Wiley Interdisciplinary Reviews: Water

WILEY

WIREs WATER

ADVANCED REVIEW OPEN ACCESS

Ecosystem Services in Drying River Networks: A Meta-Ecosystem Conceptual Model

Ignacio Pérez-Silos[1] | José Barquín[1] | Thibault Datry[2]

[1]Environmental Hydraulics Institute "IH Cantabria", University of Cantabria, Santander, Spain | [2]National Institute for Agriculture, Food, and Environment (INRAE), RiverLy Research Unit, Centre de Lyon-Grenoble Auvergne-Rhône-Alpes, Villeurbanne, France

Correspondence: Ignacio Pérez-Silos (perezsi@unican.es; nacho91ps@gmail.com)

Received: 17 October 2023 | **Revised:** 22 November 2024 | **Accepted:** 8 December 2024

Co-Editor-in-Chief: Jan Seibert | **Senior Editor:** Sonja Jähnig

Funding: This work was supported by the DRYvER project (www.dryver.eu), funded by the European Union's Horizon 2020 Research and Innovation Program (869226, to I. P. S., J. B., and T. D.).

Keywords: aquatic–terrestrial ecological interactions | cross-boundary effects | hierarchical patch dynamics | hydrological connectivity | socio-ecosystems

ABSTRACT

All river networks are virtually prone to drying, which is dramatically increasing in space and time. This threatens the functions and ecosystem services (ES) rivers provide to societies. Here, we introduce a new conceptual model of the provision of ES in drying river networks (DRN), situating drying as a pivotal element of every river network. Based on a meta-ecosystem perspective, we contend that ES provision is determined in DRN by the exchange of abiotic and biotic flows between terrestrial and aquatic ecosystems in the catchment. Specifically, we highlight three main components of the ecosystem involved: the intensity of abiotic flows, biodiversity patterns, and ecosystem functioning rates. How they vary in space and time due to changes in the hydrological connectivity in catchment-DRN determines the pattern of ES provision along the DRN. Although drying events are the cause of the great diversity of services naturally provided by DRN, we must perceive their anthropogenic increase as a major socio-ecological risk factor.

1 | Introduction

River networks cover only about 0.8% of the Earth's surface and contain around 0.01% of the world's water (Shiklomanov 1993). However, they harbor disproportionate levels of biodiversity, supporting 10% of all described species (Reid et al. 2019). They contribute substantially to global biogeochemical cycles, for example with the release of greenhouse gases into the atmosphere and the transport of carbon and nutrients from continents to oceans (Battin et al. 2023). Due to their central role in the water cycle, they are not only the main supply of clean water for humans, but also provide other *ecosystem services* (ES; see Glossary) such as flooding regulation, nutrient retention, food provisioning, or the availability of waterways (Kaval 2019). Despite their remarkable importance, growing evidence suggests the amount of streams and rivers drying due to climate change is increasing (Tramblay et al. 2021; Zipper et al. 2021). In addition, and despite poor recognition until recently, rivers and streams that naturally do not flow all year round represent the majority of river networks (Messager et al. 2021). However, our understanding of the manner in which the provision of ES is organized in drying river networks (DRN) at local and regional scales is still in its infancy, and the effects of drying on ES provision have largely been overlooked (Datry, Boulton, et al. 2018).

The flow regime paradigm describes how river flow regulates ecological patterns and processes in flowing waters through the different flow regime components such as the frequency and magnitude of floods or the duration and timing of low flow periods (Poff et al. 1997). This perspective, which exclusively focused on perennial rivers, has been recently expanded to include drying events (Leigh et al. 2016; Price et al. 2021). Indeed, in DRN, alternating cycles of flowing, nonflowing, and dry conditions (Figure 1) generate spatiotemporal patterns of flow intermittence (i.e., % of the time without water) with critical effects on their biodiversity and ecological functions depending on the magnitude, frequency, duration, timing, and rate of drying (Datry, Bonada, and Boulton 2017). The emerging recognition of the prevalence of DRN worldwide, calls for a paradigm shift in river science. However, most conceptual and applied developments of river dynamics and functioning have emerged from perennial rivers and therefore present multiple limitations when applied to DRN (Barquín et al. 2016; Boulton et al. 2016; Datry, Boulton, et al. 2018). This typically includes the existing conceptual models for ES provision in flowing waters (Boulton 2014). Few have considered drying as an important process structuring river ecosystems, and even fewer have done so from a *catchment* perspective that integrates all the socio-ecological components involved (Table 1). The development of an ES framework to manage DRN has great potential to assess impacts and identify appropriate ecosystem-based strategies to mitigate or adapt to these impacts, explore trade-offs and synergies among societal demands and ecosystem management actions, as well as analyze the relationships between ES and biodiversity (Barquín et al. 2016; Boulton et al. 2016; Datry, Boulton, et al. 2018).

In this essay, we take up the call from Boulton et al. (2016) and Datry, Boulton, et al. (2018) for comprehensive conceptual models that hypothesize ES provision in DRN including drying as a pivotal factor. To this end, we have incorporated the latest theoretical and empirical advances in *meta-ecosystem* and ES frameworks, as well as relevant aspects of lotic models proposed from the 1980s, including recent and extensive research in the field of DRN. We begin by interpreting both meta-ecosystem and ES frameworks from the logic of DRN to establish the concepts on which our model is based. Our core idea is that drying events alter profoundly hydrological connectivity, which is key to control abiotic and biotic flows within meta-ecosystems (Cid et al. 2021). In turn, drying cascades into ES provision within the catchment. To demonstrate this, we propose in the next sections a hydro-geomorphic template of the river catchment capable of conceptualizing all these interactions and identifying the key ecosystem components for potential ES provision. Indeed, we are interested in exclusively unraveling the biophysical mechanisms of the socio-ecological system for ES provision, assuming a heuristic DRN with dynamics and ecosystems in a pristine state. In the end, our conceptual model predicts the spatiotemporal patterns in potential ES provision along the DRN and across the different hydrological conditions it experiences.

2 | Foundations of the Conceptual Model: Coupling Meta-Ecosystem Theory and ES Framework in a Hydrological Catchment Perspective

Meta-ecosystem theory has provided a powerful framework in ecology to evidence how both cross-ecosystem organismal movements and resource flows drive landscape dynamics involved in the generation of ES (Gounand et al. 2018). This framework has upgraded the perspectives of *meta-population* and *meta-community* ecology in river ecosystems by considering the spatial flows of organisms, water, solutes, and sediments throughout whole catchments. Together, these flows shape the spatiotemporal organization of populations and communities, and determine ecological processes and their eventual contribution to ES when river ecosystems are considered within a socio-ecological context (Cid et al. 2020, 2021). The aim of this section is to interpret from a meta-ecosystem perspective the main DRN features on which we designed our conceptual model, as well as to understand their implications for ES provision. We present below the four theoretical foundations of our conceptual model. While Foundation 1 presents the general principles for

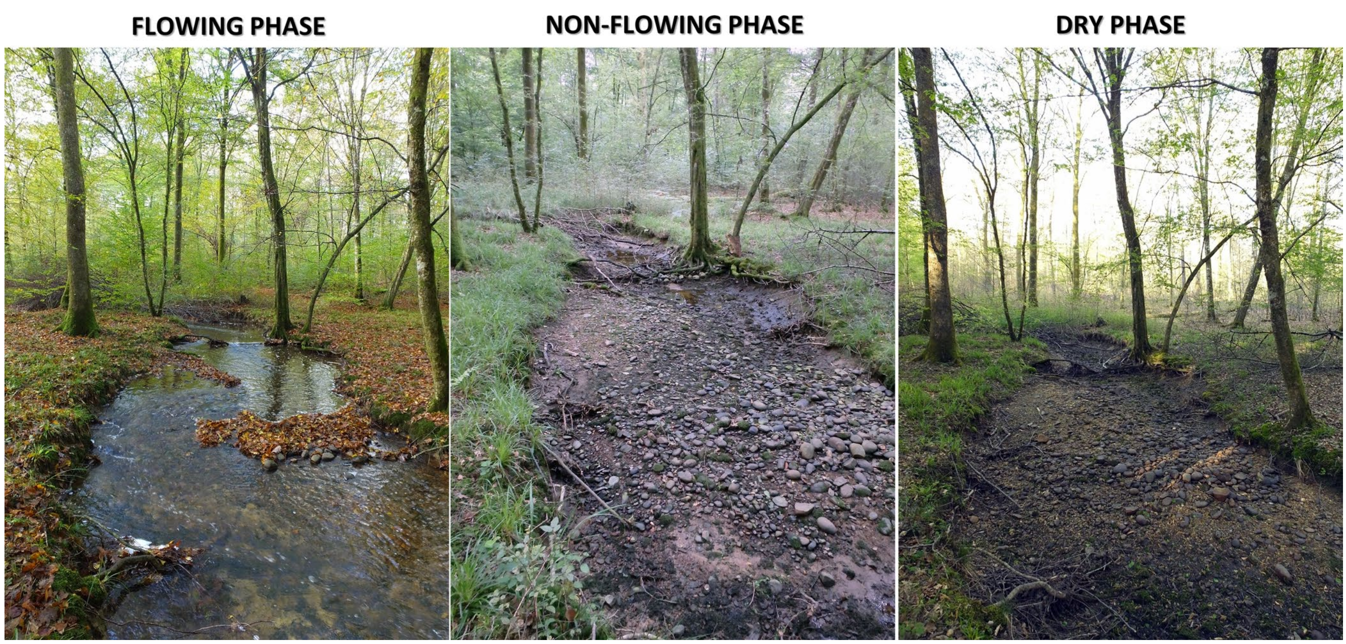


FIGURE 1 | Alternating flowing, nonflowing, and dry phases in a river network (Clauge River, Jura mountains, France. Photo credits: B. Launay).

TABLE 1 | A selection of frameworks and concepts that have been developed over the past two decades to understand the structure of ecosystem services provision within river networks.

Citation	Does it follow a catchment approach?	Does it consider drying?	Does it make hypotheses about ES provision?
Falkenmark (2000)	Yes. Nested ecosystems via water	No	No
Wipfli, Richardson, and Naiman (2007)	Yes. Nested ecosystems via water and resources	Yes, as temporal changes in water and resource flows	No
Stevenson and Sabater (2010)	Yes, but only limited to consideration of some interactions with land uses	Yes, as temporal disturbance regime for aquatic biota	Yes. Hypothetical relationships between a resource stressor (e.g., nutrient concentrations) and a suite of ES of the catchment (i.e., drinking water quality and biodiversity, fisheries production, and agricultural production)
Gilvear, Spray, and Casas-Mulet (2013)	Yes, via rehabilitation measures that include actions on terrestrial ecosystems and effects on key fluvial processes	No	Yes, based on expert-derived scoring. Benefit to ES (i.e., biodiversity, flood management, physical habitat quality, fisheries, diffuse pollution, and cultural) after a rehabilitation measure
Hohenthal et al. (2015)	Yes, but only limited to consideration of some interactions with land uses	Yes, as temporal pressure	Yes. Qualitative interactions between ES (i.e., water retention capacity, water purification capacity, water provision, wetland flood control capacity, fish provision, and agricultural production), drivers, pressures, actions, state of the ecosystem, and responses
Yeakley et al. (2016)	Yes. Existence of different zones within the catchment based on their involvement in the ES flow	No	Yes. Longitudinal provision pattern (function of the stream order) for a wide range of ES
Rawlins, de Lange, and Fraser (2018)	Yes. Linear causal pathways with certain environmental properties and disturbances of terrestrial ecosystems	No	Yes. Analysis of ES value chains (exemplified by flood attenuation)
Datry, Boulton, et al. (2018)	No	Yes. Temporal: how intermittence governs ES provision during three hydrological phases (i.e., flowing, pool, and dry)	Yes. Temporal provision (i.e., provided, lost, or altered compared with the flowing phase) for a wide range of ES (CICES v. 4.3; Haines-Young and Potschin 2018)
Stubbington et al. (2020)	No	Yes. Mainly temporal: how aquatic and terrestrial biota interact with physical assets across the continuum from flowing to dry conditions to mediate ecological processes	Yes. Narrative exposition of ES provision (extensive list) based on literature review

(Continues)

TABLE 1 | (Continued)

Citation	Does it follow a catchment approach?	Does it consider drying?	Does it make hypotheses about ES provision?
Kaletova et al. (2021)	No	Yes. Temporal: how the duration, frequency, timing, and magnitude of the aquatic states (i.e., floods, flow, connected pools, isolated pools, humid riverbed, and dry riverbed) matter in the ES provision	Yes. Qualitative temporal assessment of the provision of three ES: swimming, domestic animal watering, and surface water for irrigation purpose
Vidal-Abarca Gutiérrez et al. (2023)	Yes, but limited to some direct and indirect drivers of change that involve terrestrial ecosystems	Yes. Mainly temporal and focused exclusively on dry rivers	Yes. Narrative exposition of ES provision (extensive list) based on literature review
Oginah et al. (2023)	No	No	Yes. Damage to ES assessed by the impact of toxins on ecosystem functions

Note: We compiled the articles through a literature search on Scopus*. The search yielded 320 results, but only the following 12 were relevant to the purpose of the search. *We used keywords in the Article title, Abstract, and Keywords: "ecosystem services" AND (river OR freshwater OR stream* OR catchment OR watershed) AND ("conceptual model" OR "conceptual framework" OR "theoretical model" OR "theoretical framework").
Abbreviation: ES, ecosystem services.

ES characterization used to design the model, Foundations 2, 3, and 4 focus on the per se features of DRN: highly hierarchically organized, open (i.e., connected to other ecosystems), and temporally dynamic systems, respectively.

2.1 | Foundation 1: Spatiotemporal Template for ES Provisioning and Delivery in DRN

ES are provided and delivered within process-related landscape units such as catchments, specific habitats, or geomorphological units (i.e., *functional units* sensu; Laca 2021). However, areas that provide a specific ES might differ from those where society benefits from this service. The framework proposed by Syrbe and Walz (2012) is particularly relevant as it recognizes three types of areas in the landscape in relation to ES flows, depending on whether they initially generate the benefit (service-providing areas; SPA), simply transfer it (service-connecting areas; SCA), or definitively deliver it to society (service-benefiting areas; SBA). Within these three areas, ES may also fluctuate over time due to changes in abiotic and biotic flows involved in the ES provision, changes in societal demands, or even the time lag between the ES provision and their final delivery (Rau, von Wehrden, and Abson 2018). The rationalization behind the ES cascade model (Haines-Young and Potschin 2010) supposes that ES provision and transfers in DRN are likely driven by factors governing the biophysical structural patterns (e.g., channel morphology, substrate composition), rates of ecological processes (e.g., nutrient cycling, organic matter decomposition) and biodiversity (e.g., structure and composition of biological communities; Datry, Boulton, et al. 2018). Dynamics involving these factors should therefore essentially determine the spatial distribution of SPA, SCA, and SBA within the river catchment, as well as their ES flows over time.

