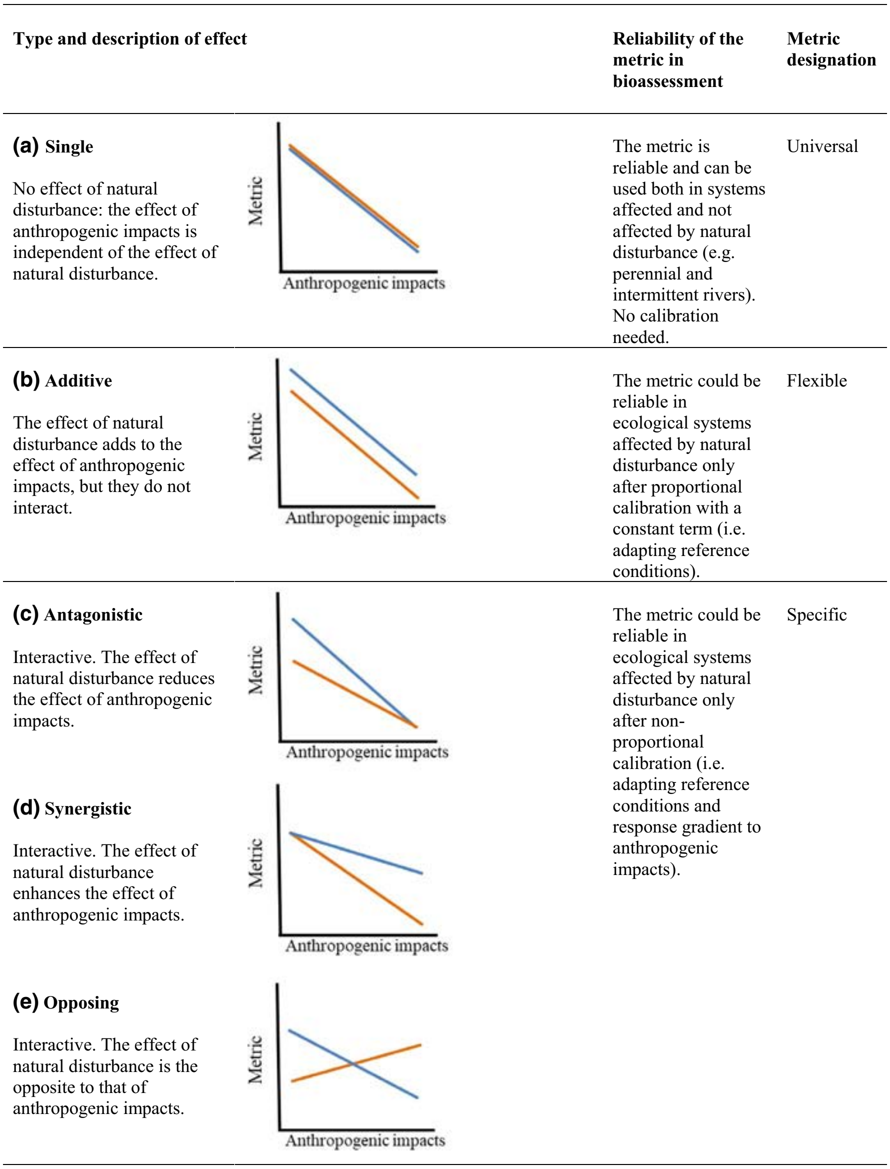

FIGURE 1 Potential effects of natural disturbances and anthropogenic impacts on a biomonitoring metric and the associated reliability for its use in bioassessment, with a special focus on intermittent rivers. Colours indicate communities not affected (blue) and affected (orange) by natural disturbance

Type and description of effect		Reliability of the metric in bioassessment	Metric designation
(a) Single No effect of natural disturbance: the effect of anthropogenic impacts is independent of the effect of natural disturbance.		The metric is reliable and can be used both in systems affected and not affected by natural disturbance (e.g. perennial and intermittent rivers). No calibration needed.	Universal
(b) Additive The effect of natural disturbance adds to the effect of anthropogenic impacts, but they do not interact.		The metric could be reliable in ecological systems affected by natural disturbance only after proportional calibration with a constant term (i.e. adapting reference conditions).	Flexible
(c) Antagonistic Interactive. The effect of natural disturbance reduces the effect of anthropogenic impacts.		The metric could be reliable in ecological systems affected by natural disturbance only after non-proportional calibration (i.e. adapting reference conditions and response gradient to anthropogenic impacts).	Specific
(d) Synergistic Interactive. The effect of natural disturbance enhances the effect of anthropogenic impacts.			
(e) Opposing Interactive. The effect of natural disturbance is the opposite to that of anthropogenic impacts.			

2006), with high seasonal variability in precipitation and thus streamflow (Bonada & Resh, 2013; Cid et al., 2017). Ten of the sites are intermittent and 10 are perennial. Sites were located in different sub-basins in the Ebro, Júcar and Catalan catchments and experience different degrees of anthropogenic impact and river regime. Sites ranged from 6 to 1,100 m a. s. l. and drained calcareous catchments with discharges ranging from 0 to 417 L/s.

