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Article title: HOW LARGE IS A RIVER? CONCEPTUALISING RIVER LANDSCAPE SIGNATURES AND ENVELOPES IN FOUR DIMENSIONS

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Abstract

River research often addresses the influence of anthropogenic and natural processes on the ecological, hydrological and geomorphological dynamics of river systems. However, here we take a river-centred approach and consider how rivers influence their landscapes by developing concepts of river landscape 'signatures' and 'envelopes'. The influence of a river penetrates well beyond its

channel into the atmosphere, across the land surface, and into the subsurface. We define a signature as an emergent property of a set of processes acting on a river landscape, and its envelope as the dynamic penetration of the signature across the landscape. The potential to recognise river signatures and envelopes is driven by unprecedented expansion in data acquisition, processing and modelling technologies. The spatial envelope of any particular signature will have fuzzy and temporally-dynamic edges, may rapidly expand and contract, may differ in its extent from other signatures, and may be highly permeable to many organisms using the river (and broader) landscape. However, an understanding of the approximate dynamic envelope of a signature is crucial to understanding the contribution of rivers at a landscape scale and to informing the sustainable management of these landscapes and their ecosystem services.

Introduction

Recently, Muehlbauer *et al.*¹ posed the question 'How wide is a stream?'. Although this may seem a simple question, river scientists trained in different disciplines might give very different answers. Muehlbauer *et al.*¹ answered it through a meta-analysis of food web data. When interpreted in relation to the theme of 'signatures and envelopes' developed in this paper, they tracked the penetration of a stream 'signature' in the food web across adjacent terrestrial environments to establish the spatial 'envelope' within which this distinctive signature could be recognised. Although in one sense this research reinforces long-held knowledge that the impact of a river extends far beyond its active channel, not least in relation to areas affected by flooding, it also raises fundamental questions about the importance as well as the spatial and temporal penetration of river systems and their services across the Earth's surface.

It is crucial to answer such questions because river landscapes are not only keystone ecosystems of global importance for humans and nature^{2,3} but they are also intensively-settled areas of the Earth's surface because of the many ecosystem services that they offer to human populations. The global network of all rivers and streams, defined as lotic systems with an average annual discharge of more than 1 m³/sec, is 7.56 million km in length and it covers an area of about 508,000 km²⁴. As a result of human pressures, large proportions of the World's rivers and floodplains have become heavily degraded and retain little natural function. For example, 50% of the human population is located on previously-functioning floodplains in Japan⁵ and 90% of Europe's former floodplains no longer function as a result of human occupation and use⁶. This coupling of human populations with landscapes whose services are dependent upon the river's disturbance regime, demonstrates how

essential it is to understand river landscape physical, chemical and biological functioning in order to lay the foundations for more harmonious management.

In this paper we conceptualise the likely spatial influences of river systems on the broader landscape, how these vary through time, and how they may be explored to support more sustainable river management. River landscapes potentially incorporate complex processes and interactions that penetrate the atmosphere, hydrosphere, biosphere and geosphere. In humid settings they are strongly driven by contemporary flood disturbances and biotic productivity gradients, but this may not be the case in more arid settings. Here, we consider how the extent and emergent properties of a river's influence on the broader landscape may be characterised using concepts of river landscape signatures and their envelopes. Following a definition of environmental signatures and their envelopes, we then consider the potential components of a river's signature and related envelopes within the landscape, and then we assess the scientific challenges that must be faced if one or more river signatures and envelopes are to be formulated and translated into tools for river landscape management.

WHAT IS A SIGNATURE?

We define a river landscape signature as an emergent property of a set of processes acting on the river landscape. While it may be a long term objective to define a single integrated signature of a river landscape, at this early stage it is more scientifically tractable to consider signatures that relate to one or more specific aspects of the landscape that can be characterised by a set of summary indices capturing the key processes and properties of a particular spatial and/or temporal pattern. The spatial envelope of any particular signature will have fuzzy and temporally-dynamic edges, it may rapidly expand and contract, may differ in its extent from other signatures, and may be highly permeable to many organisms using the river (and broader) landscape. However, an understanding of the approximate dynamic envelope of a signature is crucial to understanding the contribution of rivers at a landscape scale and to informing the sustainable management of these landscapes and their ecosystem services.

