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**Article:**

https://doi.org/10.1002/wat2.1106
Coupling virtual watersheds with ecosystem services assessment: A 21st century platform to support river research and management

(30 words max)


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Running title: Coupling virtual watersheds with ecosystem services assessment

Opinion paper (2,000-4,000 words, ≤ 5 figures/tables, 30-60 references)
ABSTRACT (250 words)

The demand for freshwater is projected to increase worldwide over the coming decades, resulting in severe water stress and threats to riverine biodiversity, ecosystem functioning and services. A major societal challenge is to determine where environmental changes will have the greatest impacts on riverine ecosystem services and where resilience can be incorporated into adaptive resource planning. Both water managers and scientists need new integrative tools to guide them towards the best solutions that meet the demands of a growing human population but also ensure riverine biodiversity and ecosystem integrity.

Resource planners and scientists could better address a growing set of riverine management and risk mitigation issues by (1) using a “Virtual Watersheds” approach based on improved digital river networks and better connections to terrestrial systems; (2) integrating Virtual Watersheds with ecosystem services technology (ARtificial Intelligence for Ecosystem Services: ARIES), and (3) incorporating the role of riverine biotic interactions in shaping ecological responses. This integrative platform can support both interdisciplinary scientific analyses of pressing societal issues and effective dissemination of findings across river research and management communities. It should also provide new integrative tools to identify the best solutions and trade-offs to ensure the conservation of riverine biodiversity and ecosystem services.
INTRODUCTION (1-2 paragraphs, 250-750 words)

Recent decades have witnessed accelerating climatic change, biodiversity loss, modifications to biogeochemical cycles, and alteration of the biophysical processes that shape the Earth’s surface. The Millennium Ecosystem Assessment provided a comprehensive review of the status of and threats to ecosystems and highlighted how biodiversity is a key contributor to numerous ecosystem functions and services. This has been widely adopted and is now central to the 2020 targets of the international Convention on Biological Diversity, aimed at halting declines in the provisioning of services. Despite recognising the scale of the problem, global water demand is still projected to exceed supply by approximately 40% by 2030. Freshwater ecosystems are among the most productive on Earth, harbouring a disproportionately large share; however, they are also especially vulnerable and there is an urgent need to reverse the biodiversity loss and ecosystem degradation they suffer.

Freshwaters are aquatic islands embedded in a terrestrial sea; their spatial structure and hydrological connectivity define many of their ecological attributes. Fluvial systems (entire catchments containing features such as streams, wetlands and lakes that are drained by their river networks) provide critical ecosystem provisioning (e.g., clean water, fisheries), regulating (e.g., flood control, waste assimilation) and cultural services (e.g., recreation), all essential to human societies. For example, at the beginning of the 21st century, large dams contributed 20% of the world’s electricity supply and irrigated agriculture produced 40% of the world’s food, yet a naturally variable and interconnected flow regime is generally seen as a necessity for sustaining riverine biodiversity and ecosystem functioning. These competing demands and other anthropogenic stressors have resulted in freshwater ecosystems having among the largest projected extinction rates on the planet, comparable to tropical rainforests and coral reefs. Moreover, future climate change and the demands of a growing and increasingly urbanised and affluent human population will exacerbate pressure on riverine biodiversity and the ecosystem services they support over the coming decades.

Maximizing societal returns from fluvial landscapes while simultaneously ensuring resilience and aquatic biodiversity conservation is a formidable challenge for sustainable development. Water managers require tools to guide them through complex natural resource decisions that seek to improve ecological status, predictability of flood risk, and ecosystem resilience. Meeting the conflicting demands of a growing human population while protecting the integrity of riverine ecosystems will require new approaches, bringing together research and resource management by capitalising on the increasing availability of high-resolution scientific data and on computational advances that enable their effective analysis. This article outlines the case for a coupled digital platform (Fig. 1) that integrates analytical models of aquatic-terrestrial ecosystems (Virtual Watersheds) with a robust ecosystem services assessment technology (such as ARtificial Intelligence for Ecosystem Services: ARIES). This coupled platform serves two fundamental needs: (1) providing readily usable tools and decision support for water managers and resource planners, using currently available data; (2) providing a framework to organize past, and guide future research that links biodiversity, ecosystem functioning and services.