2.2 | Macroinvertebrate data

Macroinvertebrates were collected five times per site (i.e. *n* = 100 samples) at six-week intervals between April and December 2015, to capture the assemblages present during flowing phases and in disconnected pools. In total, 91 samples were taken because five sites were dry between one or three occasions. Samples were collected using a 250 μm-mesh D-net across all available microhabitats (i.e. different mineral and organic substrates), following the national standard quantitative sampling protocol (MAGRAMA, 2013). Samples were preserved in 4% formaldehyde, and the macroinvertebrates identified to the lowest taxonomic resolution possible, usually genus, but with some Chironomidae and Ceratopogonidae identified to subfamily or tribe. Overall, 194 macroinvertebrate taxa were identified.

Macroinvertebrate effect and response traits were characterized. Effect traits describe the potential contribution of macroinvertebrate organisms to ecosystem functioning through the trophic transfer of resources and energy from basal to higher organisms (Suding et al., 2008). Response traits characterize the resistance and resilience of communities to disturbances and, thus, inform on community responses to environmental changes (McLean et al., 2019; Suding et al., 2008). For the effect traits, trophic characteristics of each genus (i.e. grazers, miners, xylophagous, shredders, gatherers, active and passive filterers, predators, parasites and others) were gathered from the Freshwater

Information Platform (http://www.freshwaterecology.info; Moog, 2002; Schmidt-Kloiber & Hering, 2015). Response traits were compiled from Tachet, Richoux, Bournaud, and Usseglio-Polatera (2010; Table S1). For each genus, traits were assigned using a fuzzy coding approach (i.e. a degree of affinity assigned to each trait category, according to the frequency of occurrence within the genus; Chevenet, Doléadec, & Chessel, 1994). For genera without traits or for taxa not identified to genus, the averaged data from other genera within the same family or from family-level traits were used. This was the case for 24 taxa identified to genus, as well as for the Chironomidae and Ceratopogonidae identified to subfamily or tribe (see Data Accessibility Statement). Prior to analysis, fuzzy-coded data were converted into percentages of affinity for each trait.

2.3 | Characterization of flow intermittence and anthropogenic impacts

The degree of flow intermittence at each site was obtained from different descriptors. First, TREHS (Temporary Rivers Ecological and Hydrological Status) software (http://www.lifetrivers.eu/products/trehs-software/; Gallart et al., 2017) was used to classify the rivers' regime and to identify potential hydrological alterations (Table S2) to differentiate sites affected by natural flow intermittence from those with human-driven flow intermittence. The degree of flow intermittence during the study period (i.e. from April 2015 until December 2015) was calculated from temperature data loggers (UA-002 HOBO), from which is possible to infer the aquatic phases (Gungle, 2006). Two data loggers were installed at each site: one in a riffle, to determine the day flow ceased and resumed, and one in a pool, to identify the day the reach dried completely. Data were used to calculate two descriptors of flow intermittence for each site: the number of days in the disconnected pool phase since the last sample was taken (DP_i), and the total number of zero-flow days (i.e. disconnected pool or dry riverbed) during the 30-week study period (ZF_T).

The extent of anthropogenic impacts at each site was measured using the number of impacts in the Mediterranean reference criteria (MRC), which include invasive species, diffuse pollution sources, land-use intensity, riparian vegetation, river geomorphology, instream habitat conditions and hydrological alterations (Sánchez-Montoya et al., 2009). To facilitate interpretation, the number of MRC index impacts (i.e. 0 = non-impacted, to 20 = extremely impacted) was used as a descriptor variable (hereafter, number of impacts; see Table S3 for more details). Physicochemical parameters of each river were also measured in every sampling occasion, and were the following: dissolved oxygen, conductivity, temperature, phosphates, nitrates and Chl-a (Table S2). However, only the number of impacts was used as it represented a broad spectrum of impacts and was correlated with most of the physicochemical parameters in our dataset (Table S2) and elsewhere (Sánchez-Montoya et al., 2009).

2.4 | Metrics calculation

Two types of metrics were calculated for each sample to characterize biotic responses to flow intermittence and the anthropogenic impacts: widely used and functional. As widely used metrics, taxonomic richness based on invertebrate families (Sfam) or genera (Sgen) and several tolerance-based biological indices used in the Iberian Peninsula were calculated: IBMWP (Alba-Tercedor et al., 2002), IASPT (Jáimez-Cuéllar et al., 2002), and IMMi-T (Munné & Prat, 2009; Table 1).

For the functional metrics, functional redundancy (i.e. FR; the number of taxa or individuals contributing similarly to an ecosystem function, here a trophic function) and response diversity (i.e. RD; how functionally similar taxa respond to natural disturbance and anthropogenic impacts; Suding et al., 2008) were calculated (Figure 2). For FR metrics, using a classification of macroinvertebrates into functional trophic groups (i.e. effect traits; see Appendix S1) was used to obtain the average abundance (ab) and trait richness (i.e. presence–absence; pa) for the entire community and each trophic group: omnivorous, shredders, predators, grazers, gatherers and filterers (Figure 2, Table 1). For RD, traits related to resilience and resistance strategies (i.e. response traits; see Appendix S1) were used to estimate functional richness (FRic, Villéger, Mason, & Mouillot, 2008) and functional dispersion (FDis, Laliberté & Legendre, 2010; hereafter, RD) for the whole community and each trophic group, all of them using abundance (ab) measures (Figure 2, Table 1).