The extraction of signatures from complex spatial and temporal data sets is now being accomplished in many areas of the environmental sciences, providing a sound foundation for considering how this type of approach might be adopted to explore the extent and character of river influences on the broader landscape. Some recent, relevant examples from different environmental science disciplines are assembled in Table 1.

ENVELOPES OF A RIVER'S SIGNATURE ON THE LANDSCAPE

River research has already generated many signatures that provide a starting point for multidisciplinary studies. Perhaps the most long-established is the classification of river types by geomorphologists. Since the 1950s, geomorphologists have identified types of river channel as emergent signatures of the formative processes of flow energy and sediment dynamics⁷, and of the sediments, landforms and physical habitats that comprise the envelopes of their active channels and genetic floodplains⁸. As signatures and envelopes, river channel and floodplain types represent the outcomes of river biophysical processes acting across well-defined areas of the land surface. Furthermore, because river flow intensity, sediment erosion-transfer-deposition, and plant colonisation-growth vary longitudinally, laterally and through time within river corridors, distinct signatures arise as mosaics of intertwined vegetation, sediments and landforms, dominated by particular sets of physical processes within different parts of the river and floodplain⁹. At the same time, linkages between river bedform, planform shape, flow regime and fluxes of organisms, material and energy across the river-riparian ecosystem are intrinsically oscillatory, both in space and time¹⁰⁻¹². Indeed, signatures and envelopes expand and contract with time, with the borders of riverine ecosystems not being where they are generally accepted to be. For example, although most of the aquatic subsidy remains within 1 m of the stream edge, a 10% aquatic signal can still be present at distances up to 350 m away from the stream bank, corresponding to an area encompassing about three quarters of all land in a given catchment¹ (J. Muehlbauer, unpubl. data).

Thus, a river's landscape signature is not limited to envelopes of physical processes and forms at the land surface. As noted by Sponseller *et al.*¹³ (p. 1):

'The distribution and movement of water can influence the state and dynamics of terrestrial and aquatic ecosystems through a diversity of mechanisms. These mechanisms can be organized into three general categories wherein water acts as (1) a resource or habitat for biota, (2) a vector for connectivity and exchange of energy, materials, and organisms, and (3) as an agent of geomorphic change and disturbance'.

We argue that in order to advance scientific understanding of the landscape-scale imprint of rivers, research needs to go further than these three water-related mechanisms. It needs to extend beyond the land surface to explore river signatures and their envelopes within the atmosphere and in the sub-surface, and to extend beyond physical processes to the full array of biological, biogeochemical and related ecological processes that are a product of the river's impact on the landscape.

To fully integrate the behaviour of systems as diverse, complex and dynamic as riverine landscapes, called macrosystems¹⁴, will fundamentally challenge present and future research activities. Macrosystems are hierarchically organized, heterogeneous and interactive, with human activities as key processes that accelerate timescales, shape linkages, and introduce novel system components¹⁴. To study riverine landscapes as macrosystems requires collaborative research networks, demands advanced sensor and remote sensing technologies, and incorporates the challenge of processing immense data sets. Ultimately, this will improve understanding and prediction of rapid environmental change and support environmental policy at relevant scales.

As a starting point, Figure 1 illustrates the main physical river processes that drive the four dimensional imprint of rivers on the landscape (upstream to downstream; across the river, its floodplain and valley; above and below the land surface; through time) and the terminology we use to refer to different parts of the river corridor. Table 2 lists the main river-influenced physical processes; their vertical linkages with the atmosphere, vegetation cover, land surface, alluvial sediments and bedrock; their maximum spatial extent; and examples of other (secondary) processes that are affected by the specific river-influenced physical processes that are listed. Concurrently, there are key biological processes, depending on and interacting with these physical processes, which drive the landscape imprint of rivers.