ECOLOGICAL NETWORKS, FLUVIAL LANDSCAPES AND RIVERINE ECOSYSTEM SERVICES
Understanding how riverine ecosystem services are affected by human actions is a long-standing challenge. Analysis of ecosystem services must address the complex and often indirect links between organisms and processes (Fig. 2). Although significant advances have been made towards understanding the relationship between freshwater biodiversity and ecosystem functioning in the last decade, these studies have been largely restricted to simple species-poor assemblages in small-scale laboratory microcosms. Such studies fill an obvious knowledge gap in disentangling specific drivers and responses, but their narrow focus does not contribute to our understanding of the same relationships at larger spatial scales.

Ecosystem processes in riverine ecosystems may be resistant to local declines in species richness due to high levels of functional redundancy. However, more recent evidence suggests that the focus on single processes, rather than a more realistic evaluation of the multiple processes that define ecosystem functioning, may have caused an overestimation of this apparent robustness. Decades of biomonitoring research have shown that different species have different performance response curves across environmental gradients. Thus, a greater level of biodiversity may be needed at larger scales to maintain functioning ecosystems. This has important implications for scaling up (or down) findings from local to regional spatial scales, and may suggest ways to bridge the gap between biodiversity, ecosystem functioning and services. Biotic interactions are often the main determinant of ecosystem processes at local scales, whereas environmental drivers are usually assumed to have an increasingly important role at the river network scale and beyond (i.e., river basins that contain several streams of more than 1st order). Understanding how these local-to-regional responses change functional attributes of river ecosystems is essential for understanding and predicting the consequences of environmental change for river ecosystem services.

Remarkable scientific progress has also been achieved over the last decade increasing our understanding on the organisation of riverine biodiversity and processes across scales, including: (1) the role of river network structure and topology to explain habitat creation and maintenance through geomorphological processes, (2) the importance of hierarchical patch dynamics on the biocomplexity of river ecosystems, (3) the dependency of biodiversity on hydrological dynamics, and (4) the role of spatial heterogeneity, connectivity, and asynchrony in riverine ecological dynamics. However, the development of analytical GIS tools capable of incorporating these theoretical advances within a digital numerical framework still lags far behind, which prevents linking biological structure and function to the hydro-morphological characteristics of river networks.

Most current assessments and evaluations of ecosystem services (e.g. LUCI, INVEST, ARIES) incorporate analytical tools that deal with ecosystem services linked to catchment or terrestrial processes (e.g., Irrigation, Drinking water, Hydroelectric energy production; Fig. 2). Few incorporate approaches in which models include in-stream elements (i.e., biofilm, macroinvertebrates or fish) to characterise ecosystem services that are mainly generated within the riverine domain (e.g., Water purification, Fisheries; Fig. 2). New approaches are needed to improve our understanding of how biodiversity and functioning are linked with the provision of riverine ecosystem services. Effective ecosystem service analytical tools should be able to (1) work at a range of scales and integrate results while recognising river network topology and structure, (2) integrate existing and new data from different sources, and (3) be flexible enough to employ different models according to data availability.
CREATING THE ANALYTICAL FRAMEWORK FOR RIVER-TERRESTRIAL ECOSYSTEMS

Assessment of riverine ecosystem services requires complete and accurate digital representations of entire river networks (GIS hydrography or stream layers). Robust analytical capabilities are also needed to bring together the roles of different ecosystem components and interactions on the provisioning of riverine ecosystem services (Fig. 2). However, many existing digital river networks (at regional or national scales) are based on incomplete river networks (omitting headwaters) or have limited analytical capabilities. A wide variety of methods can be used to derive synthetic hydrography from Digital Elevation Models (DEM; e.g., ArcHydro, TauDEM and HEC-GeoHMS); however, creating a digital river network from DEMs is not the same as building a digital numerical framework which can incorporate different analytical capabilities (Box 1).