2.5 | Statistical analysis

Two datasets were analysed. One considered all data collected during aquatic phases (i.e. flow and disconnected pools), to identify metrics that respond to anthropogenic impacts independently of flow. The second dataset included only flowing-phase samples, as required in current river biomonitoring protocols. To determine the reliability of each metric to detect anthropogenic impacts across a gradient of flow intermittence, linear mixed-effects models (LME) were fitted with a Gaussian error distribution to model all metric responses. Before analyses, to reduce distribution skewness and improve linearity, a square-root-transformation was applied to Sfam, Sgen and IBMWP, and a log- or square-root-transformation was applied to almost all functional metrics. Predictor variables (i.e. the number of impacts, DP_i and ZF_T) were standardized to mean = 0 and *SD* = 1 to allow for model coefficient comparison.

For all the aquatic phases dataset, the LMEs were fitted using the number of impacts, DP_i and ZF_T and their pairwise interactions as fixed factors (i.e. DP_i × number of impacts, and ZF_T × number of impacts). For the flowing-phase dataset, the same analysis was performed, but excluding DP_i. All models included site as a random factor to account for the non-independence of samples collected from the same location. A multimodel inference approach was adopted to quantify the predictor's standardized effect sizes and significance. See Appendix S2 for more details.

TABLE 1 Community metrics used in this study

Type of metric	Metric	Description	Type of data
Widely used	Sfam	Taxon richness at the family level	pa
	Sgen	Taxon richness at the genus level	pa
	IBMWP	Iberian Biological Monitoring Working Party (Alba-Tercedor et al., 2002)	pa
	IASPT	Iberian Average Score Per Taxon (Jáimez-Cuéllar et al., 2002)	pa
	IMMi-T	Multimetric index for Mediterranean rivers (Munné & Prat, 2009)	pa
Functional redundancy	FR	Functional redundancy of the entire community	pa, ab
	FR.omnivorous	Functional redundancy of the omnivorous functional group	pa, ab
	FR.shredders	Functional redundancy of the shredder functional group	pa, ab
	FR.predators	Functional redundancy of the predator functional group	pa, ab
	FR.grazers	Functional redundancy of the grazer functional group	pa, ab
	FR.gatherers	Functional redundancy of the gatherer functional group	pa, ab
	FR.filterers	Functional redundancy of the filterers (filterers) functional group	pa, ab
Response diversity	RD	Response diversity of the entire community	ab
	RD.omnivorous	Response diversity of the omnivorous functional group	ab
	RD.shredders	Response diversity of the shredders functional group	ab
	RD.predators	Response diversity of the predators functional group	ab
	RD.grazers	Response diversity of the grazers functional group	ab
	RD.gatherers	Response diversity of the gatherers functional group	ab
	RD.filterers	Response diversity of the filterers (filterers) functional group	ab
	FRic	Functional richness of the response traits	ab

Note: Functional redundancy (FR) and response diversity (RD) metrics were calculated using effect and response traits, respectively. *Type of data*: FR and RD were calculated as the average abundance (ab) and/or richness (i.e. presence–absence; pa) for each functional trophic group and for the entire community. *Omnivorous* taxa had mixed feeding habits, including a variety of shredding, grazing and gathering affinities. See Section 2 for further details.

For each metric, the combined effect type was determined using the regression coefficient sign (+ or −) and p-value of individual predictors and their interactions (Feld et al., 2016). Under this framework, a non-significant interaction term and one significant predictor coefficient indicate a single effect, whereas two or more significant single predictor coefficients indicate an additive effect. Interactive (antagonistic, synergistic or opposing) effects were identified by a significant ($p < .05$) or potential (p-value between .05 and .25) interaction and a single interaction explaining the conditional goodness of fit (rc^2) ≥ 5% of variance. Negative coefficients for individual predictors with a positive interaction coefficient indicated an antagonistic effect. Negative individual predictor and interaction coefficients indicated a synergistic effect. Different coefficient signs between individual predictors indicated an opposing effect. Effective metrics should be responsive to anthropogenic impacts (i.e. explaining a high percentage of total variance and the marginal goodness of fit or $r^2m > 0.20$), and show a similar pattern across a gradient of flow intermittence, which is reflected by non-interactive responses.

For all predictors (i.e. number of impacts, ZF_T and DP_i), null models were used to determine whether observed functional metric responses to anthropogenic impacts reflected taxonomic variation (i.e. the probability of finding more or fewer