2.2 | Foundation 2: Biophysical Structural Patterns in DRN Arise From a Catchment Patch Hierarchy That Shapes Ecological Processes, Biodiversity, and ES Flows in River Ecosystems

Meta-ecosystem theory acknowledges that local- and regional-scale factors interact to determine the dynamics of environmental conditions and biota in a given landscape (Gounand et al. 2018). DRN are commonly organized as a dendritic structure of nodes and branches in which biophysical and ecological patterns and processes are influenced by the downstream flow of water (Townsend 1996). This implies that the environmental template for biotic communities in any segment of the DRN not only reflects local conditions but also upstream conditions due to the relevance of routing processes (Boulton et al. 2017; Montgomery 1999). Routing processes are driven by regional factors acting at the catchment scale that determine flow patterns (i.e., climate, geology, topography, and vegetation; Poff et al. 1997). The interaction between local and regional factors in DRN causes river ecosystems to simultaneously exhibit both routing-induced continuous and patchy-discontinuous features (Townsend 1996). As DRN are strongly hierarchical systems, at coarse spatiotemporal scales top-down processes mediated by routing-derived features dominate over local controls such as tributary junctions or abrupt changes in the geomorphic structure (Poole 2002; Thorp, Thoms, and Delong 2006). Although DRN is composed of a set of unique and discontinuous patches, micro-scale patterns in patches are constrained by macro-scale geomorphic patterns which vary more linearly along the catchment (Poole 2002; Townsend 1996).

The importance of these hierarchical relationships lies in the recognition of an underlying set of continuous factors that determine at large scales the ecological patterns and processes for headwaters to river mouths or confluences (Rodriguez-Iturbe et al. 2009; Sponseller, Heffernan, and Fisher 2013). Some of the most influential models of river ecology have used this pattern of longitudinal variation to explain factors from sediment dynamics and landforms distribution (Wohl et al. 2015) to carbon processing (Battin et al. 2008), hydrological connectivity (Boulton et al. 2017), or the structure and composition of stream communities (Vannote et al. 1980). The relative spatial position of each reach in the DRN would roughly determine the dominant biophysical structural patterns and ecological processes and, consequently, the ES that can be potentially provided by the associated biodiversity.

2.3 | Foundation 3: DRN Are Extremely Open Systems in Which ES Provision and Delivery Are Also Controlled by Other Neighboring Ecosystems

The catchment can be seen as a single meta-ecosystem in which water, by acting as a geological and meteorological factor (Likens and Bormann 1974), drives an exchange of matter, energy, and organisms between terrestrial and river ecosystems (O'Sullivan et al. 2022). River ecosystems behave mainly as receivers of these spatial flows because of the pervasive gravitational movement of water towards the DRN (Bracken and Croke 2007; Covino 2017; Tonkin et al. 2018), although exports in the lateral direction driven not only by water (see the flood pulse of Junk, Bayley, and Sparks 1989) but also by biotic-driven dynamics (e.g., Bultman et al. 2014 or Helfield and Naiman 2006), can be significant. The biophysical patterns and ecological processes of river ecosystems are therefore largely determined by this intimate connection with terrestrial ecosystems (e.g., hydrology or water temperature; O'Sullivan et al. 2022).

Consequently, many of the spatial flows involved in the generation of ES are mediated by terrestrial ecosystems of the catchment, so the ES delivered in the DRN are not always produced by the river ecosystem itself. In fact, the SPA may be located in other ecosystems such as riparian and hillside forests or wetlands. In this case, the river ecosystem would mainly act as a link or a mere beneficiary of the ES (i.e., SCA and SBA respectively).

2.4 | Foundation 4: DRN Are Temporally Dynamic Systems in Which the Flow Regime Determines ES Provisioning and Transfers Over Time

Events such as floods, low flows, or flow intermittence are induced by quantitative changes in the hydrological connectivity of the catchment (Bracken and Croke 2007). By generating expansion and contraction cycles in the DRN (Datry et al. 2016; O'Sullivan et al. 2022), flow variability shapes the longitudinal, lateral, and vertical hydrological connectivity along the DRN. From a meta-ecosystem perspective, this fact alters abiotic and biotic flows between terrestrial and river ecosystems and the habitat mosaics of the DRN (Boulton et al. 2017). At a catchment scale, flow variation controls the carbon and nutrient dynamics, but also erosion–sedimentation patterns, by changing inputs to the DRN as well as rates of cycling or transport (i.e., the telescoping model, the flood pulse and the pulse-shunt concepts, and the natural sediment regime paradigm; Raymond, Saiers, and Sobczak 2016; Fisher et al. 1998; Tockner, Malard, and Ward 2000; Wohl et al. 2015). In addition, hydrological connectivity also alters the movement and dispersal of organisms through/between DRN and neighbor ecosystems (Tockner, Malard, and Ward 2000). These variations in flow alter habitat conditions and meta-population and -community dynamics (e.g., mass effects during drying; Jaeger, Olden, and Pelland 2014), producing cascading responses from populations to communities that affect most of the ecological processes occurring at the reach scale (Larned et al. 2010).

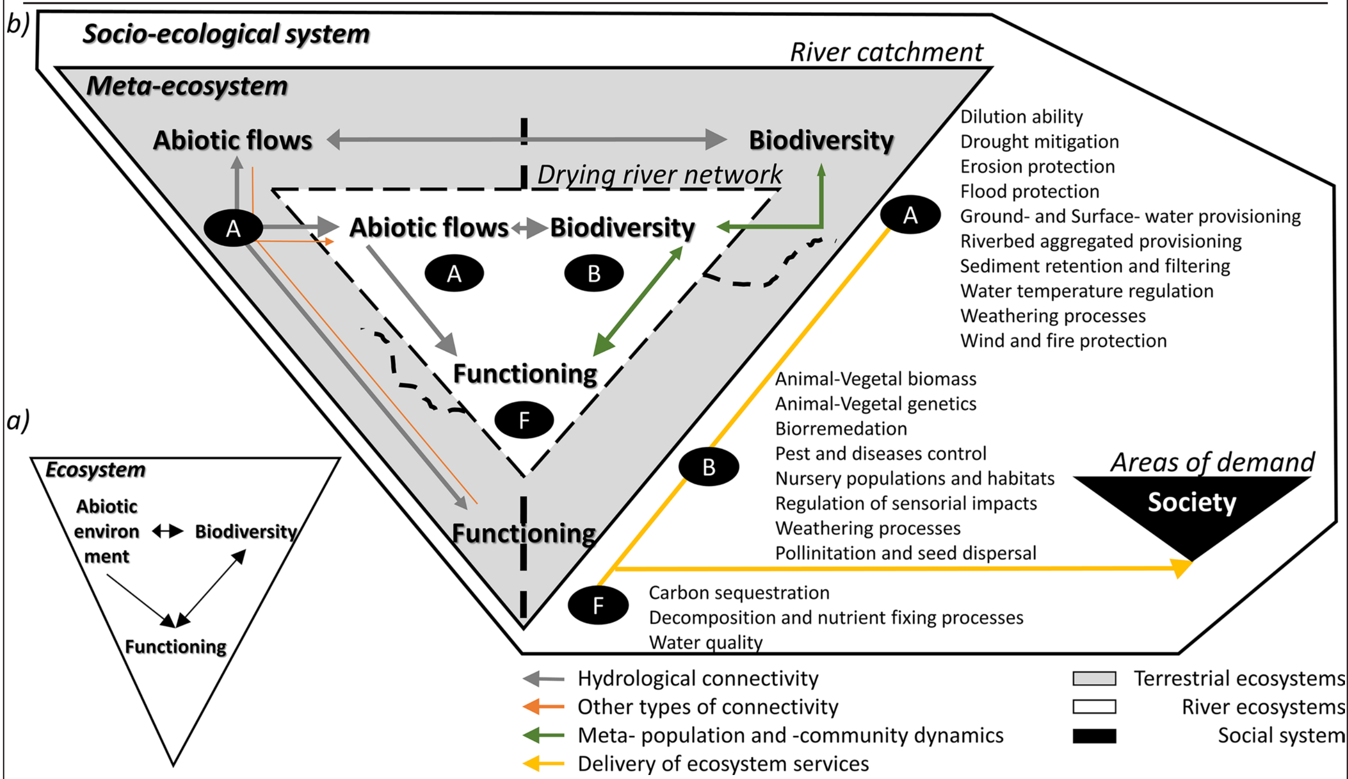
Because of all these multiscale effects, flowing and drying regimes are key factors for determining the temporal pattern of ES generation in SPA (Datry, Boulton, et al. 2018; Kaletova et al. 2021; Talbot et al. 2018). Furthermore, changes in hydrological connectivity alter the transfer of water-borne ES from SPA to SBA, which is particularly relevant in DRN where flow cessation may even disable SCA. Varying spatial arrangements of intermittence may also produce different suites or magnitudes of ES provision. As input/circulation rates of water, resources, or biota vary longitudinally along the DRN, ecological functions such as organic matter cycling would differ between DRN where hydrological connectivity changes differently in space and time due to drying. In fact, the spatial pattern of network drying has been hypothesized by Datry, Boulton, et al. (2018) as the main driver in the distribution of SPA, SCA, and SBA at a catchment scale for DRN.

3 | Rationalization of the Conceptual Model

Our conceptual model assumes that provisioning and regulating ES associated with DRN depend fundamentally on three key ecosystem components: the intensity of abiotic flows (e.g., water, sediment, or solar energy), the biodiversity patterns in space and time, and the ecosystem functioning rates. ES provision would have a stronger or lighter dependence on each of these three components depending on the biophysical interactions that determine their generation (Box 1). For example, while dilution capacity or erosion protection are governed by the occurrence of certain abiotic flows (i.e., water inputs and their properties such as soil erodibility; Terrado et al. 2014), biomass provision or bioremediation are more related to biodiversity because they depend strongly on organisms' biological activities (i.e., growth or physiological rates; Zieritz et al. 2022). Water quality and carbon sequestration arise from the interaction via food webs between biological communities and circulating abiotic flows, often involving other ecosystem components such as soils or sediments (Keeler et al. 2012). In this case, both ES are closely dependent on ecosystem functioning properties like nutrient recycling rates, organic matter dynamics or river metabolism.

According to Foundation 1, the spatiotemporal variation in the intensity of abiotic flows, biodiversity patterns, and ecosystem functioning rates determine ES provision and delivery in DRN. We suggest that the dynamics associated with these three key ecosystem components are driven by hydrological connectivity and meta-population and -community dynamics, across the catchment and the DRN (Box 1). More specifically, the core concept of our model is that hydrological connectivity is the

BOX 1 | Functioning of the socioecological system of the river catchment from a meta-ecosystem perspective.



(a) Outline of the current paradigm on the relationships between biodiversity and ecosystem functioning in an ecosystem. (b) Representation of the socio-ecological functioning of a fluvial catchment system using a meta-ecosystem perspective. The thickness and size of the arrows represent the importance of the relationships between the different components of the ecosystem. In this study, we just consider those provisioning and regulating ES from CICES closely linked to the DRN (see Table S1 for the ES equivalences), either because they are directly produced by the river ecosystem and associated ecosystems (i.e., riparian and floodplain areas), or because the benefit they generate is delivered to society in the DRN itself.

Within an ecosystem (a), biodiversity not only responds to its environment, but also drives ecosystem functioning and has the capacity to bring about changes in its abiotic environment (Loreau 2010; Plas 2019). From an ecological point of view (b), a hydrological catchment is a meta-ecosystem in which terrestrial and river ecosystems are connected by multiple abiotic and biotic flows. In this sense, exploring the interactions between the environment, biodiversity, and functioning within a meta-ecosystem requires broadening the above perspective by including how flows between ecosystems determine the dynamics associated with these three ecosystem components (Scherer-lorenzen et al. 2022). First, the environment of a DRN is shaped by the abiotic flows that originate in the catchment and circulate through the DRN. These flows are mainly driven by water (i.e., hydrological connectivity), but other factors such as gravitation, wind, or organisms are often also involved. In addition, abiotic flows are mediated by terrestrial biodiversity before reaching the DRN, so some of them are partially or fully influenced by the functioning of the terrestrial ecosystem. Second, in relation to biodiversity, both local (i.e., niche selection and biotic interactions within a river channel) and regional (i.e., dispersal of organisms across the catchment and the DRN) mechanisms interact to shape the spatial and temporal organization of meta-populations and -communities in the DRN. Third, ecosystem functioning within the DRN is determined by abiotic flows coming from the catchment and the DRN, as well as the functional organization of biodiversity in food webs.

Meta-ecosystems are integrated into socioecological systems when the biophysical interactions exerted by the biological components of the ecosystems produce benefits that are demanded and delivered to society. In this sense, depending on the type of biophysical interactions, ES are more closely related to one of the above-mentioned ecosystem components, which we consider key to ES provision in DRN:

A—Intensity of abiotic flows: abiotic provisioning and regulating ES where biodiversity acts by mediating (e.g., reducing or concentrating) an abiotic flow.

B–Biodiversity pattern: biotic provisioning and regulating ES (those originally considered as supporting ES; see Reid et al. 2005) narrowly driven by physical, chemical, and biological transformations of matter and energy that involve a specific organism and their interactions with abiotic flows and other organisms.

F—Ecosystem functioning: regulating ES related to the sum of multiple ecological processes involving interactions between ecosystems or several of their components.

basal factor that ultimately controls abiotic and biotic flows (i.e., meta-population and meta-community dynamics that set biodiversity patterns) between the catchment and the DRN and, consequently, functioning rates in the river ecosystem. On the one hand, hydrological connectivity determines abiotic flows acting as a transport vector and agent of geomorphic change, which also shapes the physical habitat for biodiversity (Sponseller, Heffernan, and Fisher 2013). On the other hand, hydrological connectivity controls meta-population and meta-community dynamics by acting as a local resource and disturbance agent for biota (Sponseller, Heffernan, and Fisher 2013), but also as an agent of fragmentation of DRN (Datry et al. 2023). Our conceptual model uses current perspectives and models of river ecology to consider the spatiotemporal variations in the three key ecosystem components for ES provision (see Section 3.1). We interpret these models based on two gradients that capture the dimensions of the variability of hydrological connectivity and its influence on the ecosystem components and dynamics involved (i) drainage area, because of the existence of a catchment hierarchy that determines a longitudinal pattern of variation in hydrological connectivity along the DRN (Altermatt 2013; Foundation 2), including the connection to other ecosystems (Foundation 3); (ii) flowing-drying, because it reflects the dynamism of the DRN as a consequence of temporal changes in its hydrological connectivity (Boulton et al. 2017; Foundation 4).

3.1 | Key Ecosystem Components and Processes for ES Provision in DRN

Regarding abiotic flows (Figure 2a1, b1), we use the conceptual model proposed by Boulton et al. (2017) to characterize the spatiotemporal variations in the hydrological connectivity. The model captures connectivity dynamics from other river models, such as the hyporheic corridor concept (Stanford and Ward 1993) or the flood pulse concept (Junk, Bayley, and Sparks 1989), and is particularly interesting because it extends the perspective to DRN. We also use the natural sediment regime concept (Wohl et al. 2015) to summarize sediment dynamics and we extract from the river continuum concept (Vannote et al. 1980) the proposed pattern of incident solar radiation.