Virtual watersheds (Box 1) offer advantages over other approaches because they explicitly account for river network structure and topology, incorporating a wide range of terrestrial-riverine interactions at different spatial scales (Fig. 3). Virtual watersheds create near-complete digital synthetic river networks (e.g., stream layer or hydrography), often improving on national level hydrography. By using virtual watersheds and its accompanying digital synthetic hydrography, an analyst can route information downstream (such as water, sediment or pollutants) or upstream (such as migrating fish). Moreover, all parts of the landscape within a Virtual Watershed are inter connected to simulate the movement of gravity-driven elements such as water and sediment, or animal movement, which includes using least environmental cost technology. All cells (i.e., smaller homogenous units in a DEM) within a Virtual Watershed are topographically characterised to identify landforms, including their elevation, relative to the channel network, elevation relative to other areas (concavities, convexities), flow convergence, slope steepness, etc. This is used to identify relevant landforms for riverine ecosystems such as riparian zones, floodplains, terraces, alluvial fans and erosional features. Finally, the synthetic hydrography is richly attributed with stream and watershed information so that any digital information (e.g., vegetation cover or land uses) can be transferred to the river network across a range of different scales. This is facilitated by the discretization of landforms and other features at different spatial scales, ranging from individual hillsides and river buffers (DEM cells below $10^{-1} \text{ km}^2$), river segments (variable, but commonly below $10^{-1} \text{ km}$), sub-catchments (variable, $10^1 - 10^2 \text{ km}^2$), catchments (any scale) or even whole landscapes (multiple catchments).

Virtual Watersheds have been developed across a diverse set of landscapes and projects that build upon the uniquely rich analytical capabilities of this approach (Box 1). For example, in the Simonette River watershed ($6,000 \text{ km}^2$; north central Alberta) the Alberta Provincial Government required the identification of variable width riparian zones for regulatory purposes in relation to road erosion and sediment delivery (and transport) to streams. NetMap’s Virtual Watershed was integrated with existing national-level LiDAR based hydrography to map variable width riparian zones that included floodplains, wetlands, in-stream wood recruitment areas and zones that influenced water thermal loading, allowing evaluation of cumulative watershed effects. A virtual watershed was built for the Matanuska-Susitna catchment ($65,000 \text{ km}^2$) in south central Alaska to create a more complete and accurate hydrography (using a blend of 5 m and 1 m DEMs) to delineate salmon habitats. NetMap’s valley floor and riparian delineation tools were also used to identify floodplains and
riparian areas. This work provided the foundation for a basin level ecosystem valuation analysis for fisheries, floodplains and riparian zones.\textsuperscript{41}

**BOX 1**

**Building Virtual Watersheds**

Virtual Watersheds are built using NetMap \url{www.terrainworks.com} as an add-in in ArcGIS. They were developed with numerous agency and NGO partners in the western U.S. for the purposes of addressing fluvial and riparian processes, aquatic habitat characteristics, erosion-sedimentation processes and the effects of roads, urbanization, wildfire and climate change on river networks. Virtual Watersheds are a geo-spatial simulation of riverine landscapes within computer hardware and software which contain components necessary to enumerate a variety of watershed landforms and processes, and human interactions with them. The components of a Virtual Watershed include a digital elevation model (DEM) of the highest resolution available, synthetic hydrography (e.g., river network derived from DEMs) and their coupling using a data structure to support the required analytical capabilities. A virtual watershed is more than a stream layer or hydrography and it is characterized by five analytical capabilities (Fig. 3): 1) landform characterization, every cell in a DEM is characterized topographically (floodplains, hillslopes, etc.); 2) discretization, the digital hydrography and DEM surface are subdivided into facets of appropriate spatial scales; 3) attribution, assigning of watershed and stream attributes to individual segments within the digital hydrography; 4) connectivity, all DEM cells need to be connected to all others to allow information transfer (river network – terrestrial); 5) routing, transfer of information up and downstream in the river network.