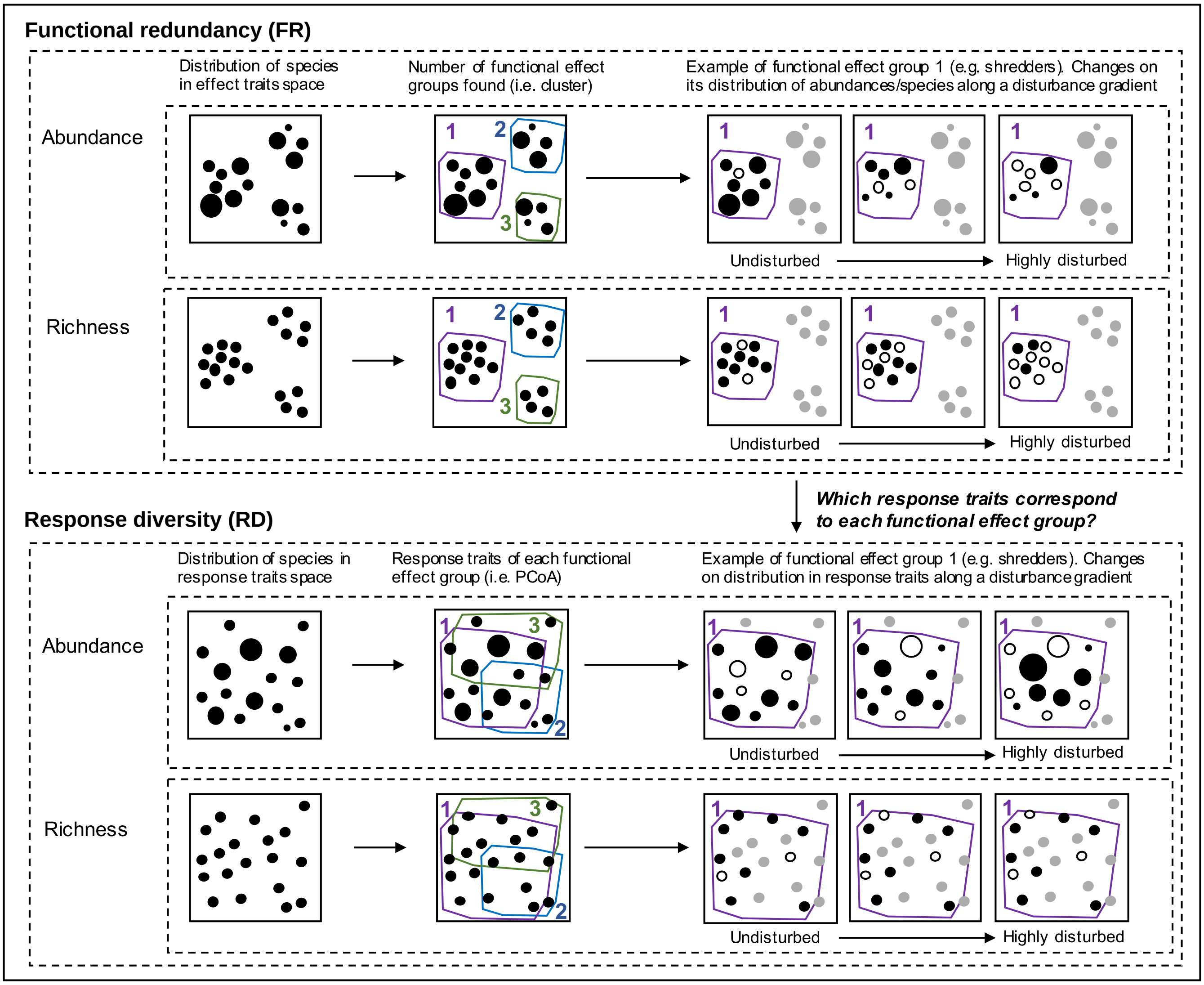

FIGURE 2 Analytical framework for the functional metrics used in this study (i.e. functional redundancy, FR, and response diversity, RD). For FR functional trophic groups were used as effect traits. For RD biological traits related to resilience and resistance strategies were used as response traits (Table S1). Both FR and RD are represented as the average abundance (ab) or trait richness (i.e. presence–absence; pa) for each functional group. Circle size is proportional to abundance. Black circles: species present; white circles: species absent; grey circles: species not included in the functional effect group of the example (i.e. shredders). PCoA, Principal Coordinate Analysis

abundance or trait categories due to the number of taxa; see Appendix S3).

All analyses were conducted in R version 3.4.1 (R Core Team, 2015), using the packages “lme4” (Bates, Maechler, Bolker, & Walker, 2015), “MuMIn” (Barto'n, 2017) and “variancePartition” (Hoffman & Schadt, 2016). The code and functions used to run these analyses are available at Data Accessibility Statement.

3 | RESULTS

Overall, metrics decreased with increasing the number of impacts and with flow intermittence predictors (i.e. DP_i and ZF_T; Table 2 and Table 3). However, responses varied between metrics and between datasets (i.e. flowing phase and all aquatic phases).

3.1 | Widely used metrics

All widely used metrics were negatively related to the number of impacts, explaining >50% of total variance (Tables S4 and S5). A single effect of the number of impacts on the flowing phase dataset (but not all the aquatic phases dataset) was found for IBMWP (Figure 3h, Table 3). For other widely used metrics, the most common effect was the antagonistic (Figure 3, Tables 2 and 3). All widely used metrics from both datasets were identified as responsive metrics ($r^2m > 0.20$), with r^2m values ranging from 0.39 to 0.54 for all the aquatic phases dataset (Table 2) and from 0.24 to 0.43 for flowing phase samples (Table 3). According to the criteria in Figure 1, IBMWP is reliable for flowing phase assessments in both perennial and intermittent rivers (i.e. universal metric; Table 4), whereas other widely used metrics would require calibration before use in intermittent rivers.