Biodiversity patterns are characterized from two perspectives. On the one hand, spatiotemporal variations in their functional composition allow us to capture the implications for ecosystem functioning. In this sense (Figure 2a2), we use the conceptual basis established by the river continuum concept (Vannote et al. 1980),

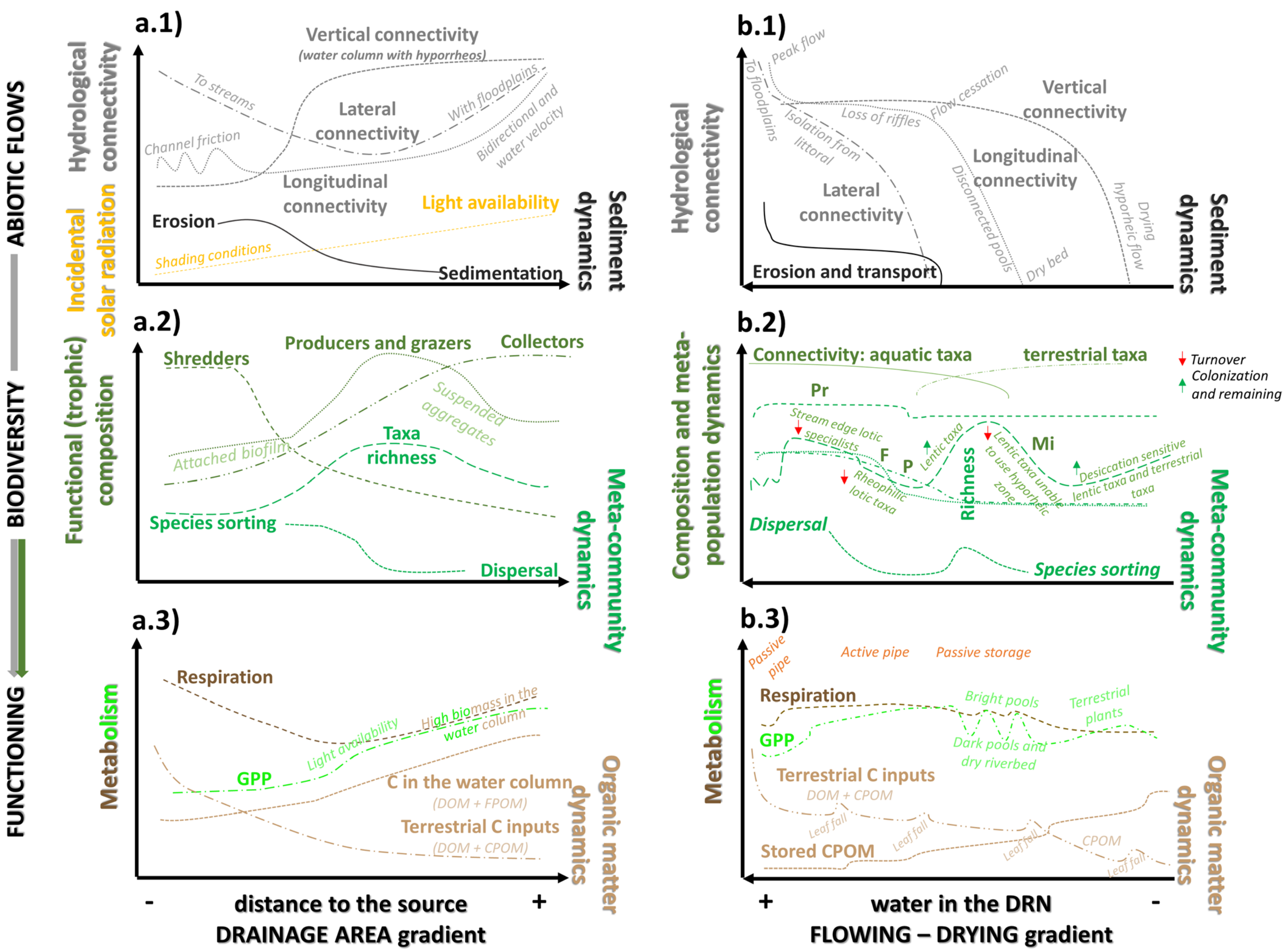


FIGURE 2 | Spatiotemporal patterns (a and b, respectively) associated with key ecosystem components and processes for ES provision in DRN: (1) abiotic flows, (2) biodiversity, and (3) functioning (the arrows in the left margin between these key ecosystem components symbolize the main direction of the interactions between them, as set out in Box 1). Each dynamic, process, or pattern described (represented by different colors) is treated independently in each graph. That is, the magnitude represented on the *y*-axis is not comparable between different dynamics, processes, or patterns. C, carbon; CPOM, coarse particulate organic matter; DOM, dissolved organic matter; FPOM, fine particulate organic matter; F, fungi; GPP, gross primary production; Mi, macroinvertebrates; Pr, prokaryotes; P, protozoa.

reinforced by recent meta-ecosystem modeling approaches (Jacquet, Carraro, and Altermatt 2022), to determine how changes in resource flows translate into local and regional changes in functional community composition. We extend this perspective by adding other key biological components to metabolic dynamics (i.e., microbial lifestyles; Battin et al. 2008). In addition (Figure 2b2), we incorporate temporal changes in the community induced by the occurrence of various hydrological phases using insights from DRN research (Boulton 2003; Larned et al. 2010; Steward, Datry, and Langhans 2022). On the other hand, meta-community dynamics allow us to capture the role of different local and regional mechanisms in the composition of fluvial communities and to explore different patterns such as migrations, taxa richness, or colonization after drying events. To this end, we use as a reference the hypothesis proposed and tested by Brown and Swan (2010) for meta-community patterns along the DRN (Figure 2a2) and Datry, Bonada, and Heino (2016) to account for habitat fragmentation because of flow intermittency (Figure 2b2).

Finally, we characterize the spatiotemporal dynamics of organic matter (Figure 2a3, b3) using the framework developed by Casas-Ruiz et al. (2020). Based on the pulse–shunt concept (Raymond, Saiers, and Sobczak 2016), this framework spatializes at the network level the dominant sources of organic matter, as well as the domain of its transport or processing, depending on the hydrological conditions of the catchment (i.e., high and low flow). Using the models proposed by Battin et al. (2008) and Hotchkiss et al. (2015), we also derive the longitudinal patterns of how organic carbon is metabolized along the DRN. Of particular interest is the meta-ecosystem perspective proposed by Battin et al. (2008) when making explicit the connection with other ecosystems. From a temporal point of view (Figure 2b3), we use the river wave concept (Humphries, Keckeis, and Finlayson 2014), which characterizes river metabolism under different flowing conditions by combining the river continuum concept (Vannote et al. 1980), the riverine productive model (Thorp and Delong 1994) and the flood pulse concept (Junk, Bayley, and Sparks 1989). Additionally, to infer metabolic ratios under no-flowing conditions, we incorporate concepts more or less independently developed for temporary rivers (but not only): trophic interactions within their food webs (McIntosh et al. 2017), organic matter storage during hydrological contractions in dry streambed (Catalán et al. 2022), their colonization by terrestrial vegetation (von Schiller et al. 2017), as well as more integrative views of the functioning of these rivers as meta-ecosystems (Datry et al. 2017).

4 | The Conceptual Model Building Blocks: Functional Units, Geomorphic States and Flow Stages

The river catchment is considered as an array of geomorphic patches, formed by regional acting factors such as catchment geomorphology and climate, hydrologically connected to each other. Geomorphic patches result from shifts in geomorphic processes that govern abiotic flows and constitute physical habitat type, structure, and dynamics (Montgomery 1999). Each type of geomorphic patch has a specific ecological potential that roughly shapes biodiversity and ecosystem functioning. This portrayal of the river catchment extends the vision proposed by Thorp, Thoms, and Delong (2006) by incorporating a meta-ecosystem perspective and the specific elements to explore ES patterns and dynamics in river ecosystems. Geomorphic patches are here equivalent to functional units. They capture and aggregate the biotic and abiotic interactions that take place in functional process zones at the scale needed to generate ES. Since the three key components for ES provision change among functional units (i.e., geomorphic patches), according to Foundation 1, both the ES they generate and their role in the ES flow also differ between functional units.

We considered the four process domains proposed by Montgomery (1999) as the most basic set of functional units of the river catchment: hillslopes, floodplains, riparian zones, and river channels. They have been also highlighted by Petersen (1999) for their relevance in characterizing hydrological connectivity between terrestrial and river ecosystems (Figure 3a). This spatial segregation of the catchment allows us to track the potential ES flow between the SPA functional unit, characterized by some specific abiotic and biotic conditions that determine the generation of ES, and the SBA functional unit. By delocalizing the provision and delivery of ES, we cover the requirements mentioned in Foundation 3. As described in Foundation 2, both biophysical interactions and hydrological connectivity also change more or less predictably along the DRN depending on geomorphological factors. Our model considers only three different strata in the DRN (i.e., the traditional and widespread division in headwaters, piedmont areas, and lowlands; Leopold, Wolman, and Miller 1964) for the sake of simplification, although they should be seen as representative “states” within a spatial gradient of geomorphic change (Figure 3a). We consider that biophysical interactions and, consequently, the patterns, processes, and dynamics associated with the three key ecosystem components for ES provision within each geomorphic state, are homogeneous for each type of functional unit.

According to Foundation 4, the connectivity of the abiotic and biotic flows involved in the key ecosystem components for ES provision vary temporally, as they depend on how water moves through the functional units of the catchment (i.e., hydrological connectivity). We consider three possible flow stages for the DRN: flowing, nonflowing, and dry phases, following the common description of flow states in DRN (Allen et al. 2020), as well as flood events. For simplicity and understandability, we argue that producing a conceptual model based on these main three flow stages will be a major step forward for river scientists and managers. For each of the hydrological phases considered, our model makes explicit the changes in water pathways that occur among functional units (Figure 3b). However, DRN do not dry homogeneously, but typically do so following one of these spatial patterns (Boulton et al. 2017): (i) drying of headwaters due to cessation of rainfall and feeding of piedmont and lower river channels by alluvial or karstic aquifers; (ii) drying of piedmont river channels due to infiltration into the alluvial aquifer greater than the water supplied by the headwater drainage network; and (iii) contraction of the DRN from lowlands. In our model, we consider these spatial patterns of transition between the three flow stages, as the hydrological phase of the functional units (flowing or nonflowing) can differ between geomorphic states. Thus, our model also reflects how incident and internal abiotic and biotic flows involved in the key ecosystem components for

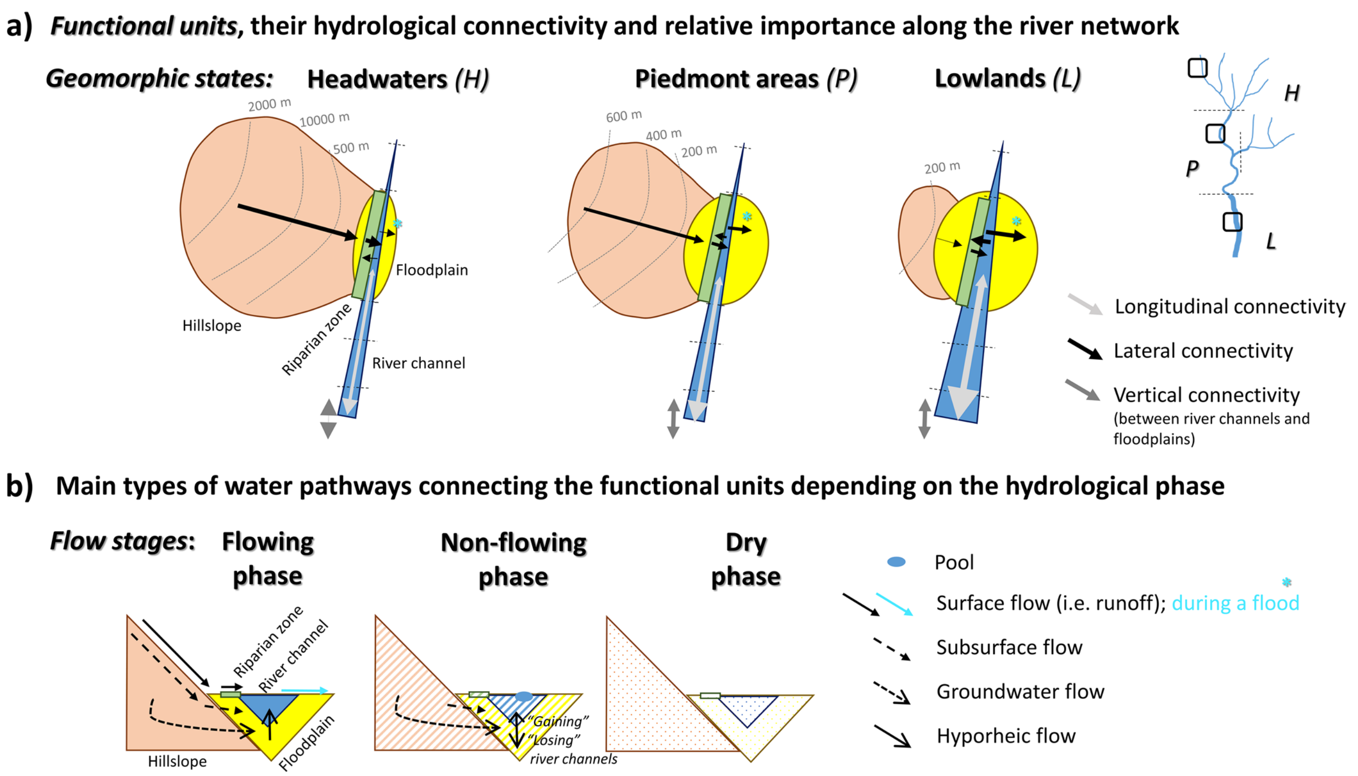


FIGURE 3 | Plan (a) and transverse (b) views of functional units (hillslopes, floodplains, riparian zones, and river channels) and (a) their relative longitudinal, lateral, and vertical hydrological connectivity in an idealized single-thread DRN (i.e., headwaters, piedmont zone, and lowlands; the size of each functional unit represents the relative importance of its dominant processes within each geomorphic state), (b) the types of water pathways that connect the functional units depending on the flow stage of the DRN. For reasons of visualization, in (a) only hillslopes, floodplains, and riparian zones, are shown for a single river channel. In addition, both hillslopes and riparian zones are only shown for the right bank of the river channel. Figure inspired by Boulton et al. (2017).

ES provision vary with the spatial arrangement of perennial and nonperennial reaches in the DRN.

5 | Characterizing ES Provision in DRN: General Model Predictions

Our conceptual model considers the intensity with which ES are provided along the DRN, as well as how ES provision varies depending on the flow (Tables 2 and 3). On one hand, we identify the ecosystem or biological component implied in the generation of the ES, as well as the functional unit supporting the biophysical interaction (i.e., SPA). For each ES, the spatial pattern of its provision along the DRN depends on how the key ES-generating component varies within the functional unit of each of the three geomorphic states (i.e., drainage area gradient shown in Figure 2a). On the other hand, we identify the changes in hydrological connectivity that occur during transitions between the flow stages in the functional units that generate and transfer ES (i.e., SPA and SCA, respectively). For each ES, the temporal pattern of its provision under different flow conditions depends on how the key ES-generating component varies during each of the three flow stages in the associated functional units (i.e., flowing–drying gradient shown in Figure 2b).