**ASSESSING RIVERINE ECOSYSTEM SERVICES USING ARIES**

The ARIES approach has several advantages over other methods in the assessment of riverine ecosystem services since it provides (1) spatial explicit information on modalities of ecosystem services sources, sinks and flows, (2) actual ecosystem service use versus potential use, (3) flexible statement on ecosystem services values (4) simultaneous analysis of ecosystem services trade-offs, and (5) uncertainty estimates.\textsuperscript{42} ARIES\textsuperscript{19} (Box 2) was developed in response to the need to extend the Millennium Ecosystem Assessment conceptual model (which classifies ecosystem services as “supporting,” “regulating,” “provisioning,” and “cultural”)\textsuperscript{43} to support a systematic emphasis on beneficiaries. This reduces the occurrence of erroneous “double counting” of ecosystem services values\textsuperscript{44} and provides improved characterisation of the spatial locations of ecosystem services provision, beneficiaries, and spatial flows.\textsuperscript{45}

An ARIES assessment requires the mapping of concrete and spatially explicit beneficiary groups, and a thorough explicit characterization of the set of processes that link a beneficiary group with specified source ecosystem(s) through a clearly identified spatio-temporal flow. For example, the water supply service includes separate processes for each water use in an area, such as irrigation, domestic, or industrial use. This approach improves detail, scale and dynamics of ecosystem services models.\textsuperscript{46} ARIES models the spatiotemporal transport and delivery of ecosystem service benefits through dynamic flow models, based on algorithms that use the production function output along with quantification of demand as inputs. In this multi-stage approach, amounts of a service carrier produced in source (supply) regions flow to beneficiaries where demand is explicitly quantified. Flows reach beneficiaries
along physical or informational flow paths, which result from spatially explicit and dynamic physical processes.

A precondition for the effective use of ecosystem services in decision-making is to acknowledge, quantify and communicate the uncertainties that are inherent to any modelling task. ARIES is designed to use probabilistic initial conditions for most of its models, using Bayesian belief networks in place of the production functions adopted in other approaches. An end user obtains information on uncertainty via dynamic portions of Aries models that use methods including Monte Carlo simulation and variance propagation. Importantly, only the components of overall uncertainty that relate to missing data or known data quality issues can be dealt with effectively in such a probabilistic model. Accounting for uncertainty that relates to the structure of the causal dependencies that define the Bayesian models is not possible, although context-specific model assemblage rules can be used (Box 2).

At present, ARIES comprises models addressing eight ecosystem services (carbon sequestration and storage, riverine flood regulation, coastal flood regulation, aesthetic views and open space proximity, water supply, sediment regulation, subsistence fisheries, and recreation). Water service models have incorporated explicit water demand, simulating water-delivery dynamics that take into account precipitation, evapotranspiration, infiltration, runoff, and rival use. Water budgets computed for a particular region account separately for demand for irrigation, livestock, residential consumption and tourism, often using “best practice” manuals and heuristic criteria when primary data is not available. ARIES model development uses a bottom-up approach, based on detailed collaborative case studies; this knowledge is generalised to yield “global” models, providing a broader characterization of many ecosystem services at a wider variety of locations based on limited data input requirements from users. These simpler models provide a default “bottom line” in the ARIES environment, allowing the system to produce results of adjustable detail in almost any geographic region using global data, but automatically switching to more detailed models when the knowledge base and data allow. A variety of well-known, open source physical process models are integrated into the ARIES model base. For example, the water components currently rely on a fully distributed, relatively simple surface water model that uses the curve number method\(^7\) to predict infiltration, evapotranspiration, runoff and groundwater recharge from globally available elevation, land cover and soil data.

By bringing together the capabilities of Virtual Watersheds and ARIES provides immense potential to increase our understanding of the relationships between riverine biodiversity and ecosystem functioning and services. The large-scale meta-modelling ARIES framework, based on a flexible modular assembly process, would be greatly expanded by coupling it with the Virtual Watershed approach (Box 2). Virtual Watersheds capabilities coupled to the ARIES’ model repository can greatly expand the conceptual resolution of the system and allow more widespread and economical exploitation of its decision-making potential. The Virtual Watershed design complements ARIES because it adds increasing spatial resolution and relevant information on environmental properties of catchments and river networks across scales. This coupled platform could host models that include in-stream elements (e.g., biofilm) that provide key functions (i.e., nutrient retention) in the provision of riverine ecosystem services (i.e., Water purification; Fig. 2) at different spatial scales (from single river reaches to entire river networks).
STEPS AHEAD: INTEGRATING EXISTING AND NEW DATABASES