The Land Surface

At the land surface, river flows erode, transport and deposit sediment particles ranging in size from boulders and cobbles to silts and clays. Coarser sediment particles underpin the landforms of the river channel and floodplain, while finer sediments are retained within the matrix of coarser particles or become stabilised by plants and other organisms. Sediment 'connectivity signatures' and 'functional connectivity styles' have been proposed to capture the timing, magnitude and quality of sediment at the reach scale¹⁵, allowing assessment of reactions to disturbances in sediment connectivity arising from activities such as dam removal or reservoir sediment flushing. Furthermore, fine sediment, a heterogeneous mixture of fine inorganic and organic materials, can have a distinctive biogeochemical signature and plays a fundamental role in the geomorphological, hydrological and ecological functioning of fluvial systems¹⁶, linking physical, chemical and biological processes at different scales and connecting hillslopes, floodplains, riparian zones and the active channel¹⁷.

Flows of water and sediment interact with vegetation to provide much more than distinct surface morphologies. Interaction with vegetation and other organisms that use vegetation as a substratum gives rise to waterborne organic matter dynamics including processing of fine particulate organic matter and inorganic sediments by invertebrates¹⁸ and propagule dispersal¹⁹. Vegetation plays a crucial role in these interactions as a source of organic material, a strong control on the microclimate and soil moisture regime, and an important retention-stabilisation structure for mineral sediment and organic material, including fine sediment, which underpins soil and further vegetation development²⁰. Furthermore, these interactions between flow, sediment, vegetation and transported materials drive the physical (hydraulic and morphological) habitats that are present, the degree to which they turn over and are rejuvenated, and the biogeochemical processes they support, from ecological to evolutionary time scales²¹.

Signatures that capture key properties of these interactions and their spatial-temporal envelopes should reveal the environmental importance of the river at the land surface and the strength of its impact along and across river corridors.

The Subsurface

At geological time scales, mutual interactions among deposition and erosion cycles, driven by longterm river morphodynamics and tectonic and climate-driven processes, create the setting for contemporary geomorphological and ecological river evolution. By acting at the spatial scale of the entire valley to floodplain depth and width, these long-term interactions fundamentally influence present river dynamics, especially for the largest river systems on Earth²². In the shorter term, since river flow dynamics induce sediment dynamics that build the alluvial deposits underlying river channels, floodplains and terraces, these alluvial deposits inevitably possess properties (calibre, stratigraphy, permeability) that reflect the river type with which they are associated as well as the bedrock materials from which the sediments were derived. The properties of the alluvial sediments and related processes such as colmation, in turn affect rates and pathways of water exchanges between the surface and subsurface²³, and because fine sediments are chemically active, sedimentbound nutrients and contaminants affect biogeochemical processes and ecosystem functioning and health. There is considerable potential to derive signatures and envelopes for these subsurface environments that capture key properties of the river's imprint upon them.

The Atmosphere

The most neglected sphere in terms of river landscape influence is the atmosphere. Although climate may have a topographic signature within river catchments²⁴, the impact of rivers on climate has received relatively little attention. Since rivers carve major topographic features (i.e. river catchments, valley networks) into the land surface, there is an inevitable, significant impact of rivers on near-surface atmospheric circulation patterns and local climate properties that are governed by

this large-scale river-controlled topography^{25,26}. At a finer spatial scale, the morphological and vegetation properties of the valley bottom provide complex corridors of roughness features that heavily influence local wind fields²⁷, the microclimate at the ground surface, and above-ground dispersal processes and habitat characteristics. At a broader spatial scale, rivers have been recently recognised as fundamental coupling agents for biogeochemical cycles between the atmosphere, continents and oceans²⁸. From a biological perspective, the airscape above river corridors is a neglected but potentially key area for long distance movement of birds and bats as well as a major habitat for terrestrial invertebrates and the adult stages of aquatic insects²⁹. Preliminary data from the Tagliamento river in NE Italy demonstrates an almost even distribution of insects up to 30 m above the land surface, which was the maximum height investigated (Sukodolova et al. pers. comm.), although living insects may be found kilometres from the land surface. Aerobiology is an important research domain that needs to integrate river landscapes as major drivers of biological and ecological processes in the atmosphere³⁰. Most life history functions of aquatic insects such as emergence, dispersal, mating, and egg deposition are restricted to the short terrestrial period. Because mortality of aquatic insects is disproportionately high during the terrestrial phase, the airscape above the river-floodplain surface is a critical, albeit unexploited, habitat for creating and maintaining aquatic biodiversity⁶.