Several predictions can be derived about the spatiotemporal pattern of ES provision in DRN, both the ES that are provided by its river ecosystems and those that are provided by terrestrial ecosystems and delivered in the DRN. For example, ES such as flood and erosion protection in hillslopes, which involves the regulation of abiotic flows associated with steep slopes (i.e., sediment generation and runoff) occur mostly in headwater areas during flowing phase, as lateral hydrological connectivity with river channels is very high (Figure 2a1; Table 3). However, ES linked to the buffering of abiotic flows requires depositional morphologies, with gentle slopes and more porous materials, and therefore become more important in the lower and middle river channels of the DRN, where vertical hydrological connectivity is higher (e.g., flood protection and drought mitigation through dry river channels, floodplains, and piedmont hillslopes; Figure 2a1; Table 3). As another example, concerning carbon sequestration, its efficiency and the associated ES should vary spatiotemporally in the DRN due to ecosystem functioning. Incoming and circulating flows of matter and energy along the DRN determine the functional structure of the river community and, generally in the temperate zone, lead to higher heterotrophy in headwaters (i.e., low carbon sequestration ES because the carbon emitted to the atmosphere by biomass respiration is greater than that fixed by primary producers) compared to lowlands (Figure 2a3; Table 3). Drying reduces longitudinal and lateral–vertical hydrological connections, so the ability of DRN to store carbon may increase, at least temporally, as organic matter accumulates in river channels and terrestrial carbon inputs into the river ecosystem

TABLE 2 | Expected spatiotemporal patterns for provisioning ecosystem services in drying river networks.

Ecosystem service (ES)	Ecosystem, biological components implied	SPA: functional unit where the ES is generated	SCA: functional unit connecting supply with potential demand (*pathway referred to the connection with/between river channels*)			SBA: functional unit where the ES is delivered	Spatial variation in ES provision			Temporal variation in ES provision		
			F	N	D		H	P	L	F	N	D
Vegetal biomass production (VB)	Aquatic and semi-aquatic wild plants	River channel		River channel		River channel	⇗	⇗	⇗	⇣+	−	0
			River and hyporheic flows	*Pools—hyporheic flow*	*0*							
	Terrestrial wild plants (i.e., no crops)	Floodplain, riparian zone, river channel	Floodplain, riparian zone	Floodplain, riparian zone, river channel		Floodplain, riparian zone, river channel	⇗	⇗	⇗	⇣−	+	+
			–	*Exposed river channel*	*Dry river channel*							
Animal biomass production (AB)	Aquatic and semi-aquatic wild animals (i.e., no aquaculture)	River channel		River channel		River channel	⇗	⇗	⇗	⇣+	−	0
			River and hyporheic flows	*Pools—hyporheic flow*	*0*							
	Terrestrial wild animals	Floodplain, riparian zone, river channel	Floodplain, riparian zone	Floodplain, riparian zone, river channel		Floodplain, riparian zone, river channel	⇗	⇗	⇗	⇣−	+	+
			–	*Exposed river channel*	*Dry river channel*							
Vegetal genetic materials (VG)	Aquatic and semi-aquatic wild plants	River channel		River channel		River channel	↗	↗↘	↘	+	−	0
			River and hyporheic flows	*Pools—hyporheic flow*	*0*							
	Terrestrial wild plants	Floodplain, riparian zone, river channel	Floodplain, riparian zone	Floodplain, riparian zone, river channel		Floodplain, riparian zone, river channel	↗	↗	↗	−	+	+
			–	*Exposed river channel*	*Dry river channel*							

(Continues)

TABLE 2 | (Continued)

Ecosystem service (ES)	Ecosystem, biological components implied	SPA: functional unit where the ES is generated	SCA: functional unit connecting supply with potential demand (*pathway referred to the connection with/between river channels*)			SBA: functional unit where the ES is delivered	Spatial variation in ES provision			Temporal variation in ES provision		
			F	N	D		H	P	L	F	N	D
Animal genetic materials (AG)	Aquatic and semi-aquatic wild animals	River channel		River channel		River channel	⇗	⇗⇘	⇘	⇣+	–	0
			River and hyporheic flows	*Pools—hyporheic flow*	*0*							
	Terrestrial wild animals	Floodplain, riparian zone, river channel	Floodplain, riparian zone	Floodplain, riparian zone, river channel		Floodplain, riparian zone, river channel	↗	↗↘	↘	⇣–	+	+
			–	*Exposed river channel*	*Dry river channel*							
Surface water provisioning (SW)	Biophysical structure of the catchment	Hillslope, floodplain		River channel		River channel	⇗	⇗	⇑	⇡+	–	0
			River flow	*Subsurface, hyporheic flow*	*0*							
Groundwater provisioning (GW)	Biophysical structure of the catchment	Hillslope, floodplain		Hillslope-floodplain		Hillslope, floodplain	⇗	⇗	⇑	⇡+	–	0
			Subsurface, hyporheic flow	*Subsurface, hyporheic flow*	*0*							
	Biophysical structure of the DRN	River channel		River channel		Floodplain, riparian buffer, river channel	⇒	⇗	⇑	0	–	+
			0	*Hyporheic flow*	*Hyporheic flow*							
Riverbed aggregated provisioning (RP)	Biophysical structure of the catchment	Hillslope		River channel		Floodplain, riparian zone, river channel	⇒	⇗	⇑	⇣–	+	+
			River flow	*0*	*0*							

Note: The spatial pattern of each ES provision is expressed through arrows, indicating its evolution from headwaters to lowlands. This is achieved by using the relative position of the arrow (lower symbolizes less provision and higher symbolizes more provision) and its inclination (symbolizes whether the longitudinal variation within each geomorphic state occurs in a more or less pronounced manner). Single lines show uncertainty in our predictions. Temporal relevance in ES provision is indicated by (+)—highly relevant, (–)—provision reduced, or (0)—inactive. The dashed arrow adjacent to the flowing phase symbol shows the behavior of the ES during a flood event: upwards (⇡), ES provision rises, while downwards (⇣), ES provision decreases. The equivalence with the CICES classes (Haines-Young and Potschin 2018) of the ES presented in the table can be found in Table S1.
Abbreviations: ES, ecosystem services; F, flowing phase; N, nonflowing phase; D, dry phase; H, headwaters; P, piedmont areas; L, lowlands; SBA, service benefiting areas; SCA, service connecting areas; SPA, service providing areas.

TABLE 3 | Expected spatiotemporal patterns for regulating ecosystem services in drying river networks.

Ecosystem service (ES)	Ecosystem, biological components implied	SPA: functional unit where the ES is generated	SCA: functional unit connecting supply with potential demand (*pathway referred to the connection with/between river channels*)			SBA: functional unit where the ES is delivered	Spatial variation in ES provision			Temporal variation in ES provision		
			F	N	D		H	P	L	F	N	D
Bioremediation (BR)	Riparian and floodplain vegetation (i.e., riparian forest, meadows, etc.)	Floodplain, riparian zone	River channel			River channel	↗	↗↘	↘	⇡+	+	0
			Sub-surface flows and overflow	*Subsurface flow*	*0*							
	Aquatic biota: macrophytes, algae, and biofilm in the river channel	River channel	River channel			River channel	⇘	⇒	⇒	⇣+	–	0
			River and hyporheic flows	*Pools—hyporheic flow*	*0*							
Regulation of sensorial impacts (SI)	Riparian and floodplain vegetation, as well as animals, but especially tree cover	Floodplain, riparian zone	Riparian zone			Floodplain, riparian zone, river channel	⇒	⇒	⇒	+	+	0
			–	–	–							
	Aquatic biota: macrophytes, algae, and biofilm in the river channel	River channel	In situ			River channel	↘	↘	→	⇣+	0	0
			River and hyporheic flows	*0*	*0*							
Erosion protection (EP)	Catchment vegetation, but especially tree cover (i.e., hillside forest)	Hillslope	Riparian zone			Hillslope, floodplain, riparian zone, and river channel	⇓	⇘	⇒	⇡+	–	–
			Sub-surface flows (and gravitational-non-water)	*0 (gravitational-non-water)*								
	Riparian vegetation, but especially tree cover (i.e., riparian forest)	Riparian zone	River channel			River channel	⇘	⇒	⇘	⇡+	–	0
			River flow	*Pools*	*0*							

(Continues)

TABLE 3 | (Continued)

Ecosystem service (ES)	Ecosystem, biological components implied	SPA: functional unit where the ES is generated	SCA: functional unit connecting supply with potential demand (*pathway referred to the connection with/between river channels*)			SBA: functional unit where the ES is delivered	Spatial variation in ES provision			Temporal variation in ES provision		
			F	N	D		H	P	L	F	N	D
Sediment retention and filtering (SR)	Riparian vegetation, but especially tree cover (i.e., riparian forest)	Riparian zone		River channel		River channel	⇘	⇘	⇘	⇣+	–	0
			Sub-surface, hyporheic flows	*Subsurface, hyporheic flow*	*0*							
	River ecosystem: macrophytes, algae, biofilm, and rest of death biomass	River channel		River channel		River channel	⇗⇘⇗	⇗	⇒	⇣–	–	0
			River and hyporheic flows	*Hyporheic flow*	*0*							
Drought mitigation (DR)	Biological retention structures, but especially mature forests and wetlands	Hillslope		Hillslope		River channel	⇒	⇗	⇘	⇣+’	–	0
			Subsurface flow	*Subsurface flow*	*0*							
	Floodplains, favored by the presence of wetlands and meadows	Floodplain		Floodplain		River channel	⇗⇘⇗	⇑	⇘	⇡–	+	0
			Sub-surface, hyporheic flows	*Subsurface, hyporheic flow*	*0*							
Flood protection (FP)	Catchment vegetation, but especially mature forest	Hillslope		River channel		Hillslope, floodplain, riparian zone, river channel	⇘	⇓	⇒	⇡+	0	0
			Surface and river flows	*0*	*0*							
	Floodplains, especially when they are covered by floodplain forests and wetlands	Floodplain		River channel		Hillslope, floodplain, riparian zone, river channel	⇗⇘⇗	⇑	⇒	⇡0	0	0
			River overflow	*0*	*0*							
	Biophysical structure of the DRN	River channel		River channel		Hillslope, floodplain, riparian zone, river channel	⇗	⇗	⇑	–	–	+
			River flow	*River flow*	*River flow*							
Wind and fire protection (WF)	Riparian and floodplain vegetation, but especially wet forests); river ecosystem	Floodplain, riparian zone, river channel		Floodplain, riparian zone, river channel		Hillslope	⇗	⇗	⇗	⇡+	–	–
			–	–	–							

(Continues)

TABLE 3 | (Continued)

Ecosystem service (ES)	Ecosystem, biological components implied	SPA: functional unit where the ES is generated	SCA: functional unit connecting supply with potential demand (*pathway referred to the connection with/between river channels*)			SBA: functional unit where the ES is delivered	Spatial variation in ES provision			Temporal variation in ES provision		
			F	N	D		H	P	L	F	N	D
Pollination and seed dispersal (PL)	Native biota and biophysical structure of the river ecosystem (water and wind)	Floodplain, riparian zone, river channel	Floodplain, riparian zone, river channel			Hillslope, floodplain, riparian zone, river channel	→	→	→	⇡+	−	−
			River flow (i.e., *hydrochory*)	*Exposed river channel*	*Dry river channel*							
Nursery populations and habitats (PH)	Aquatic and semi-aquatic biota	River channel	River channel			River channel	⇗	⇘	⇒	+	−	0
			River flow	*Pools—hyporheic flow*	*0*							
	Terrestrial biota	Floodplain, riparian zone, river channel	Floodplain, riparian zone	Floodplain, riparian zone, river channel		Hillslope, floodplain, riparian zone, river channel	→	→	→	⇣−	−	+
			–	*Exposed river channel*	*Dry river channel*							
Pest and disease control (PD)	Terrestrial and river native ecosystems	Floodplain, riparian zone, river channel	In situ			Floodplain, riparian zone, river channel	↗	↘	→	⇡+	−	0
			River flow	*Pools—hyporheic flow*	*0*							
Weathering processes (WS)	Biophysical structure of the catchment: biological and P/Q meteorization	Floodplain, riparian zone, river channel	In situ			Floodplain, riparian zone, river channel	⇘	⇒	⇒	⇡+	−	−
			River flow	*Pools—hyporheic flow*	*0*							
Decomposition and fixing processes (DS)	Aquatic, semi-aquatic, and terrestrial micro biota	Floodplain, riparian zone, river channel	In situ			Floodplain, riparian zone, river channel	→	↗	↗	⇣+	+	−
			River flow	*Hyporheic flow exposed river channel*	*Dry river channel*							
		River channel	River channel			Floodplain, riparian zone	⇗⇘⇗	⇑	⇒	⇡0	0	0
			River overflow	*0*	*0*							
Water quality (WQ)	Aquatic biota: animals, macrophytes, algae, and biofilm	River channel	River channel			River channel	⇘	⇘	⇘	⇣+	−	0
			River flow	*Pools—hyporheic flow*	*0*							

(Continues)

TABLE 3 | (Continued)

Ecosystem service (ES)	Ecosystem, biological components implied	SPA: functional unit where the ES is generated	SCA: functional unit connecting supply with potential demand (*pathway referred to the connection with/between river channels*) F	N	D	SBA: functional unit where the ES is delivered	Spatial variation in ES provision H	P	L	Temporal variation in ES provision F	N	D
Dilution ability (DI)	Biophysical structure of the catchment	River channel	River channel *River flow*	*Pools*	*0*	River channel	⇒	⇗	⇑	⇡+	–	0
Carbon sequestration (CS)	In-stream biomass (algae, periphyton, benthic invertebrates, fish, and POC)	River channel	River channel *River and hyporheic flows*	*Pools—hyporheic flow—exposed river channel*	*Dry river channel*	River channel (atmosphere)	→	↗	→	⇣–	–	+
	Standing biomass (e.g., mature forests), large downed wood, and soils	Floodplain, riparian zone	River channel *River overflow*	*0*	*0*	River channel (atmosphere)	⇗⇘⇗	⇑	⇒	⇡+	+	–
Water temperature regulation (TR)	Catchment vegetation, but especially tree cover	Hillslope, floodplain	Hillslope *Sub-surface, hyporheic flows*	*Subsurface, hyporheic flows*	*0*	River channel	→	↘	→	⇣–	+’	0
	Riparian vegetation, but especially tree cover (i.e., riparian forest)	Riparian zone	River channel *River flow (through air: by incidental radiation)*	*Pools-hyporheic (through air: by incidental radiation)*	*0*	River channel	⇗	⇘	⇘	⇣–	+	0

Note: The spatial pattern of each ES provision is expressed through arrows, indicating its evolution from headwaters to lowlands. This is achieved by using the relative position of the arrow (lower symbolizes less provision and higher symbolizes more provision) and its inclination (symbolizes whether the longitudinal variation within each geomorphic state occurs in a more or less pronounced manner). Single lines show uncertainty in our predictions. Temporal relevance in ES provision is indicated by (+)—highly relevant, (–)—provision reduced, or (0)—inactive. The dashed arrow adjacent to the flowing phase symbol shows the behavior of the ES during a flood event: upwards (⇡), ES provision rises, while downwards (⇣), ES provision decreases. (’) The ES has got a temporal delay and it could be generated in the previous phase. Single lines show uncertainty in our predictions. The equivalence with the CICES classes (Haines-Young and Potschin 2018) of the ES presented in the table can be found in Table S1.