TABLE 2 Linear mixed-effects model results from the aquatic phase dataset

	Intercept	No. impacts	ZF_T	DP^i	No. impacts × ZF_T	No. impacts × DP_i	R^2m	R^2c	Effect type: No. impacts × ZF_T	Effect type: No. impacts × DP^i
Sfam	5.488	−0.105*	−2.725	−0.003	0.262 (.)	–	0.39	0.77	Antagonistic	Single
Sgen	6.392	−0.135*	−3.529	−0.006	0.355 (.)	−0.0001	0.45	0.75	Antagonistic	Single
IBMWP	0.973	−0.024*	−0.379	−0.002	0.056 (.)	0.0001	0.31	0.82	Antagonistic	Single
IASPT	0.982	−0.032*	−0.762	−0.004*	0.083 (.)	0.0003	0.44	0.73	Antagonistic	Additive
IMMiT	1.045	−0.045*	−1.116*	−0.005*	0.126*	0.0002	0.54	0.86	Antagonistic	Additive
FR.pa	1.316	−0.006	−0.265	0.001	−0.031 (.)	−0.0002	0.22	0.22	Synergistic	ns
FR.ab	3.949	0.064*	1.481	−0.005	0.187	–	0.23	0.47	Single	Single
FR.omnivorous.pa	1.453	−0.085*	−2.332*	−0.004	0.278*	–	0.32	0.62	Antagonistic	Single
FR.shredders.pa	1.093	−0.043*	−0.272	−0.01	–	0.001 (.)	0.23	0.36	Single	Antagonistic
FR.predators.pa	3.913	−0.092*	−3.085*	0.001	0.244 (.)	–	0.39	0.65	Antagonistic	Single
FR.grazers.pa	1.671	−0.016	−0.161	−0.005*	–	0.0004	0.10	0.57	ns	Single
FR.gatherers.pa	9.262	−0.274*	−7.735*	−0.02	0.922*	−0.004 (.)	0.34	0.56	Antagonistic	Synergistic
FR.filterers.pa	1.492	−0.023	−0.914	−0.005	0.099 (.)	0.001 (.)	0.13	0.28	Antagonistic	Antagonistic
FR.omnivorous.ab	4.476	−0.328*	−5.028	−0.033	1.498*	−0.003	0.33	0.64	Antagonistic	Single
FR.shredders.ab	2.097	−0.083*	−0.171	−0.01	–	–	0.09	0.26	Single	Single
FR.predators.ab	5.261	−0.133*	−3.665	0.004	0.471*	–	0.20	0.39	Antagonistic	Single
FR.grazers.ab	5.307	−0.103	−1.879	−0.014	0.761*	0.001	0.15	0.42	Antagonistic	ns
FR.gatherers.ab	6.592	0.061	1.242	−0.016	0.292	−0.001	0.06	0.43	ns	ns
FR.filterers.ab	4.616	−0.069	−3.565	−0.044	0.307	0.009*	0.15	0.19	ns	Antagonistic
RD.ab	1.101	−0.002*	−0.037*	0	0.006*	−0.00002	0.36	0.36	Antagonistic	Single
RD.omnivorous.ab	0.059	−0.003	−0.012	0	–	–	0.03	0.08	ns	ns
RD.shredders.ab	0.111	−0.008*	−0.005	−0.002	–	0.0002 (.)	0.17	0.23	Single	Antagonistic
RD.predators.ab	0.465	−0.004	−0.043	0.001	–	−0.0004*	0.33	0.33	ns	Opposing
RD.grazers.ab	0.452	−0.007*	−0.145	0	0.005	–	0.11	0.10	Single	Single
RD.gatherers.ab	0.156	−0.005*	0.010	0	–	–	0.16	0.16	Single	Single
RD.filterers.ab	0.287	−0.016*	−0.372	0.001	0.028	–	0.29	0.45	Single	Single
FRic	0.235	−0.011*	−0.194	0	0.023 (.)	–	0.35	0.71	Antagonistic	Single

Note: R^2m: marginal goodness of fit. R^2c: conditional goodness of fit. (–): not selected in the top model. ns: non-significant effect. Significant *p*-values (<.05) are indicated as * for all variables. Potential *p*-values (i.e. between .05 and .25) are also indicated for interactions as (.). No. impacts: the number of impacts. DP_i: number of days in the disconnected pool phase since last sample was taken. ZF_T: total number of zero flow days. See Table 1 for further details about metrics.

TABLE 3 Results of linear mixed-effects models from the dataset including only the flowing phase

	Intercept	No. impacts	ZF_T	No. impacts × ZF_T	R^2m	R^2c	Effect type
Sfam	5.467	−0.104*	−2.441	0.258 (.)	0.36	0.71	Antagonistic
Sgen	42.014	−1.546*	−45.606*	4.187*	0.43	0.65	Antagonistic
IBMWP	0.972	−0.023*	−0.151	—	0.24	0.82	Single
IASPT	0.965	−0.03*	−0.674	0.083 (.)	0.32	0.71	Antagonistic
IMMiT	0.997	−0.039*	−1.058*	0.126*	0.40	0.87	Antagonistic
FR.pa	1.303	−0.005	−0.307*	−0.021	0.14	0.14	Single
FR.ab	3.988	0.073*	1.699	0.141	0.20	0.51	Single
FR.omnivorous.pa	3.562	−0.209*	−4.541	0.662 (.)	0.25	0.47	Antagonistic
FR.shredders.pa	1.131	−0.043*	−0.283	—	0.15	0.21	Single
FR.predators.pa	3.975	−0.101*	−3.662*	0.294*	0.41	0.56	Antagonistic
FR.grazers.pa	1.705	−0.019	−0.001	—	0.04	0.50	ns
FR.gatherers.pa	3.094	−0.058*	−1.532*	0.195*	0.38	0.58	Antagonistic
FR.filterers.pa	1.584	−0.025*	−1.078	0.050	0.33	0.42	Single
FR.omnivorous.ab	4.473	−0.346*	−5.472	1.922*	0.45	0.76	Antagonistic
FR.shredders.ab	1.944	−0.066	0.995	—	0.03	0.35	ns
FR.predators.ab	5.199	−0.133*	−2.482	0.376 (.)	0.24	0.45	Antagonistic
FR.grazers.ab	5.231	−0.099*	−0.199	0.600*	0.07	0.25	Antagonistic
FR.gatherers.ab	6.637	0.072	1.519	—	0.05	0.53	ns
FR.filterers.ab	4.576	−0.035	−3.027	—	0.04	0.07	ns
RD.ab	0.211	−0.005*	−0.026	0.008 (.)	0.43	0.43	Antagonistic
RD.omnivorous.ab	0.063	−0.003	−0.015	—	0.03	0.03	ns
RD.shredders.ab	0.123	−0.009*	0.016	—	0.15	0.18	Single
RD.predators.ab	0.463	−0.004	−0.017	0.022 (.)	0.06	0.06	Antagonistic
RD.grazers.ab	0.448	−0.007*	−0.223	0.017	0.08	0.08	Single
RD.gatherers.ab	0.155	−0.005*	0.011	—	0.18	0.25	Single
RD.filterers.ab	0.101	−0.007*	−0.118	0.011	0.28	0.39	Single
FRic	0.239	−0.011*	−0.197	0.027 (.)	0.37	0.63	Antagonistic