The spatial framework provided by the Virtual Watershed-ARIES platform is essential to produce spatial explicit information on multiple levels of biological organisation and ecosystem functions required to improve our understanding on the relationship among riverine biodiversity, ecosystem functioning and ecosystem services. A key advantage of the proposed Virtual Watershed-ARIES platform is that it could incorporate existing and new data from many different sources. This allows significant progress in river research and management issues all around the world with current available data. For example, biomonitoring and hydromorphological data gathered through national or regional monitoring programmes (e.g. hydrology, water quality) could be easily integrated and modelled in Virtual Watersheds. Additionally, most funding bodies are now moving towards public repositories for datasets collected from projects they fund (e.g., http://www.evo-uk.org/). Findings from increasingly popular citizen science could also constitute and important data source; for instance Riverfly Monitors gather standardised macroinvertebrate data at different spatial scales across the UK (http://www.riverflies.org/) which could be easily integrated into the dual digital platform to provide alternative measures of biological diversity. Citizen science data is often collected from the same site over time, providing a temporal component of biodiversity and ecosystem functioning. These time series allow effects of policy change on biodiversity, and ecosystem functioning to be assessed. Remote sensing information from different sources (e.g. LANDSAT, MERIS, SENTINEL, SPOT-5 and others) could provide series of data on land use and land cover dynamics or riparian forest condition covering a range of spatial scales. There is also a growing amount of environmental digital information available through different interconnected web portals (e.g., GEOSS, GBIF, BIOFRESH) that could also be used to calculate biophysical characteristics to entire river networks worldwide.

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BOX 2

The ARIES approach to intelligent model integration

In ARIES, observation is the unifying paradigm that allows models of physical objects, processes and quantities to be independently developed, stored, found and assembled into end-user data-flows. A model is seen as a strategy to observe a concept, which applies equally to datasets and computed models. ARIES runs at the user side as a client software with limited requirements, accessing a distributed network where many models may be available to observe the same concept. Explicit semantics guides the assembly of the best possible workflow that will compute the requested observation, based on a user query as simple as “observe social dynamics of water in watershed X”. The resolution process builds a decision tree to identify the most suitable model and, in turn, any other concepts required by it, until a computable workflow is built. To match models to contexts, ARIES adopts a sophisticated, multiple criteria ranking algorithm that can mix objective criteria (such as spatio-temporal resolution or currency) with user-provided rankings of reliability and quality. Specific, detailed models and data are chosen over more general alternatives as long as data exist to run them. Differences in representation (e.g., units or spatial projections) are negotiated transparently. In the current ARIES model base, modelling paradigms such as GIS, system dynamics and Bayesian networks coexist with agent-based models to provide a variety of possible interpretations for the complex phenomena that underlie ecosystem service. When data allow, detailed models are built with no user intervention.
Biodiversity indicators currently used to reflect the state of the environment are structural in nature and cover only a few levels of biological organisation, situated mainly at the level of populations and/or communities.\textsuperscript{49} Information on other levels of biodiversity and ecosystem functioning (e.g., genes-to-ecosystems; Fig. 4) are less commonly used. However, future advances on river research will need to produce data spanning multiple levels of biological organisation and ecosystem functions based on a spatially explicit design. This is because it is difficult to predict ecosystem functioning by simply extrapolating across levels of biological organisation due to emergent properties in complex systems.\textsuperscript{50} The proposed platform could provide the basis for setting (pressure-driven or natural) gradients and control-impact analysis to elucidate effects of human impacts on biodiversity and ecosystem functioning. Molecular data will be essential in this multi-level approach, such as environmental DNA,\textsuperscript{51} to account for key species maintaining ecosystem functioning and services. Molecular approaches are also pivotal to understand how microbial diversity changes throughout river networks.\textsuperscript{52} Research on the population genetic diversity of keystone species or ecosystem engineers (e.g., trout at the top of the food web and alder at the base) at a river network scale (e.g., metacommunity dynamics) or comparing growth rates (RNA:DNA ratios) of indicator species that have disproportionate effects across driver-pressure gradients could also help to explain the relationships between biodiversity and ecosystem functioning and services. Moreover, a reasonable starting point for introducing biotic interactions into the Virtual Watershed modelling practise is to use a trait-based approach, rather than one that is taxonomically explicit: this also frees us of the “curse of the Latin binomial”\textsuperscript{53} and improves the potential generality of the approach. This is supported because of the evident redundancy that occurs in running waters, at least for single processes and/or services, and the existence of “super-traits” such as body-size, which determines both the structure and dynamics of freshwater food webs.