Abbreviations: ES, ecosystem services; F, flowing phase; N, nonflowing phase; D, dry phase; H, headwaters; P, piedmont areas; L, lowlands; POC, particulate organic matter; SBA, service benefiting areas; SCA, service connecting areas; SPA, service providing areas.

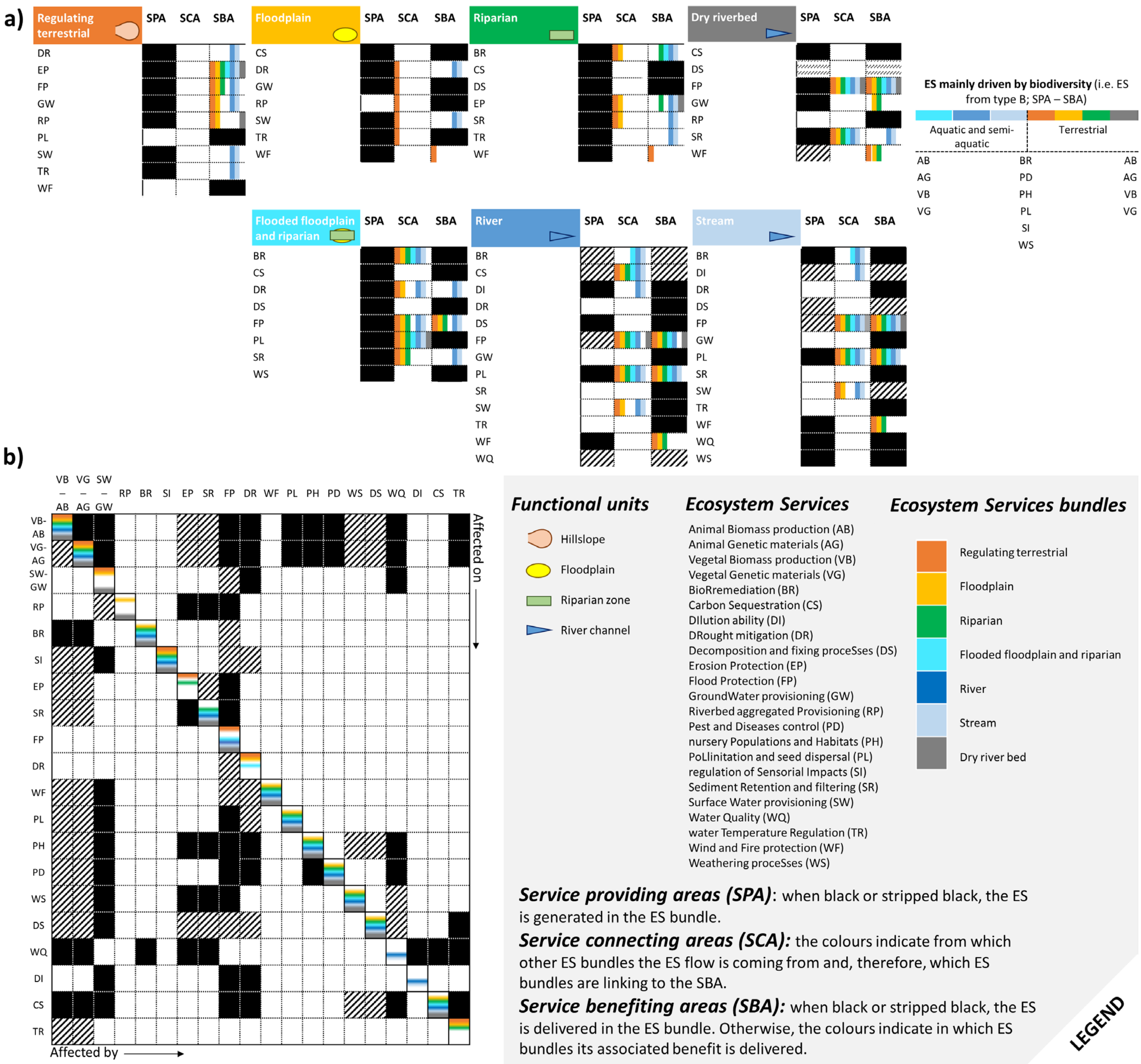


FIGURE 4 | (a) The different ES bundles that interact at the catchment scale for delivering ES along the DRN and associated ecosystems. ES bundles are differentiated by color. In the case of river, stream, and dry river bed ES bundles, black indicates greater ES provision than stripped and multi-stripped black. (b) Matrix with bilateral relationships between ES (black: Strong effect, strip black: Soft effect, white: No effect). The colors appearing in the crosses between the same ES represent the ES bundles in which the ES is generated (i.e., SPA).

decrease, resulting in the river becoming less heterotrophic (Figure 2b3; Table 3).

6 | Identifying ES Bundles: Making Explicit the Relationships Between Ecosystems

As mentioned above, many ES are provided at once in the same spatiotemporal context (e.g., flood and erosion protection in headwater hillslopes, drought mitigation, and flood protection in floodplains and piedmont hillslopes, or instream carbon sequestration in lowlands and during drying). In addition, different biological components may be associated with each other in the functional unit in which they generate the ES (Tables 2 and 3). This means that several ES are provided simultaneously in space and/or time, constituting an *ES bundle* (Raudsepp-Hearne, Peterson, and Bennett 2010). Our conceptual model identifies the presence of seven ES bundles associated with the ES provision along the DRN (Figure 4a). Working with ES bundles allows homogeneous units in the catchment for ES provision to be identified and to make explicit the dependences among ecosystems. As such, we show how the four strictly and mixed terrestrial ES bundles (i.e., regulating terrestrial, floodplain, riparian, and flooded floodplain and riparian ES bundles) are highly relevant in the ES provision along the DRN. More than 60% of the ES provided by these bundles are eventually delivered to the river ecosystem (i.e., SBA in river channels; Figure 4a). Furthermore, some of the ES provided by

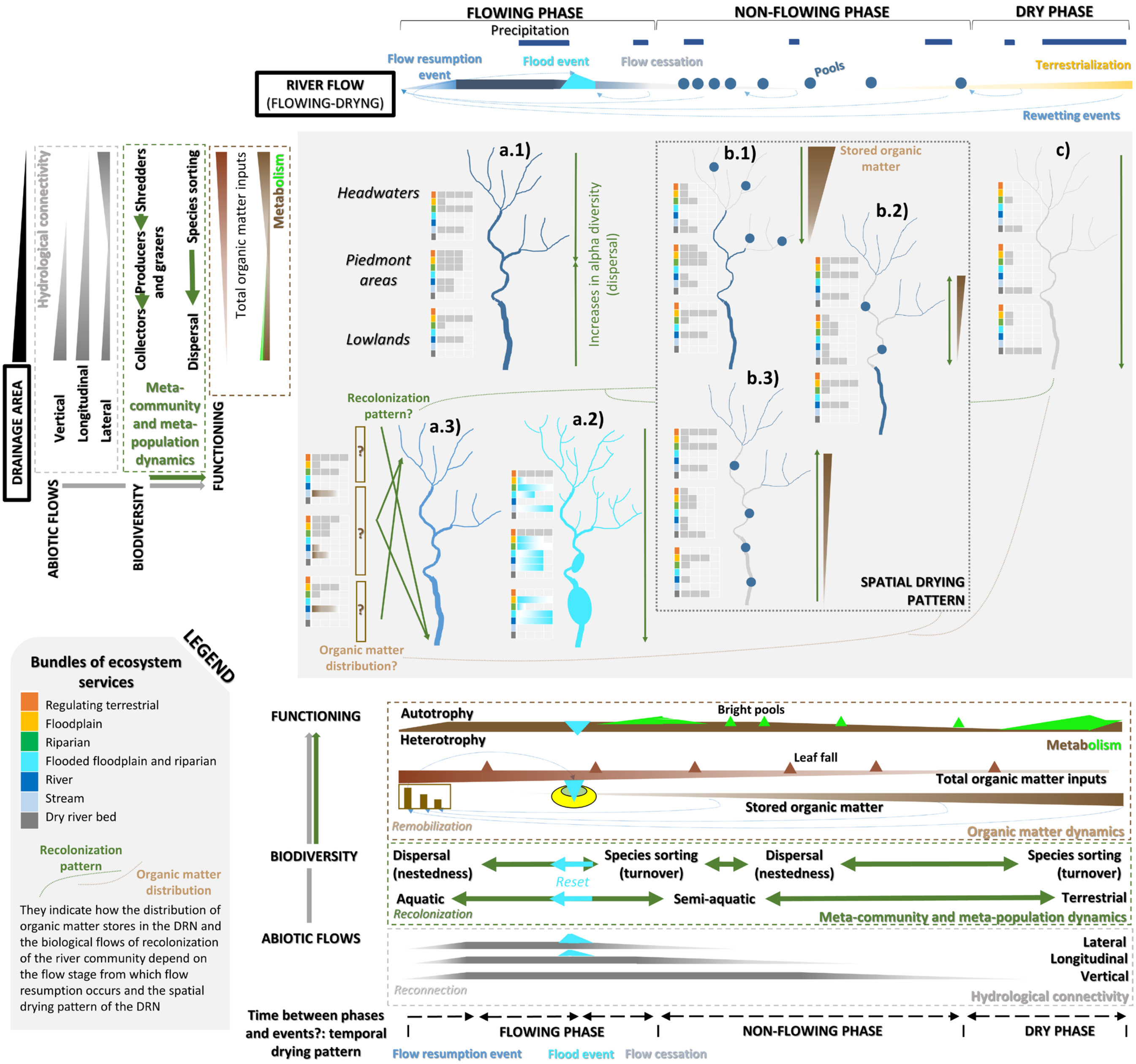


FIGURE 5 | Conceptual model for ES provision in DRN. The model represents the relevance of the different ES bundles (see Figures 4 and S2 to identify the ES of each ES bundle) for three flow stages (i.e., flowing phase, nonflowing phase, and dry phase) and two types of events (i.e., floods and flow resumption; a2 and a3, respectively) along three geomorphic states of the DRN (i.e., headwaters; piedmont areas; lowlands): The greyer cells, the greater the importance of the ES bundle. In a2, the light blue color highlights a greater intensity in the ES provision from regulating terrestrial and flooded floodplain and riparian ES bundles, while in river and stream ES bundles it highlights higher provision of surface water provisioning, lower provision of water quality and bio-remediation, and neutral provision of carbon sequestration. In a3, the brown gradient indicates how the ES provision of the river and stream ES bundles varies depending on the amount of organic matter accumulated in the DRN: The higher the amount of organic matter, the lower the provision of water quality and carbon sequestration ES. The conceptual model explains the temporal variations in the ES bundles based on the changes that occur in three key ecosystem components for ES provision (i.e., abiotic flows, biodiversity, and ecosystem functioning) due to river flow variations (river flow), but also because their spatial variations along the DRN (drainage area). The intensity of these changes (e.g., amount of organic matter that accumulates in the DRN, changes in biotic communities, etc.) depends on the relative duration of each phase and the time that elapses between the different events under consideration (i.e., type of flow resumption, duration between floods when the DRN is in moderate flows, duration until flow cessation, duration in the disconnected pools phase, duration in the dry phase, and timing-type of the rewetting event).

the regulating terrestrial, floodplain, and riparian ES bundles determine the physical matrix of the river ecosystem (e.g., controlling water and solid flows), affecting directly or indirectly much of the ES provided by the strictly river ES bundles along the DRN (Figure 4b). For example, carbon sequestration and water quality are ES provided by instream ES bundles, which are directly linked to the biotic activity derived from the composition and structure of the river communities (i.e., biomass and biodiversity). However, both ES are also highly controlled by other processes occurring in riparian or hillside forests, such as water temperature, shadow generation, or hydrological regulation (Bernhardt et al. 2022).

7 | Spatiotemporal Dynamics for ES Provision in DRN

7.1 | From Flowing Phase to Nonflowing and Dry Phases

Efficient hydrological connectivity in the longitudinal, lateral, and vertical dimensions sustains the regulating terrestrial, riparian, and floodplain ES bundles fully active (Figure 5a), when all river channels are flowing. Most ES provided by these ES bundles regulate the inflows of water, materials (i.e., sediments, dissolved, and coarse particulate organic matter; DOM and CPOM respectively), and energy (i.e., thermal energy) from terrestrial ecosystems. The importance of each ES bundle along the DRN depends on the extent to which the functional unit associated with the ES bundle is connected to the river channel unit (Figure 3a). In turn, flowing waters in functional units promote the existence of rich aquatic communities ranging from rheophilic and desiccation-sensitive taxa to more generalist taxa (Datry et al. 2014; Sarremejane, Messager, and Datry 2022). Both factors determine the dominance of stream and river ES bundles in headwater and lowland river channels, respectively (Figure 5a). The presence of a wide variety of feeding modes allows food webs to use the full range of allochthonous resources from terrestrial functional units (Harvey and Altermatt 2019). Organic matter transported is actively processed along the DRN (Casas-Ruiz et al. 2020), which occasionally becomes a net carbon source (i.e., low carbon sequestration ES; Song et al. 2018), but also a biogeochemical reactor for nutrient cycling, bioremediation, and weathering ES (Battin et al. 2008).

During drying, lateral hydrological connectivity decreases rapidly leading to disconnection with many of the abiotic flows from terrestrial ecosystems (Boulton et al. 2017). This first results in a partial deactivation of regulating terrestrial, floodplain, and riparian ES bundles because of the loss of runoff-dependent SCA (e.g., flood and erosion protection ES during low flows or the nonflowing phase; Figure 5b). Eventually, these ES bundles become inactive during the dry phase (Figure 5c). In contrast, longitudinal hydrological connectivity in the DRN decreases slowly because it is mainly fed by vertical flows from the aquifers (Boulton et al. 2017). When flow cessation occurs, the disruption of longitudinal hydrological connectivity fragments the DRN into a mosaic of lentic and completely dry habitats (i.e., disconnected pools; Datry et al. 2016) and breaks down the transport of organic matter along the DRN because the sediment retention ES is greatly increased (von Schiller et al. 2017). At the same time, it increases biotic connectivity for a wide range of semi-aquatic and terrestrial organisms, which contribute to regional biodiversity (genetic material ES) and to their specific provisioning ES (Steward, Datry, and Langhans 2022).