Note: See Table 2 for further details.

3.2 | New functional metrics

The number of impacts explained >50% of the variance for most functional metrics but, in some cases, ZF_T, DP_i and their interactions with the number of impacts explained a similar percentage (Tables S4 and S5). A single effect of the number of impacts was observed for several FR and RD metrics (Tables 2 and 3): FR.ab, FR.shredders.ab, RD.grazers.ab, RD.gatherers.ab and RD.filterers.ab for all the aquatic phases dataset, and FR.ab, FR.shredders.pa, FR.filterers.pa, RD.shredders.ab, RD.grazers.ab, RD.gatherers.ab and RD.filterers.ab for the flowing phase dataset. Among them, the most responsive metrics (r^2m > 0.20) were FR.ab (r^2m = 0.23) and RD.filterers.ab (r^2m = 0.29) from all the aquatic phase dataset, and FR.filterers.pa (r^2m = 0.33) from the flowing phase dataset (Table 4). Following our criteria (Figure 1), FR.ab, FR.filterers.pa and RD.filterers.ab represent universal metrics (Table 4), with FR.ab and RD.filterers.ab reliable for samples collected in both flowing and disconnected pool phases, and FR.filterers.pa reliable only for flowing phase samples.

For other functional metrics showing significant responses to predictors, the number of impacts and ZF_T resulted in interactive effects. For the aquatic phase dataset, nine metrics showed an antagonistic response and one synergistic (Table 2), whereas for the flowing phase dataset, all interactive metrics showed an antagonistic response (Table 3). We also observed interactions between the number of impacts and DP_i resulting in four antagonistic, one synergistic and one opposing effect on the aquatic phase metrics (Table 2). Among them, several functional metrics were identified as responsive metrics (r^2m > 0.20), with r^2m values ranging from 0.20 to 0.39 in the aquatic phases dataset, and from 0.24 to 0.45 in the flowing phase dataset (Table 4). According to our criteria (Figure 1), these metrics could be reliable in intermittent rivers after non-proportional calibration.

Null models indicated that all predictor terms had non-random effects on FR.pa, FR.ab and FR.omnivorous.pa models including all aquatic phases (Table S6) and, thus, functional metric responses reflected anthropogenic impacts and/or flow intermittence, not taxonomic variation. For the flowing phase dataset, several metrics had non-random effects on all model terms (i.e. FR.ab, FR.omnivorous.

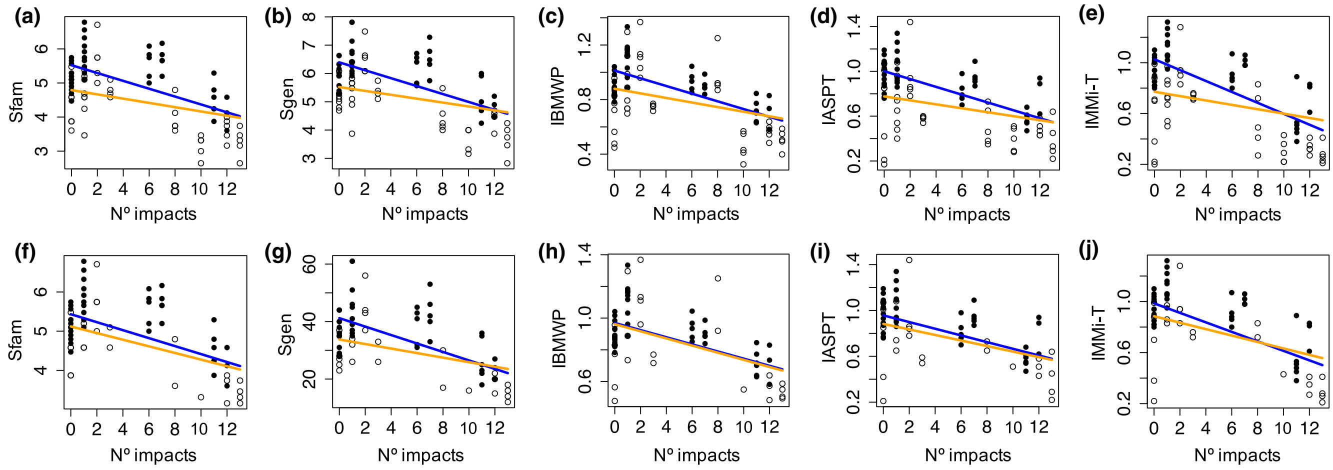

FIGURE 3 Plots showing the individual response of the five widely used metrics from the aquatic phases dataset (Sfam, Sgen, IBMWP, IASPT and IMMi-T; a to e, respectively; Table 1) and the flowing-phase dataset (f to j) along an anthropogenic impacts gradient (N° impacts). Full circles represent perennial rivers and empty circles intermittent ones. Fitted values for LMEs models are represented as blue lines for perennial rivers and as orange lines for intermittent rivers. All responses were antagonistic except for h, for which a single effect was observed