In order to develop a deeper understanding of the nature, spatial extent, and temporal variability of river influences on the broader landscape, scientists need to define biogeophysical and biogeochemical river signatures within and between the atmosphere, vegetation, land surface and subsurface spheres (Figure 1) and the envelopes within which they operate, including their temporal as well as their spatial distributions and dynamics.

TOOLS FOR INVESTIGATING AND EXTRACTING SIGNATURES

New Methods of Data Acquisition

Given the rapid development of ground, airborne and satellite environmental sensors, the time is right to pursue this research. The potential to extract emergent properties of a river's landscape from high resolution remotely-sensed spatial data sets and detailed time series data is enormous³¹. For example, Figure 2 shows some different river landscape signatures extracted using established analyses of Landsat data for part of the Tagliamento River in NE Italy. Figure 2 visualises the river's signature in relation to land surface roughness (Figure 2A), actively growing (leaf-covered) vegetation (Figure 2B), surface wetness (Figure 2C) and seasonal thermal dynamics (Figure 2D). However, disentangling scientifically-meaningful information from one or more remotely-sensed data sets requires 'connecting the dots' of ground data³² so that they jointly underpin signature extraction. Extracting and linking information from disparate sources requires sophisticated statistical analyses and modelling tools that not only focus on emergent river signatures and their envelopes but also make allowance for sensor and other errors and the spatial and temporal data gaps that are inevitably present. As new monitoring networks are designed, 'existing and novel techniques in sampling, sensing and modelling need to be applied in a co-ordinated fashion at relevant locations to improve process understanding and reveal general outcomes'³³ (p. 239). At the same time, increasingly sophisticated laboratory experiments can allow biophysical process interactions, usually inferred from field observations, to be investigated in a controlled way^{34,35}, generating new hypotheses that can be pursued through data mining, field investigations and mathematical modelling. Finally, unmanned air vehicles, drone swarms, radar, advanced sensors to trace animal movements, and stable isotopes facilitate studying landscape signatures of rivers, as well as disentangling the underlying key hydrological, geomorphological, and ecological drivers.

New Methods of Analysis and Synthesis

To exploit effectively this river landscape 'data revolution', it is necessary (i) to develop innovative methods for the assimilation and synthesis of remotely-sensed and field monitored data with experimental field and laboratory observations; (ii) to devise new statistical and mathematical modelling tools capable of identifying signatures of river landscape processes and their envelopes and of simulating their functioning under different environmental settings; and (iii) to develop management tools that make effective use of the outputs from these multi-disciplinary scientific endeavours.

Many challenges must be faced, including issues of equifinality in signatures, whereby different combinations of processes and process-form interactions deliver similar landscape results³⁶ and the subtle signatures arising from self-organisation processes that are imposed upon the physical template^{37,38}. The diagnosis of river landscape signatures and their dynamic envelopes is an exciting field for future scientific research that can provide a new generation of tools to inform and support river and landscape management.

Conclusion

A hierarchy of signatures and envelopes emanate from the actions of rivers on the Earth's surface. In the long term, erosion and deposition of sediment by the river produces drainage basins, valleys, floodplains and river channels that comprise most of the World's land surface. These extensive surface forms have different topographic signatures and envelopes. They also have a fundamental impact on near-surface atmospheric circulation and hydrological processes, and they are underlain by near-surface sedimentary structures that are frequently a direct product of the actions of the river. This set of physical processes, characteristics and their associated signatures and envelopes support and constrain crucial biogeochemical processes; the dispersal of organic and inorganic matter, species, diseases; and colonisation by plants and animals. As a result, further signatures develop within dynamic envelopes and these feed back into surface, above and below ground physical processes.