Our conceptual model considers lentic habitats as patches of stream and river ES bundles whose magnitude of ES provision is reduced in comparison to the flowing phase (Figure 5b). Shifts to lentic conditions cause a rapid increase in the importance of species sorting, so species turnover may be observed more commonly (Datry, Bonada, and Heino 2016). The proportion of predators increases as prey become concentrated in contracting pools (Boulton and Lake 2008). This implies a reduction in filter feeding and shredding feeding modes more associated with flowing phases (Bogan and Lytle 2007). These changes in the community assemblage, together with changes in the water physicochemistry (especially higher temperatures, lower dissolved O_2, and higher evaporation and concentration processes; Gómez et al. 2017), alter the processing of the accumulated organic matter. Fermentation and accumulation of toxic compounds in anoxic pools (Boulton and Lake 1990; von Schiller et al. 2011) and nutrient uptake by microbes in standing pools (Corti et al. 2011; Timoner et al. 2012) are common during the nonflowing phase, which reduces water quality and the carbon sequestration ES (e.g., CH_4 release).

However, the dry riverbed ES bundle emerges in dry patches because the ES that it provides depends on the river channel remaining totally or partially dry: riverbed aggregated provision, decomposition and fixing processes for soil formation, groundwater provisioning through aquifer recharge, or flood protection (Stubbington et al. 2020). Here, organic material from riparian zones is mainly stored passively (Catalán et al. 2022), as its processing is limited to photooxidation (del Campo, Gómez, and Singer 2019) and the heterotrophic exoenzymatic activity of the hyporheic environment as a consequence of the terrestrialization of the dry river bed community (Arce et al. 2019). This processing is strongly conditioned by the intensity of lateral hydrological contractions during the flowing phase (the greater the contraction, the greater the importance of passive storage and therefore the lesser the degradation of CPOM), as well as by the riparian phenology (Catalán et al. 2022). Furthermore, the dry riverbed ES bundle is also enhanced by the photosynthetic activity of the terrestrial vegetation and biota that colonizes the river channels (Steward, Datry, and Langhans 2022; von Schiller et al. 2017). In consequence, as DRN enters the dry phase, the dry riverbed ES bundle becomes more dominant (Figure 5c), and the DRN works as a temporary carbon storage (i.e., increases carbon sequestration ES; Datry, Foulquier, et al. 2018; Stubbington et al. 2020). Both the duration of the flow cessation period and the spatial pattern of drying at the DRN scale may be controlling the volume of this carbon storage. Headwater river channels are often covered by riparian forests, which means that a higher proportion of leaf biomass ends up reaching the river channel unit (Datry, Foulquier, et al. 2018; Vannote et al. 1980). If leaf fall also coincides with dry phase, a greater amount of organic matter will be deposited in the riverbed (Datry, Foulquier, et al. 2018; von Schiller et al. 2015). Therefore, DRN with drying headwaters (Figure 5b1) may have a greater potential to store carbon than DRN drying in lower sections (Figure 5b2, b3).

7.2 | Floods, Rewetting, and Flow Resumption Events

Heavy precipitation events can trigger river floods (Figure 5a2). In headwaters, the increase in lateral hydrological connectivity implies more important flows from hillslope and riparian zone units towards river channels, so regulating terrestrial and riparian ES bundles temporarily increases. This also greatly enhances longitudinal connectivity: the DRN functions as a passive pipe in which the short residence times of organic matter prevent it from being processed by the river community, transporting it downstream without significant alterations (Casas-Ruiz et al. 2020). In contrast, lateral connectivity in the piedmont and lowlands becomes very important in the opposite direction to normal (i.e., from river channels units towards the riparian and floodplain functional units; Figure 3a; Junk, Bayley, and Sparks 1989), determining the emergence of the flooded floodplain and riparian ES bundle. This ES bundle works as a temporary water storage, so not only contributes to recharge floodplain aquifers and reduce flooding downstream (i.e., flood protection and drought mitigation ES; Thomas and Nisbet 2007), but also favors the deposition of nutrients and carbon storage in the retentive biostructures of floodplain and riparian units (Sutfin, Wohl, and Dwire 2016).

When channels are under nonflowing and dry phases, the longitudinal, lateral, and vertical hydrological connectivity of the DRN could be completely or partially re-established during rewetting events depending on the intensity of precipitation (Figure 5a3). Here, and assuming that the flow is not high enough to make the DRN function mostly as a passive pipe (i.e., as in Figure 5a2), ES provision in river and stream ES bundles is altered with respect to the flowing phase (Figure 5a1). While water flow resumption also determines the immediate recovery of ES mainly driven by abiotic flows (e.g., surface water provisioning, dilution ability, or weathering processes ES), provision of ES closely related to aquatic biodiversity and ecosystem functioning may be delayed. Despite functional redundancy, this is insufficient to compensate for certain levels of biodiversity loss (Crabot et al. 2021) and full ES provision is conditional on the reestablishment of the river community. In this sense, meta-community dynamics are characterized by high dispersal from refuge areas (e.g., pools, tributaries, logs, sediments, or patches that have remained wet; Chester and Robson 2011) to recolonize the newly re-established lotic habitats. However, this depends on the dispersal strategies of the species and the spatial distribution of refuges supporting the source of colonists, as well as the temporal extent of the dry phase (Datry et al. 2017).

Flow resumption also involves the downstream mobilization of sediments, organisms, and organic matter accumulated during the dry phase, and the reactivation of CPOM, DOM, and nutrient inputs from terrestrial functional units (Mulholland and Hill 1997). Large pulses of resources transform the DRN into a punctual biogeochemical reactor for organic matter transfer and transformation (Datry, Larned, and Tockner 2014; von Schiller et al. 2017). However, in many cases, the lack of aquatic shredders and fungi due to the previous drying hinders the decomposition of organic litter, which is mostly exported downstream without processing (Corti and Datry 2012). In this context, the mobilization of these terrestrial labile compounds involves high O_2 consumption and CO_2 release (Datry, Foulquier, et al. 2018). Therefore, rewetting and subsequent flow resumption may initially reduce the provision of surface water quality and carbon sequestration ES, especially when it occurs rapidly (but not under extreme flow conditions that export the scarcely degraded CPOM out of the DRN) and there is a large amount of accumulated organic matter in the DRN's passive storage (Catalán et al. 2022). These conditions are often produced by flashy hydrographs and should be more frequent in DRN that have remained dry in the headwaters for a prolonged period of time compared to those drying from lowlands (Figure 5b1–b3). If rewetting events result from extreme flows that trigger floods activating lowland floodplains, they can (under sufficiently warm temperature conditions and organic matter accumulation) lead to a plummeting of dissolved O_2 in the DRN, causing invertebrate and fish mortality, and high CH_4 emissions (Hladyz et al. 2011).

8 | Conclusions and Future Prospects

We have developed a conceptual model for understanding ES provision in DRN based on the interactions between terrestrial and river ecosystems, as well as the movement of water through the landscape. Our model is a suitable framework for posing hypotheses involving the biophysical components of the catchment and how they could determine potential benefits to society in a context of increasingly challenging drying and human impacts. In particular, it reveals three critical applications that we consider especially relevant to guide integrated catchment management and future river research:

- Predicting global ES dynamics in the context of global change. Very important ES for human societies, such as the provision of drinking water and fish, or the self-purification capacity, disappear during drying phases. Others, such as carbon sequestration, are strongly determined by the type of DRN drying pattern and their provision could be negatively affected by more unstable climate regimes. If DRN remains dry for prolonged periods, they would temporarily store a lot of organic matter. Flow resumption events will therefore have a high capacity to punctually release greenhouse gases, as well as deliver unprocessed material to coastal ecosystems that could lead to significant changes in emission balances (Bauer et al. 2013). Thus, while our conceptual model highlights the importance of natural drying in shaping the great diversity of ES typically provided by DRN, the increase in drying due to climate change or other alterations of the hydrological cycle should be perceived as a major risk factor that increases the vulnerability of its associated socio-ecosystems.
- Identifying ecosystem-based management priorities and actions. Our conceptual model points to the prominent role of terrestrial and semi-aquatic ecosystems in many of the ES that are harvested by society in DRN. Mature forests in headwaters, floodplains in piedmont and lowland areas actively connected to river channels, and riparian forests along the DRN should be at the center of any integrated catchment plan to properly manage DRN and their associated socio-ecosystems.
- Evaluating human impacts on DRN. Our conceptual model could characterize different types of impacts on DRN in terms of how they affect the three key ecosystem components involved in ES provision. It is possible to assess not only which ES are directly or indirectly affected by each impact, but also their general effects depending on their

location in the catchment-DRN and the temporal dynamic of the DRN.

Our conceptual model hypothesizes potential ES provision along a heuristic DRN in which both the ecosystems and landforms of the catchment are assumed to be in a pristine state. It is necessary to interweave the biophysical mechanism here developed within the social dynamics to achieve the whole perspective of the river catchment as a socio-ecological system. We suggest two main additions to the model:

- Incorporating the demand for and transfer of ES to society. This would make it possible to determine the interdependencies of society and the ecosystems associated with the DRN in terms of: the ES society demands, how ES are exploited through interventions in the environment, and how these pressures may affect not only other ES provided by the DRN but also its own spatiotemporal configuration (e.g., anthropogenic drying; Datry et al. 2023).
- Incorporating new ES bundles specific to anthropogenic landscapes. Land use-cover changes may configure novel ecosystems characterized by the provision of other sets of ES. For example, monoculture plantations in hillslopes that focus on the provision of vegetal biomass, but limit the provision of regulating ES (Pérez-Silos, Álvarez-Martínez, and Barquín 2021); or reservoirs that replace river and stream ES bundles to provide specific provisioning ES such as water and energy supply, or regulating ES as flood protection (Tundisi 2018).

Finally, we find it also interesting to develop the following aspects to include new elements and conditions, with the aim of capturing the particularities of a greater variety of DRN, as well as to work with them at finer scales:

- Incorporating new functional units based on other hydrogeomorphic patches of the catchment-DRN. These would allow us to characterize local factors (e.g., confluences, gorges, plains, or estuaries) that add discontinuities to the proposed gradients for the key ecosystem components for ES provision in DRN. By disaggregating river channel units at smaller scales (e.g., anabranch channels or sequences of riffles and pools), we could also consider the specific contribution of more detailed functional process zones to ES, as well as the influence of bottom-up processes or a wider range of human pressures along the DRN (Poole 2002).
- Characterizing other types of hydrological regimes. Our conceptual model can be applied to a wide range of DRN (from rivers that remain dry for a long time and suffer flash floods to mostly permanent rivers that only dry out in the headwaters), but the frameworks on which it is based are primarily focused on temperate and subtropical rivers originating in mountain areas. DRN belonging to other biogeographic regions and/or topographic conditions may need to introduce variations in dynamics such as organic matter decomposition, nutrient recycling rates, temperature inversions, or defrost-freeze cycles (e.g., rivers in subpolar zones or glacier-fed alpine rivers).

Nomenclature

Abiotic flow: Spatial flow of energy (e.g., thermal and light solar radiation) or nonliving matter (e.g., resource flows of inorganic nutrients, detritus and organisms dying, and water). Abiotic flows can be driven by passive physical processes or organismal movement.

Biological component: Living components of the biosphere. We use this term irrespective of the scale of aggregation to which we refer (i.e., organism, population, community, or ecosystem).

Bundle of ecosystem services (ES bundle): A set of associated ES that are linked to a given ecosystem, habitat, or biological community and that usually appear together repeatedly in time and/or space (Raudsepp-Hearne, Peterson, and Bennett 2010).

Catchment (or watershed): An area of land that drains all the streams and rainfall to a common outlet such as the outflow of a reservoir, mouth of a bay, or any point along a river channel (USGS).

Ecosystem services (ES): Direct and indirect benefits that people derive from the ecological functioning of ecosystems (De Groot, Wilson, and Boumans 2002). In this work, we focus only on potential ES provision (i.e., not including social demand) and we consider that ES are the result of dynamic biophysical interactions between abiotic flows (e.g., water flow and cessation, resources, sediments) and biological components (organisms, functions). Within this context, we intentionally exclude cultural ES because they are highly context-dependent as they are mainly driven by local socio-ecological factors (Stubbington et al. 2020). We use the Common International Classification of Ecosystem Services (Haines-Young and Potschin 2018) as a basis for defining the ES, although we introduce modifications to adapt them to the needs of our conceptual model.

Functional units: Spatial units that meet the spatial scale required by the biological component to generate the biophysical interaction involved in generating an ES (Laca 2021).

Meta-community: A set of local communities that are linked by the dispersal of multiple potentially interacting species (Leibold et al. 2004).

Meta-ecosystem: A set of ecosystems connected by spatial flows of energy, material, and organisms (Gounand et al. 2018).

Meta-population: A set of local populations of a single species that are linked by dispersal (Hanski 1998).

Service benefiting areas (SBA): Spatial units where the benefits from ES are required in a given landscape (Syrbe and Walz 2012). As we only consider ES potentiality, we use SBA to refer to spatial units in which ES is potentially delivered to society.

Service connecting areas (SCA): Spatial units connecting providing areas with benefiting areas in a given landscape (Syrbe and Walz 2012).

Service providing areas (SPA): Spatial units that are the sources of ES in a given landscape (Syrbe and Walz 2012)

Author Contributions

Ignacio Pérez-Silos: conceptualization (lead), investigation (lead), writing – original draft (lead), writing – review and editing (equal). **José Barquín:** conceptualization (supporting), funding acquisition (supporting), investigation (supporting), project administration (supporting), supervision (lead), writing – review and editing (equal). **Thibault Datry:** conceptualization (supporting), funding acquisition (lead), investigation (supporting), project administration (lead), supervision (lead), writing – review and editing (lead).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analysed in this study.

Related WIREs Articles

Hydrologic ecosystem services: Linking ecohydrologic processes to human well-being in water research and watershed management

River ecosystem conceptual models and non-perennial rivers: A critical review

Intermittent rivers and ephemeral streams: Perspectives for critical zone science and research on socio-ecosystems

The waterscape continuum concept: Rethinking boundaries in ecosystems

References

Allen, D. C., T. Datry, K. S. Boersma, et al. 2020. "River Ecosystem Conceptual Models and Non-Perennial Rivers: A Critical Review." *WIREs Water* 7, no. 5: 1–13. https://doi.org/10.1002/wat2.1473.

Altermatt, F. 2013. "Diversity in Riverine Metacommunities: A Network Perspective." *Aquatic Ecology* 47: 365–377. https://doi.org/10.1007/s10452-013-9450-3.

Arce, M. I., C. Mendoza-Lera, M. Almagro, et al. 2019. "A Conceptual Framework for Understanding the Biogeochemistry of Dry Riverbeds Through the Lens of Soil Science." *Earth-Science Reviews* 188, no. January 2018: 441–453. https://doi.org/10.1016/j.earscirev.2018.12.001.

Barquín, J., D. Miller, L. Benda, R. McCleary, T. J. Cai, and Y. Ji. 2016. "Building Virtual Watersheds: A Global Opportunity to Strengthen Resource Management and Conservation." *Environmental Management* 57, no. 3: 722–739. https://doi.org/10.1007/s00267-015-0634-6.

Battin, T. J., L. A. Kaplan, S. Findlay, et al. 2008. "Biophysical Controls on Organic Carbon Fluxes in Fluvial Networks." *Nature Geoscience* 1: 95–100. https://doi.org/10.1038/ngeo602.