pa, FR.predators.pa, FR.omnivorous.ab, FR.predators.ab and FRic models; Table S7), and null models indicated that the number of impacts term had non-random effects on all models except for FR.shredders.ab and FR.filterers.ab (Table S7).

4 | DISCUSSION

Our results showed that natural disturbances (i.e. flow intermittence) could confound biological quality assessments by altering metric responses to anthropogenic impacts. Most of our widely used and new functional metrics decreased with increasing anthropogenic impacts, but showed an interactive antagonistic response with flow intermittence. Thus, most metrics would not accurately indicate the biological quality of intermittent rivers, and would require calibration (Figure 1c). However, the widely used IBMWP index and few functional metrics could provide reliable biological assessments in intermittent rivers when applied during the flowing phase, and the functional redundancy based on the whole community abundance (FR.ab) remained effective even in disconnected pools.

Compared to perennial rivers, aquatic communities in intermittent rivers typically support fewer taxa and a higher proportion of generalists, due to environmental harshness (Bogan et al., 2017; Soria, Leigh, Datry, Bini, & Bonada, 2017). As a result, the usefulness of many widely used biomonitoring metrics based on taxon diversity is limited, especially when using standard values obtained from perennial rivers (Chiu et al., 2017; Prat et al., 2014). Similar limitations of widely used metrics have been observed in other naturally disturbed ecosystems such as when using riparian plant communities as indicators in intermittent rivers (Bruno, Gutiérrez-Cánovas, Sánchez-Fernández, et al., 2016) or when using invertebrates in estuaries (Elliott & Quintino, 2007) or saline rivers (Gutiérrez-Cánovas et al., 2019). Nonetheless, our results suggested that one widely used metric, the IBMWP index, could be applied in intermittent rivers during flowing phases. This aligns with other studies in mediterranean-climate rivers (e.g. Mazor, Stein, Ode, & Schiff, 2014; Munné & Prat, 2011; Prat et al., 2014), which suggest that widely used metrics may work at intermittent sites if flowing phases are sufficiently long and predictable (Gallart et al., 2012, 2017). For example, Munné and Prat (2011) found no differences for IBMWP between perennial and intermittent rivers during wet years, as flow permanence in intermittent rivers was high. However, during dry years, IBMWP values varied considerably even if samples were collected during flowing phases (Munné & Prat, 2011). Thus, the wide spatial and temporal hydrological variability within intermittent rivers (e.g. different dry phase duration at different locations at different years) could produce misleading bioassessment results in most cases (Chessman, Jones, Searle, Growns, & Pearson, 2010; Mazor, Purcell, & Resh, 2009; Papastergiadou & Manolaki, 2012), especially in less predictable, seasonal climate types (Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017). Hence, to avoid misleading biological quality assessments in intermittent rivers, either existing metrics need to be recalibrated (e.g. by incorporating long-term variability in these metrics) or new metrics, as those presented here, require development (Munné & Prat, 2011; Stubbington et al., 2018).

Most of our new functional metrics responded differently at perennial and intermittent sites, as evidenced by antagonistic effects. Our results align with recent studies considering flow intermittence and salinity as natural disturbances combined with other anthropogenic impacts (Belmar et al., 2019; Gutiérrez-Cánovas et al., 2019). The fact that intermittent rivers often showed a weaker reduction in functional metrics may reflect strong trait filtering in naturally disturbed ecosystems (Mouillot et al., 2013). Moreover, traits enabling species' persistence in certain naturally disturbed environments may contribute to be co-tolerance of other disturbances (Vinebrooke et al., 2004). In intermittent rivers, resistance and resilience traits that enable species to persist in highly variable flow conditions might also

TABLE 4 Selection of the most responsive metrics ($r^2_m > .20$) in detecting anthropogenic impacts in perennial and intermittent rivers

Metric designation	Type of metric	Valid for both flowing and disconnected pool conditions?	Metric
Universal (i.e. no calibration needed)	Functional	YES	FR.ab
		NO, only valid during flowing phase	FR.filterers.pa RD.filterers.ab
	Widely used	NO, only valid during flowing phase	IBMWP
Specific (i.e. non-proportional calibration; adapting reference conditions and response gradient to anthropogenic impacts)	Functional	YES	FR.pa FR.omnivorous.pa FR.shredders.pa FR.predators.pa FR.gatherers.pa FR.omnivorous.ab FR.predators.ab RD.ab RD.predators.ab FRic
	Widely used	YES	Sfam Sgen IASPT IMMi-T

enable them to persist under certain anthropogenic impacts (Belmar et al., 2019; Bonada & Resh, 2013). For example, macroinvertebrates with mechanisms for tolerating low dissolved oxygen concentrations may in turn be indicative of either flow intermittence or organic pollution (Stubbington et al., 2017). Thus, metrics that indicate adaptations to flow intermittence could be used for biomonitoring anthropogenic impacts only if they are calibrated differently for perennial and intermittent rivers.