Ultimately, we must aim to answer the question 'How large (wide, deep, high, and old) is a river?' in the context of a range of crucial processes and their signatures that underpin the delivery of river landscape ecosystem services and their temporal persistence. A substantive multi-disciplinary effort is required to both advance scientific understanding to address this aim and to use these advances to underpin improved river landscape restoration and management. If realised, this could revolutionise the way we design responses to pressures, allowing us to devise strategies to achieve maximum benefits from river landscapes for both humans and river ecosystem depends upon functions that extend across the entire river landscape - upstream, to the sides, below and above the river - and that vary through time. Furthermore, the delivery of river ecosystem services to humans depends upon functions that extend across the entire river landscape. As a result, key river landscape signatures and their envelopes need to set a context for any management or rehabilitation strategies. To achieve this, informative but simple signatures and envelopes need to be extracted that convey the essence of the underlying complexity and help to support measures that carefully balance the needs of humans and river ecosystems.

Finally, to ensure full recognition of the importance of river landscapes, it is crucial to understand how particular signatures may attract organisms from beyond their envelope. The permeability of envelopes may be particularly high when the broader landscape is affected by extreme conditions of, for example, water availability, temperature, exposure, or when the envelopes contribute to navigation of species across the land surface. This means that river landscapes, their signatures and envelopes, need to be recognised as major contributors to sustaining landscape functions at the broadest terrestrial scale.

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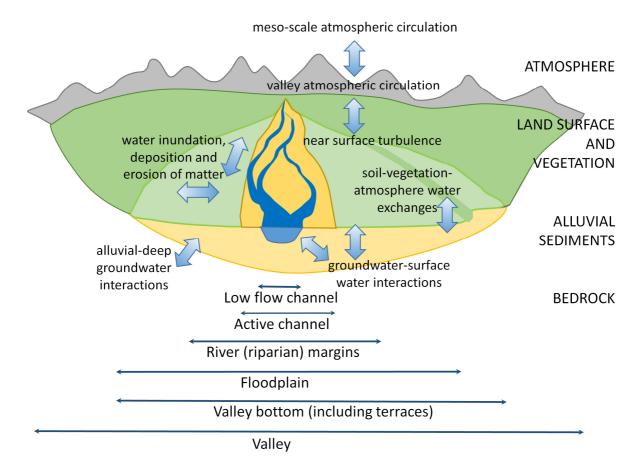


Figure 1: The main physical river processes that drive the multi-dimensional imprint of rivers on the landscape and the terminology used in the text to refer to different parts of the river corridor.

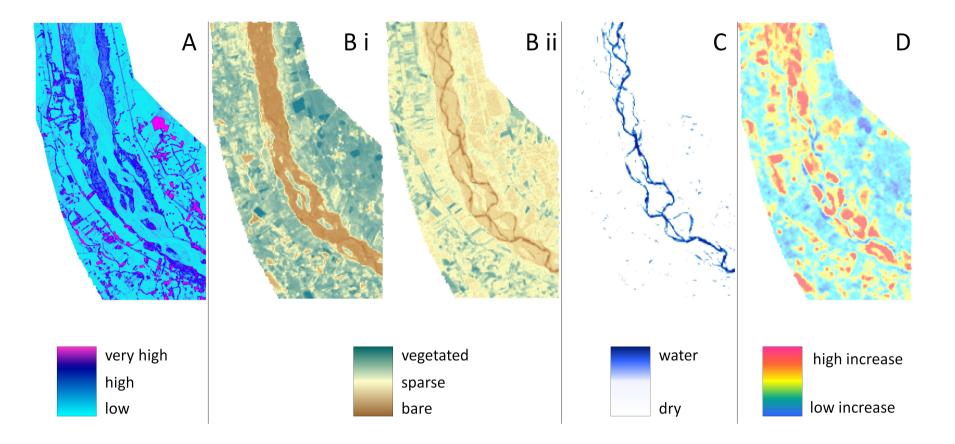


Figure 2: Varying river corridor signatures along a reach of the Tagliamento River, Italy in 2000-2001.

- A: surface roughness (standard deviation of vegetation canopy height from airborne lidar data (January 2001).
- B: surface 'greenness' (normalised difference vegetation index, NDVI from Landsat7 data: Bi August 2001, Bii December 2000.
- C: surface 'wetness' (modified normalised difference water index, MNDWI from Landsat7 data, December 2000).
- D. seasonal increase in surface temperature between winter and summer (difference in the Landsat7 thermal band: change between December
- 2000 and August 2001).