Battin, T. J., R. Lauerwald, E. S. Bernhardt, et al. 2023. "River Ecosystem Metabolism and Carbon Biogeochemistry in a Changing World." *Nature* 613, no. 7944: 449–459. https://doi.org/10.1038/s41586-022-05500-8.

Bauer, J. E., W. J. Cai, P. A. Raymond, T. S. Bianchi, C. S. Hopkinson, and P. A. G. Regnier. 2013. "The Changing Carbon Cycle of the Coastal Ocean." *Nature* 504, no. 7478: 61–70. https://doi.org/10.1038/nature12857.

Bernhardt, E. S., P. Savoy, M. J. Vlah, et al. 2022. "Light and Flow Regimes Regulate the Metabolism of Rivers." *Proceedings of the National Academy of Sciences of the United States of America* 119, no. 8: 1–5. https://doi.org/10.1073/pnas.2121976119.

Bogan, M. T., and D. A. Lytle. 2007. "Seasonal Flow Variation Allows "Time-Sharing" by Disparate Aquatic Insect Communities in Montane Desert Streams." *Freshwater Biology* 52, no. 2: 290–304. https://doi.org/10.1111/j.1365-2427.2006.01691.x.

Boulton, A. J. 2003. "Parallels and Contrasts in the Effects of Drought on Stream Macroinvertebrate Assemblages." *Freshwater Biology* 48, no. 7: 1173–1185. https://doi.org/10.1046/j.1365-2427.2003.01084.x.

Boulton, A. J. 2014. "Conservation of Ephemeral Streams and Their Ecosystem Services: What Are We Missing?" *Aquatic Conservation: Marine and Freshwater Ecosystems* 24, no. 6: 733–738. https://doi.org/10.1002/aqc.2537.

Boulton, A. J., J. Ekebom, and G. Gíslason. 2016. "Integrating Ecosystem Services Into Conservation Strategies for Freshwater and Marine Habitats: A Review." *Aquatic Conservation: Marine and Freshwater Ecosystems* 26, no. 5: 963–985. https://doi.org/10.1002/aqc.2703.

Boulton, A. J., and P. S. Lake. 1990. "The Ecology of Two Intermittent Streams in Victoria, Australia. I. Multivariate Analyses of Physicochemical Features." *Freshwater Biology* 24, no. 1: 123–141. https://doi.org/10.1111/j.1365-2427.1990.tb00313.x.

Boulton, A. J., and P. S. Lake. 2008. "Effects of Drought on Stream Insects and Its Ecological Consequences." In *Aquatic Insects: Challenges to Populations: Proceedings of the Royal Entomological Society's 24th Symposium, LB-B1 Chapter in a Scholarly Book*, 81–102. Wallingford, UK: CABI International.

Boulton, A. J., R. J. Rolls, K. L. Jaeger, and T. Datry. 2017. "Hydrological Connectivity in Intermittent Rivers and Ephemeral Streams." In *Intermittent Rivers and Ephemeral Streams: Ecology and Management*, 79–108. London, UK: Elsevier. https://doi.org/10.1016/B978-0-12-803835-2.00004-8.

Bracken, L. J., and J. Croke. 2007. "The Concept of Hydrological Connectivity and Its Contribution to Understanding Runoff-Dominated Geomorphic Systems." *Hydrological Processes* 1763, no. February: 1749–1763. https://doi.org/10.1002/hyp.

Brown, B. L., and C. M. Swan. 2010. "Dendritic Network Structure Constrains Metacommunity Properties in Riverine Ecosystems." *Journal of Animal Ecology* 79: 571–580. https://doi.org/10.1111/j.1365-2656.2010.01668.x.

Bultman, H., D. Hoekman, J. Dreyer, and C. Gratton. 2014. "Terrestrial Deposition of Aquatic Insects Increases Plant Quality for Insect Herbivores and Herbivore Density." *Ecological Entomology* 39, no. 4: 419–426. https://doi.org/10.1111/een.12118.

Casas-Ruiz, J. P., R. G. M. Spencer, F. Guillemette, et al. 2020. "Delineating the Continuum of Dissolved Organic Matter in Temperate River Networks." *Global Biogeochemical Cycles* 34, no. 8: e2019GB006495. https://doi.org/10.1029/2019GB006495.

Catalán, N., R. del Campo, M. Talluto, et al. 2022. "Pulse, Shunt and Storage: Hydrological Contraction Shapes Processing and Export of

Particulate Organic Matter in River Networks." *Ecosystems* 26: 873–892. https://doi.org/10.1007/s10021-022-00802-4.

Chester, E. T., and B. J. Robson. 2011. "Drought Refuges, Spatial Scale and Recolonisation by Invertebrates in Non-perennial Streams." *Freshwater Biology* 56, no. 10: 2094–2104. https://doi.org/10.1111/j.1365-2427.2011.02644.x.

Cid, N., T. Erős, J. Heino, et al. 2021. "From Meta-System Theory to the Sustainable Management of Rivers in the Anthropocene." *Frontiers in Ecology and the Environment* 21, no. 1: 49–57. https://doi.org/10.1002/fee.2417.

Cid, N., J. Heino, J. Crabot, et al. 2020. "A Metacommunity Approach to Improve Biological Assessments in Highly Dynamic Freshwater Ecosystems." *BioScience* 70, no. 5: 427–438. https://doi.org/10.1093/biosci/biaa033.

Corti, R., and T. Datry. 2012. "Invertebrates and Sestonic Matter in an Advancing Wetted Front Travelling Down a Dry River Bed (Albarine, France)." *Freshwater Science* 31, no. 4: 1187–1201. https://doi.org/10.1899/12-017.1.

Corti, R., T. Datry, L. Drummond, and S. T. Larned. 2011. "Natural Variation in Immersion and Emersion Affects Breakdown and Invertebrate Colonization of Leaf Litter in a Temporary River." *Aquatic Sciences* 73, no. 4: 537–550. https://doi.org/10.1007/s00027-011-0216-5.

Covino, T. 2017. "Hydrologic Connectivity as a Framework for Understanding Biogeochemical Flux Through Watersheds and Along Fluvial Networks." *Geomorphology* 277: 133–144. https://doi.org/10.1016/j.geomorph.2016.09.030.

Crabot, J., C. P. Mondy, P. Usseglio-Polatera, et al. 2021. "A Global Perspective on the Functional Responses of Stream Communities to Flow Intermittence." *Ecography* 44, no. 10: 1511–1523. https://doi.org/10.1111/ecog.05697.

Datry, T., N. Bonada, and A. J. Boulton. 2017. "Intermittent Rivers and Ephemeral Streams." In *Intermittent Rivers and Ephemeral Streams*, edited by T. Datry, N. Bonada, and A. Boulton. London, UK: Academic Press. https://doi.org/10.1016/B978-0-12-803835-2.00001-2.

Datry, T., N. Bonada, and J. Heino. 2016. "Towards Understanding the Organisation of Metacommunities in Highly Dynamic Ecological Systems." *Oikos* 125, no. 2: 149–159. https://doi.org/10.1111/oik.02922.

Datry, T., A. J. Boulton, N. Bonada, et al. 2018a. "Flow Intermittence and Ecosystem Services in Rivers of the Anthropocene." *Journal of Applied Ecology* 55, no. 1: 353–364. https://doi.org/10.1111/1365-2664.12941.

Datry, T., R. Corti, J. Heino, B. Hugueny, R. J. Rolls, and A. Ruhí. 2017. "Habitat Fragmentation and Metapopulation, Metacommunity, and Metaecosystem Dynamics in Intermittent Rivers and Ephemeral Streams." In *Intermittent Rivers and Ephemeral Streams: Ecology and Management*, 377–403. London, UK: Elsevier. https://doi.org/10.1016/B978-0-12-803835-2.00014-0.

Datry, T., A. Foulquier, R. Corti, et al. 2018b. "A Global Analysis of Terrestrial Plant Litter Dynamics in Non-perennial Waterways." *Nature Geoscience* 11, no. 7: 497–503. https://doi.org/10.1038/s41561-018-0134-4.

Datry, T., S. T. Larned, K. M. Fritz, et al. 2014. "Broad-Scale Patterns of Invertebrate Richness and Community Composition in Temporary Rivers: Effects of Flow Intermittence." *Ecography* 37, no. 1: 94–104. https://doi.org/10.1111/j.1600-0587.2013.00287.x.

Datry, T., S. T. Larned, and K. Tockner. 2014. "Intermittent Rivers: A Challenge for Freshwater Ecology." *BioScience* 64, no. 3: 229–235. https://doi.org/10.1093/biosci/bit027.

Datry, T., H. Pella, C. Leigh, N. Bonada, and B. Hugueny. 2016. "A Landscape Approach to Advance Intermittent River Ecology." *Freshwater Biology* 61, no. 8: 1200–1213. https://doi.org/10.1111/fwb.12645.

Datry, T., A. Truchy, J. D. Olden, et al. 2023. "Causes, Responses, and Implications of Anthropogenic Versus Natural Flow Intermittence in River Networks." *BioScience* 73, no. 1: 9–22. https://doi.org/10.1093/biosci/biac098.

De Groot, R. S., M. A. Wilson, and R. M. J. Boumans. 2002. "A Typology for the Classification, Description and Valuation of Ecosystem Functions, Goods and Services." *Ecological Economics* 41, no. 3: 393–408. https://doi.org/10.1016/S0921-8009(02)00089-7.

del Campo, R., R. Gómez, and G. Singer. 2019. "Dry Phase Conditions Prime Wet-Phase Dissolved Organic Matter Dynamics in Intermittent Rivers." *Limnology and Oceanography* 64, no. 5: 1966–1979. https://doi.org/10.1002/lno.11163.

Falkenmark, M. 2000. "Competing Freshwater and Ecological Services in the River Basin Perspective: An Expanded Conceptual Framework." *Water International* 25, no. 2: 172–177. https://doi.org/10.1080/02508060008686815.

Fisher, S. G., N. B. Grimm, E. Martí, R. M. Holmes, and J. B. Jones. 1998. "Material Spiraling in Stream Corridors: A Telescoping Ecosystem Model." *Ecosystems* 1, no. 1: 19–34. https://doi.org/10.1007/s100219900003.

Gilvear, D. J., C. J. Spray, and R. Casas-Mulet. 2013. "River Rehabilitation for the Delivery of Multiple Ecosystem Services at the River Network Scale." *Journal of Environmental Management* 126: 30–43. https://doi.org/10.1016/j.jenvman.2013.03.026.

Gómez, R., M. I. Arce, D. S. Baldwin, and C. N. Dahm. 2017. "Water Physicochemistry in Intermittent Rivers and Ephemeral Streams." In *Intermittent Rivers and Ephemeral Streams: Ecology and Management*, 109–134. London, UK: Elsevier. https://doi.org/10.1016/B978-0-12-803835-2.00005-X.

Gounand, I., E. Harvey, C. J. Little, and F. Altermatt. 2018. "Meta-Ecosystems 2.0: Rooting the Theory Into the Field." *Trends in Ecology & Evolution* 33, no. 1: 36–46. https://doi.org/10.1016/j.tree.2017.10.006.

Haines-Young, R., and M. Potschin. 2010. "The Links Between Biodiversity, Ecosystem Services and Human Well-Being." In *Ecosystem Ecology: A New Synthesis*, edited by D. G. Raffaelli and C. L. J. Frid. Cambridge, UK: Cambridge University Press.

Haines-Young, R., and M. Potschin. 2018. *CICES V5. 1. Guidance on the Application of the Revised Structure*, 53. Nottingham, UK: Fabis Consulting.

Hanski, I. 1998. "Metapopulation Dynamics." *Nature* 396, no. 6706: 41–49. https://doi.org/10.1038/23876.

Harvey, E., and F. Altermatt. 2019. "Regulation of the Functional Structure of Aquatic Communities Across Spatial Scales in a Major River Network." *Ecology* 100, no. 4: e02633. https://doi.org/10.1002/ecy.2633.

Helfield, J. M., and R. J. Naiman. 2006. "Keystone Interactions: Salmon and Bear in Riparian Forests of Alaska." *Ecosystems* 9, no. 2: 167–180. https://doi.org/10.1007/s10021-004-0063-5.

Hladyz, S., S. C. Watkins, K. L. Whitworth, and D. S. Baldwin. 2011. "Flows and Hypoxic Blackwater Events in Managed Ephemeral River Channels." *Journal of Hydrology* 401, no. 1–2: 117–125. https://doi.org/10.1016/j.jhydrol.2011.02.014.

Hohenthal, J., E. Owidi, P. Minoia, and P. Pellikka. 2015. "Local Assessment of Changes in Water-Related Ecosystem Services and Their Management: DPASER Conceptual Model and Its Application in Taita Hills, Kenya." *International Journal of Biodiversity Science, Ecosystem Services and Management* 11, no. 3: 225–238. https://doi.org/10.1080/21513732.2014.985256.

Hotchkiss, E. R., R. O. Hall, R. A. Sponseller, et al. 2015. "Sources of and Processes Controlling CO_2 emissions Change With the Size of Streams and Rivers." *Nature Geoscience* 8, no. 9: 696–699. https://doi.org/10.1038/ngeo2507.

Humphries, P., H. Keckeis, and B. Finlayson. 2014. "The River Wave Concept: Integrating River Ecosystem Models." *BioScience* 64, no. 10: 870–882. https://doi.org/10.1093/biosci/biu130.

Jacquet, C., L. Carraro, and F. Altermatt. 2022. "Meta-Ecosystem Dynamics Drive the Spatial Distribution of Functional Groups in River Networks." *Oikos* 2022: e09372. https://doi.org/10.1111/oik.09372.

Jaeger, K. L., J. D. Olden, and N. A. Pelland. 2014. "Climate Change Poised to Threaten Hydrologic Connectivity and Endemic Fishes in Dryland Streams." *Proceedings of the National Academy of Sciences of the United States of America* 111, no. 38: 13894–13899. https://doi.org/10.1073/pnas.1320890111.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. "The Flood Pulse Concept in River-Floodplain Systems." In *Proceedings of the International Large River Symposium, Canadian Special Publication of Fisheries and Aquatic Sciences*, edited by D. P. Dodge, vol. 106, 110–127. Ottawa, Canada: Canadian Department of Fisheries and Oceans.

Kaletova, T., P. Rodriguez-Lozano, E. Berger, et al. 2021. "Considering Temporal Flow Variability of Non-perennial Rivers in Assessing Ecosystem Service Provision." *Ecosystem Services* 52: 101368. https://doi.org/10.1016/j.ecoser.2021.101368.

Kaval, P. 2019. "Integrated Catchment Management and Ecosystem Services: A Twenty-Five Year Overview." *Ecosystem Services* 37, no. May 2018: 100912. https://doi.org/10.1016/j.ecoser.2019.100912.

Keeler, B. L., S. Polasky, K. A. Brauman, K. A. Johnson, J. C. Finlay, and A. O. Neill. 2012. "Linking Water Quality and Well-Being for Improved Assessment and Valuation of Ecosystem Services." *Proceedings of the National Academy of Sciences of the United States of America* 109, no. 45: 18619–18624. https://doi.org/10.1073/pnas.1215991109.