Riverine ecosystem functioning can be assessed by using estimates of biomass production, organic matter breakdown or nutrient uptake rates, yet it is rarely assessed in monitoring programmes and current spatial data coverage is limited. A possible approach is to measure river ecosystem metabolism, which is essentially the sum of the metabolic rates of the organisms within the food web.\textsuperscript{54} Whole-ecosystem metabolism is a promising, cost-effective measure of ecosystem functioning, as it integrates many different ecosystem processes and is affected by both rapid (primary productivity) and slow (organic matter decomposition) energy channels of the riverine food web, as well as being able to measure responses at the higher spatial scales (e.g., reaches and above) that are more relevant to service delivery.\textsuperscript{55} This technique is increasingly being used as an indicator of fluvial ecosystem health,\textsuperscript{56} although linkages to driver-pressure gradients and baseline natural variability at a range of scales are still being investigated.\textsuperscript{57, 58}

Finally, important and rapid advances in both water management and new research could be made by layering the increasing volumes of “big data” of species assemblages and interaction networks that are emerging\textsuperscript{12, 26, 49} onto the river network in the proposed coupled platform. This would essentially produce a “network of networks” (Fig. 5). The structure of ecological interaction networks (such as food webs) provides a conceptual link between specific community assemblages and the ecosystem services they provide.\textsuperscript{59} Individual streams can be considered as a fragmented local food web, part of a larger regional food web that is embedded in a spatially explicit setting (Fig. 5). Often stream food webs are considered in isolation, when in reality they are integrated into a larger meta-network, with species moving among them at different scales across the fluvial landscape (i.e., source-sink dynamics). The
consequences of a particular stressor can be assessed in a food web framework; different stressors are associated with spatial scales and particular nodes in the web (e.g., biomagnification of organochlorine pesticides in apex predators; antibiotics within the microbial loop at the base of the web) and the particular services associated with each node or compartments in the web. Ecosystem services could be linked to particular portions of the food web, providing a useful means of rationalising and predicting impacts of stressors. For instance, drought events fragment and simplify freshwater food webs, impairing ecosystem processes and the associated services they provide, such as the ability to support the higher trophic levels. The combination of these data types into the proposed coupled platform can add significantly to our understanding of how management techniques, governmental policies, as well as environmental stressors affect the mechanisms underpinning ecological network structure and hence ecosystem functioning within fluvial landscapes.

CONCLUSION (1-2 paragraphs, 250-750 words)

We propose that a coupled Virtual Watershed-ARIES Platform (or any other platform with similar analytical capabilities) should be built at the scale of regions to entire countries to support interdisciplinary analyses on fundamental issues in relation to riverine ecosystems and the services they provide. It should be made widely available (off the shelf) to river science and management communities and contain new integrative tools to identify the best solutions and trade-offs to ensure the conservation of riverine biodiversity and ecosystem services. We believe that this coupled platform could address both the immediate problems facing resource managers and support basic research into cause-effect relationships among river biodiversity, ecosystem functioning and service provisioning. Specifically, an integrated Virtual Watershed-ARIES platform would provide the following advantages:

- Improve the delineation of complete river networks, including headwater and ephemeral channels, comprising their attribution and connections to land surfaces (e.g., building virtual watersheds)
- Provide an off the shelf (readily available) and user-friendly GIS-based analysis and decision support platform for planners and managers, addressing such applied problems as fish habitat mapping, floodplain delineation, riparian area identification, erosion predictions, etc.
- Strengthen the spatial resolution and other aspects of ecosystem service assessment by coupling the Virtual Watershed with ARIES
- Implement research programmes to assess spatially explicit relationships between biodiversity and ecosystem services, via control-impact and gradient studies, and field and mesocosm experiments coupled with existing biomonitoring, remote sensing and Citizen Science data.
- Identify spatially explicit B-ES indicators linked to the wider landscape across multiple scales (Essential Biodiversity Variables sensu GEO BON).
- Improve understanding of how multiple stressors interact spatially in river networks by mapping of pressure-affected zones to identify overlaps (i.e., multiple stressor hotspots) and how pressures propagate through the river network and across scales.
- Underpin the development of new ecosystem-level analytical tools for both stakeholder and academic communities.
• Develop new integrative modelling of drivers and responses across spatial scales to understand how the environment mould B-ES relationships, and ultimately to predict future scenarios of environmental and socioeconomic change.
ACKNOWLEDGEMENTS

This study was partly funded by the Spanish Ministry of Economy and Competitiveness as part of the project RIVERLANDS (BIA2012-33572). José Barquin is supported by a Ramon y Cajal grant (Ref: RYC-2011-08313) of the Ministry of Economy and Competitiveness. Samantha Jane Hughes is SUSTAINSYS funded post-doctoral fellow - North-07-0124-FEDER-0000044, financed by the Regional Operational Programme North (ON.2 - The New North), under the National Strategic Framework (NSRF), through the European Regional Development Fund and PIDDAC via the Foundation for Science and Technology. David Vieites is supported by the ERANET Biodiversa EC21C: European Conservation for the 21st Century. Ferdinando Villa’s ARIES work is supported by ESPA/NERC (grants ASSETS and WISER) and the Spanish Government’s Plan Nacional (grant CAUSE). Clare Gray was funded by a Queen Mary University of London Studentship and the Freshwater Biology Association. This paper is also a contribution to Imperial College’s Grand Challenges in Ecosystems and the Environment initiative. We would also like to thank to a number of colleagues who contributed early to the development of these ideas: Andrea Buffagni, Sylvain Dolédec; Jan Köhler, Thierry Oberdorff, Nikos Skoulikidis and Ryan Sponseller.
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FIGURE LEGENDS

**Figure 1.** Diagram showing components of the coupled Virtual Watershed-ARIES Platform and the dual objectives it can be used to achieve.

**Figure 2.** Diagram showing theoretical linkages between different biophysical ecosystem components (EC) and riverine ecosystem services (OM: Organic Matter; SS: Suspended Solids).

**Figure 3.** The coupling of the DEM with synthetic hydrography contains a numerical data structure that support five types of analytical capabilities (Box 1). Multiple connectivity pathways, include i) river connected, ii) Euclidean distance, iii) slope distance, iv) gravity driven flow paths and v) modified slope distance. These components comprise a virtual watershed (redrawn from the original paper).\(^{18}\)

**Figure 4.** River ecosystem components at different levels of organisation and alternative techniques (Coloured arrows) that could be used to characterise these ecosystem components. Some of these techniques could actually be applied to more than one ecosystem component (White arrows show interactions among ecosystem components; DOM: Dissolved Organic Matter; GPP: Gross Primary Productivity; ER: Ecosystem Respiration).

**Figure 5.** A “network of networks” – the spatial configuration of ecological interaction networks within a river network (redrawn from original paper).\(^{12}\) Local stream food webs for the Ashdown Forest, UK. Each individual stream food web is shown alongside regional and global food webs. Each web (local and regional) contains the same number and positioning of nodes as in the global web: macroinvertebrate taxa present within the depicted web are shown in solid black dots, whilst nodes present in the global web but absent from the depicted web are shown in grey. All streams are part of the River Medway or River Ouse catchments which are separated by the dashed line.
Figure 1.
Figure 3.
Figure 4.
Figure 5