Our results also identified functional metrics with similar responses to anthropogenic impacts in perennial and intermittent rivers (i.e. single effect), indicating their ability to detect impacts regardless of flow intermittence. The most responsive metrics during flowing phases were functional redundancy based on the whole community abundance (FR.ab) and the filterers presence–absence (FR.filterers.pa), as well as abundance-weighted response diversity of filterers (RD.filterers.ab), with FR.ab also responsive in disconnected pools. Thus, for example, the decrease in RD.filterers.ab with increasing anthropogenic impacts indicates a reduction in resistance and/or resilience traits (i.e. response traits) within this functional trophic group. The decrease in FR.filterers.pa also evidenced taxonomic homogenization within this functional trophic group as the number of anthropogenic impacts increased (Gagic et al., 2015; Laliberté et al., 2010). For example, genera such as *Chimarra* or *Ephemera* were not observed when the number of impacts increased. Our results thus indicate that metrics derived from functional trophic groups that are not affected by natural disturbances, could act as universal metrics in naturally disturbed ecosystems such as intermittent rivers.

By using the response-effect trait approach, functional metrics may provide detailed information on environmental changes and their effects on ecosystem functioning (Laliberté et al., 2010; Mouillot et al., 2013; Suding et al., 2008). Response diversity (RD) metrics might help to differentiate community responses to both natural disturbances and anthropogenic impacts, whilst functional redundancy (FR) metrics based on effect traits might help to anticipate the effects of that change on ecosystem functioning (Suding et al., 2008). For example, the decrease in FR for filter feeder taxa (FR.filterers.pa) might affect organic matter processing and thus change ecosystem functioning (Bogan et al., 2017). As a consequence, community structure might also be less resistant to environmental changes and therefore increase the vulnerability to future anthropogenic impacts (Gutiérrez-Cánovas, Sánchez-Fernandez, Velasco, Millán, & Bonada, 2015; McLean et al., 2019). Similarly, the distinct decrease of FR and RD metrics in the predator functional trophic group (i.e. FR.predators.pa, FR.predators.ab and RD.predators.ab) in intermittent rivers could signal potential effects of anthropogenic impacts on predation rates, and inform about cascade effects stemming from reduced predator abundance (Hooper et al., 2012; Rodríguez-Lozano, Verkaik, Rieradevall, & Prat, 2015).

Given the different predictability, duration and spatial patterns of the aquatic phases in intermittent rivers (Bonada & Resh, 2013; Leigh & Datry, 2017), our proposed functional metrics could contribute to improved bioassessment of these rivers. As most of the widely used metrics were not reliable during flowing phases nor disconnected pools, calibration is needed considering their response gradient to anthropogenic impacts. Even though the widely used IBMWP index detected anthropogenic impacts in intermittent rivers during flowing phases, this needs to be considered with caution as its reliability may vary between wet and dry years (Munné & Prat, 2011). In this case, information on the degree of flow intermittence, seasonal predictability and temporal patterns of flowing phases is required (Gallart et al., 2017). Compared to widely used metrics, the functional redundancy based on whole community abundance (FR.ab) could be even applied during disconnected pools. Besides, functional metrics are more accurate in detecting ecosystem degradation and may represent a step forward in the management of naturally disturbed ecosystems (e.g. Belmar et al., 2019; Bruno, Gutiérrez-Cánovas, Sánchez-Fernández, et al., 2016). These metrics might enable prediction of biological responses to intensifying anthropogenic impacts in a climate change context (Belmar et al., 2019). Therefore, water managers should start incorporating alternative functional metrics in the routine biomonitoring of naturally disturbed rivers. Regardless of the biomonitoring metrics used, distinguishing natural from human-induced flow intermittence and assessing the degree of hydrological alteration of a river is crucial (Gallart et al., 2017). Future research should test both widely used and new functional metrics in datasets encompassing multiyear time periods, across different climates, and for specific anthropogenic impacts, as well as on other taxonomic groups.

ACKNOWLEDGEMENTS

The study was supported by the LIFE+ TRivers (LIFE13 ENV/ES/000341) project. We acknowledge the contribution of FEHM lab members and students who participated in fieldwork. C.G.-C. was supported by a "Juan de la Cierva-Formación" research contract (MINECO, FJCI-2015-25785). We especially thank Rachel Stubbington for her supervision and useful suggestions that greatly improved the manuscript.

AUTHORS' CONTRIBUTIONS

M.S., C.G.-C. and N.C. conceived the ideas and designed the methodology, assisted by N.B. N.C., D.V., G.B., P.F. and P.R.-L. collected the data; R.A. identified the macroinvertebrate data; M.S. and C.G.-C. analysed the data. M.S., C.G.-C., N.B. and N.C. led the writing of the manuscript and F.G., J.L., N.P. and P.L. contributed to the drafts. All authors gave final approval for submission.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.n2z34tms5 (Soria et al., 2019).

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SUPPORTING INFORMATION

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How to cite this article: Soria M, Gutiérrez-Cánovas C, Bonada N, et al. Natural disturbances can produce misleading bioassessment results: Identifying metrics to detect anthropogenic impacts in intermittent rivers. *J Appl Ecol*. 2019;00:1–13. https://doi.org/10.1111/1365-2664.13538