Laca, E. A. 2021. "Multi-Scape Interventions to Match Spatial Scales of Demand and Supply of Ecosystem Services." *Frontiers in Sustainable Food Systems* 4: 607276. https://doi.org/10.3389/fsufs.2020.607276.

Larned, S. T., T. Datry, D. B. Arscott, and K. Tockner. 2010. "Emerging Concepts in Temporary-River Ecology." *Freshwater Biology* 55, no. 4: 717–738. https://doi.org/10.1111/j.1365-2427.2009.02322.x.

Leibold, M. A., M. Holyoak, N. Mouquet, et al. 2004. "The Metacommunity Concept: A Framework for Multi-Scale Community Ecology." *Ecology Letters* 7, no. 7: 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x.

Leigh, C., A. J. Boulton, J. L. Courtwright, et al. 2016. "Ecological Research and Management of Intermittent Rivers: An Historical Review and Future Directions." *Freshwater Biology* 61, no. 8: 1181–1199. https://doi.org/10.1111/fwb.12646.

Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. *Fluvial Processes in Geomorphology*. Mineola, TX: Dover Publications.

Likens, G. E., and F. H. Bormann. 1974. "Linkages Between Terrestrial and Aquatic." *Ecosystems* 24, Número 8: 447–456.

Loreau, M. 2010. "Linking Biodiversity and Ecosystems: Towards a Unifying Ecological Theory." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 365, no. 1537: 49–60. https://doi.org/10.1098/rstb.2009.0155.

McIntosh, A. R., C. Leigh, K. S. Boersma, P. A. McHugh, C. Febria, and E. García-Berthou. 2017. "Food Webs and Trophic Interactions in Intermittent Rivers and Ephemeral Streams." In *Intermittent Rivers and Ephemeral Streams: Ecology and Management*, 323–347. London, UK: Elsevier. https://doi.org/10.1016/B978-0-12-803835-2.00012-7.

Messager, M. L., B. Lehner, C. Cockburn, et al. 2021. "Global Prevalence of Non-Perennial Rivers and Streams." *Nature* 594, no. 7863: 391–397. https://doi.org/10.1038/s41586-021-03565-5.

Montgomery, D. R. 1999. "Process Domains and the River Continuum." *Journal of the American Water Resources Association* 35, no. 2: 397–410.

Mulholland, P. J., and W. R. Hill. 1997. "Seasonal Patterns in Streamwater Nutrient and Dissolved Organic Carbon Concentrations: Separating Catchment Flow Path and In-Stream Effects." *Water Resources Research* 33, no. 6: 1297–1306. https://doi.org/10.1029/97WR00490.

Oginah, S. A., L. Posthuma, L. Maltby, M. Hauschild, and P. Fantke. 2023. "Linking Freshwater Ecotoxicity to Damage on Ecosystem Services in Life Cycle Assessment." *Environment International* 171: 107705. https://doi.org/10.1016/j.envint.2022.107705.

O'Sullivan, A. M., K. J. Devito, L. D'Orangeville, and R. A. Curry. 2022. "The Waterscape Continuum Concept: Rethinking Boundaries in Ecosystems." *WIREs Water* 9, no. 4: 1–16. https://doi.org/10.1002/wat2.1598.

Pérez-Silos, I., J. M. Álvarez-Martínez, and J. Barquín. 2021. "Large-Scale Afforestation for Ecosystem Service Provisioning: Learning From the Past to Improve the Future." *Landscape Ecology* 36: 3329–3343. https://doi.org/10.1007/s10980-021-01306-7.

Petersen, M. M. 1999. "A Natural Approach to Watershed Planning, Restoration and Management." *Water Science and Technology* 39, no. 12: 347–352. https://doi.org/10.1016/S0273-1223(99)00353-4.

Plas, F. V. D. 2019. "Biodiversity and Ecosystem Functioning in Naturally Assembled Communities." *Biological Reviews* 94, no. 4: 1220–1245. https://doi.org/10.1111/brv.12499.

Poff, N. L. R., J. D. Allan, M. B. Bain, et al. 1997. "The Natural Flow Regime: A Paradigm for River Conservation and Restoration." *BioScience* 47, no. 11: 769–784. https://doi.org/10.2307/1313099.

Poole, G. C. 2002. "Fluvial Landscape Ecology: Addressing Uniqueness Within the River Discontinuum." *Freshwater Biology* 47, no. 4: 641–660.

Price, A. N., C. N. Jones, S. C. Zipper, and P. E. T. Al. 2021. "The Drying Regimes of Non-Perennial Rivers and Streams Geophysical Research Letters." *Geophysical Research Letters* 48: 1–12. https://doi.org/10.1029/2021GL093298.

Rau, A.-L., H. von Wehrden, and D. J. Abson. 2018. "Temporal Dynamics of Ecosystem Services." *Ecological Economics* 151: 122–130. https://doi.org/10.1016/j.ecolecon.2018.05.009.

Raudsepp-Hearne, C., G. D. Peterson, and E. M. Bennett. 2010. "Ecosystem Service Bundles for Analyzing Tradeoffs in Diverse Landscapes." *Proceedings of the National Academy of Sciences of the United States of America* 107, no. 11: 5242–5247. https://doi.org/10.1073/pnas.0907284107.

Rawlins, J. M., W. J. de Lange, and G. C. G. Fraser. 2018. "An Ecosystem Service Value Chain Analysis Framework: A Conceptual Paper." *Ecological Economics* 147: 84–95. https://doi.org/10.1016/j.ecolecon.2017.12.023.

Raymond, P. E., J. E. Saiers, and W. V. Sobczak. 2016. "Hydrological and Biogeochemical Controls on Watershed Dissolved Organic Matter Transport: Pulse-Shunt Concept." *Ecology* 97, no. 1: 5–16.

Reid, A. J., A. K. Carlson, I. F. Creed, et al. 2019. "Emerging Threats and Persistent Conservation Challenges for Freshwater Biodiversity." *Biological Reviews* 94, no. 3: 849–873. https://doi.org/10.1111/brv.12480.

Reid, W. V., H. A. Mooney, A. Cropper, et al. 2005. *Ecosystems and Human Well-Being-Synthesis: A Report of the Millennium Ecosystem Assessment*. Washington, DC: Island Press.

Rodriguez-Iturbe, I., R. Muneepeerakul, E. Bertuzzo, S. A. Levin, and A. Rinaldo. 2009. "River Networks as Ecological Corridors: A Complex Systems Perspective for Integrating Hydrologic, Geomorphologic, and Ecologic Dynamics." *Water Resources Research* 45, no. 1: 1–22. https://doi.org/10.1029/2008WR007124.

Sarremejane, R., M. L. Messager, and T. Datry. 2022. "Drought in Intermittent River and Ephemeral Stream Networks." *Ecohydrology* 15, no. 5: e2390. https://doi.org/10.1002/eco.2390.

Scherer-lorenzen, M., M. O. Gessner, B. E. Beisner, et al. 2022. "Pathways for Cross-Boundary Effects of Biodiversity on Ecosystem Functioning." *Trends in Ecology & Evolution* 37, no. 5: 454–467. https://doi.org/10.1016/j.tree.2021.12.009.

Shiklomanov, I. 1993. "World Freshwater Resources." In *Water in Crisis: A Guide to the World's Freshwater Resources*, edited by P. H. Gleick, 13–24. New York: Oxford University Press.

Song, C., W. K. Dodds, J. Rüegg, et al. 2018. "Continental-Scale Decrease in Net Primary Productivity in Streams Due to Climate Warming." *Nature Geoscience* 11, no. 6: 415–420. https://doi.org/10.1038/s41561-018-0125-5.

Sponseller, R. A., J. B. Heffernan, and S. G. Fisher. 2013. "On the Multiple Ecological Roles of Water in River Networks." *Ecosphere* 4, no. 2: 1–14. https://doi.org/10.1890/ES12-00225.1.

Stanford, J. A., and J. V. Ward. 1993. "An Ecosystem Perspective of Alluvial Rivers: Connectivity and the Hyporheic Corridor." *Journal of the North American Benthological Society* 12, no. 1: 48–60.

Stevenson, R. J., and S. Sabater. 2010. "Understanding Effects of Global Change on River Ecosystems: Science to Support Policy in a Changing World." In *Global Change and River Ecosystems—Implications for Structure, Function and EcosystemServices*, edited by R. J. Stevenson and S. Sabater, 3–18. Netherlands: Springer. https://doi.org/10.1007/978-94-007-0608-8_2.

Steward, A. L., T. Datry, and S. D. Langhans. 2022. "The Terrestrial and Semi-Aquatic Invertebrates of Intermittent Rivers and Ephemeral Streams." *Biological Reviews* 1419: 1408–1425. https://doi.org/10.1111/brv.12848.

Stubbington, R., M. Acreman, V. Acuña, et al. 2020. "Ecosystem Services of Temporary Streams Differ Between Wet and Dry Phases in Regions With Contrasting Climates and Economies." *People and Nature* 2, no. 3: 660–677. https://doi.org/10.1002/pan3.10113.

Sutfin, N. A., E. E. Wohl, and K. A. Dwire. 2016. "Banking Carbon: A Review of Organic Carbon Storage and Physical Factors Influencing Retention in Floodplains and Riparian Ecosystems." *Earth Surface Processes and Landforms* 41, no. 1: 38–60. https://doi.org/10.1002/esp.3857.

Syrbe, R. U., and U. Walz. 2012. "Spatial Indicators for the Assessment of Ecosystem Services: Providing, Benefiting and Connecting Areas and Landscape Metrics." *Ecological Indicators* 21: 80–88. https://doi.org/10.1016/j.ecolind.2012.02.013.

Talbot, C. J., E. M. Bennett, K. Cassell, et al. 2018. "The Impact of Flooding on Aquatic Ecosystem Services." *Biogeochemistry* 141, no. 3: 439–461. https://doi.org/10.1007/s10533-018-0449-7.

Terrado, M., V. Acuña, D. Ennaanay, H. Tallis, and S. Sabater. 2014. "Impact of Climate Extremes on Hydrological Ecosystem Services in a Heavily Humanized Mediterranean Basin." *Ecological Indicators* 37: 199–209.

Thomas, H., and T. R. Nisbet. 2007. "An Assessment of the Impact of Floodplain Woodland on Flood Flows." *Water and Environment Journal* 21, no. 2: 114–126. https://doi.org/10.1111/j.1747-6593.2006.00056.x.

Thorp, J. H., and M. D. Delong. 1994. "The Riverine Productivity Model: An Heuristic View of Carbon Sources and Organic Processing in Large River Ecosystems." *Oikos* 70, no. 2: 305–308.

Thorp, J. H., M. C. Thoms, and M. D. Delong. 2006. "The Riverine Ecosystem Synthesis: Biocomplexity in River Networks Across Space and Time." *River Research and Applications* 22, no. 2: 123–147. https://doi.org/10.1002/rra.901.

Timoner, X., V. Acuña, D. Von Schiller, and S. Sabater. 2012. "Functional Responses of Stream Biofilms to Flow Cessation, Desiccation and Rewetting." *Freshwater Biology* 57, no. 8: 1565–1578. https://doi.org/10.1111/j.1365-2427.2012.02818.x.

Tockner, K., F. Malard, and J. V. Ward. 2000. "An Extension of the Flood Pulse Concept." *Hydrological Processes* 14: 2861–2883.

Tonkin, J. D., F. Altermatt, D. S. Finn, et al. 2018. "The Role of Dispersal in River Network Metacommunities: Patterns, Processes, and Pathways." *Freshwater Biology* 63, no. 1: 141–163. https://doi.org/10.1111/fwb.13037.

Townsend, C. R. 1996. "Concepts in River Ecology: Pattern and Process in the Catchment Hierarchy." *Large Rivers* 10: 3–21.

Tramblay, Y., A. Rutkowska, E. Sauquet, et al. 2021. "Trends in Flow Intermittence for European Rivers." *Hydrological Sciences Journal* 66, no. 1: 37–49. https://doi.org/10.1080/02626667.2020.1849708.

Tundisi, G. J. 2018. "Reservoirs: New Challenges for Ecosystem Studies and Environmental Management." *Water Security* 4-5, no. June 2017: 1–7. https://doi.org/10.1016/j.wasec.2018.09.001.

Vannote, R. L., G. Wayne Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. "The River Continuum Concept." *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130–137.

Vidal-Abarca Gutiérrez, M. R., N. Nicolás-Ruiz, M. d. M. Sánchez-Montoya, and M. L. Suárez Alonso. 2023. "Ecosystem Services Provided by Dry River Socio-Ecological Systems and Their Drivers of Change." *Hydrobiologia* 850, no. 12–13: 2585–2607. https://doi.org/10.1007/s10750-022-04915-8.

von Schiller, D., V. Acuña, D. Graeber, et al. 2011. "Contraction, Fragmentation and Expansion Dynamics Determine Nutrient Availability in a Mediterranean Forest Stream." *Aquatic Sciences* 73, no. 4: 485–497. https://doi.org/10.1007/s00027-011-0195-6.

von Schiller, D., S. Bernal, C. N. Dahm, and E. Martí. 2017. "Nutrient and Organic Matter Dynamics in Intermittent Rivers and Ephemeral Streams." In *Intermittent Rivers and Ephemeral Streams: Ecology and Management*, 135–160. London, UK: Elsevier. https://doi.org/10.1016/B978-0-12-803835-2.00006-1.

von Schiller, D., D. Graeber, M. Ribot, et al. 2015. "Hydrological Transitions Drive Dissolved Organic Matter Quantity and Composition in a Temporary Mediterranean Stream." *Biogeochemistry* 123, no. 3: 429–446. https://doi.org/10.1007/s10533-015-0077-4.

Wipfli, M. S., J. S. Richardson, and R. J. Naiman. 2007. "Ecological Linkages Between Headwaters and Downstream Ecosystems: Transport of Organic Matter, Invertebrates, and Wood Down Headwater Channels." *Journal of the American Water Resources Association* 43, no. 1: 72–85.

Wohl, E., B. P. Bledsoe, R. B. Jacobson, et al. 2015. "The Natural Sediment Regime in Rivers: Broadening the Foundation for Ecosystem Management." *BioScience* 65, no. 4: 358–371. https://doi.org/10.1093/biosci/biv002.

Yeakley, J. A., D. Ervin, H. Chang, et al. 2016. "Ecosystem Services of Streams and Rivers." In *River Science: Research and Management for the 21st Century*, 335–352. Hoboken, NJ: Wiley. https://doi.org/10.1002/9781118643525.ch17.

Zieritz, A., R. Sousa, D. C. Aldridge, et al. 2022. "A Global Synthesis of Ecosystem Services Provided and Disrupted by Freshwater Bivalve Molluscs." *Biological Reviews* 44: 1967–1998. https://doi.org/10.1111/brv.12878.

Zipper, S. C., J. C. Hammond, M. Shanafield, et al. 2021. "Pervasive Changes in Stream Intermittency Across the United States." *Environmental Research Letters* 16, no. 8: 084033. https://doi.org/10.1088/1748-9326/ac14ec.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.