Table 1: Some example publications from different science areas that are concerned with environmental signatures. The table summarises the information analysed to extract each signature and provides reference to the source article (the table is arranged by year of publication and then by alphabetical order of first author)

Science Area(s)	Signature	Information Analysed	Reference number and publication year
Biogeomorphology	Vegetation zonation patterns in tidal salt- marshes are a signature of biogeomorphic feedbacks	Two dimensional biogeomorphic modelling of mutual interactions among tides, sediment transport, morphology and vegetation distributions in salt-marshes to generate vegetation zonation patterns that are compared with those observed in nature	39, 2015
Remote Sensing	Radar signatures of surface roughness, land cover and soil wetness.	Backscattering observations from different sensors and bands	40, 2015
Geomorphology	Morphological signatures of melt- driven hydrology in cold desert environments	Diagnostic landforms of the magnitude and persistence of flow response of cold deserts are identified from information on land surface form, water sources, deposits, erosion rate and discharge behaviour	41, 2015
Biogeomorphology	Landforms as signatures of biotic influences on geomorphology	Considers four criteria that indicate that landforms are extended, composite phenotypes of biota	42, 2015
Biogeochemistry	Signature of permafrost thaw	DOC radiocarbon age, biolability, and composition in small streams	43, 2015
Geomorphology, Climatology	Landslide signature of a major typhoon	Extraction of topographic properties before and after the typhoon to assess landslide topographic change and link this to the slope-area characteristics of catchments	24, 2015
Hydrology, Biogeochemistry, Remote Sensing	Signature of human impact on a wetland landscape	Lidar data and soil maps analysed to 44, investigate changes in size distribution and spatial organisation of wetlands associated with wetland loss and restoration activities	
Geomorphology	Signature of continental drainage capture	Lithology, indices of long profile concavity, valley floor width to height ratio, stream- length gradient	45, 2014
Geomorphology	Landscape topographic	Multifractal analysis of Digital Elevation	46, 2014

	signature	Model data	
Hydrology	Signature of streamflow variability	Seasonal water balance behaviour, hydroclimatic indices of aridity, precipitation timing, snowiness, soil and vegetation classes	47, 2014
Biogeochemistry	Signatures of freshwater carbon pools	Carbon stable isotopes	48, 2014
Biology	Signature of the biological stream width based on aquatic subsidies to terrestrial food webs	Stream to land food web and surrogate subsidy data	1, 2014
Genetics	Genetic diversity signature of past climates and geological history	Fish genetic data across the North American Great Plains	49, 2014
Geology	Signature of range- divide migration and breaching	Low-temperature apatite cooling ages and elevation profiles	50, 2014
Geomorphology	Topographic signatures of geomorphic processes	Airborne and terrestrial lidar data	51, 2014
Geomorphology	Morphodynamic signatures of braiding mechanisms	Volumetric changes in sediment storage extracted from multi-temporal topographic surveys	52, 2013
Geomorphology	Fluvial signature extraction based on channel width, sinuosity and slope	High resolution imagery available in Google Earth and Bing Maps	53, 2013
Genetics	Signature of landscape- scale range expansion of the white-footed mouse	Skull morphological and genetic information	54, 2013
Biology, Geomorphology	Geomorphological signature of ecosystem engineering species	Review and theoretical consideration of the factors that affect the likelihood of a geomorphic signature arising from the activities of ecosystem engineer species	55, 2012
Geomorphology	Signature of an optimal channel network	Assessment of whether any 'optimality criterion' results in the development of the widely-recognised tree-like network with concave longitudinal channel profiles	56, 2012

Geomorphology	Topographic signature of Quaternary tectonic uplift	Analyses of slope and river channel morphometric indices	57, 2012
Biology	Signature of natural geographic barriers on populations of an economically important freshwater fish: the Striped Snakehead	Genetic data reveals signatures of the history of river connectivity and anthropogenic activities.	58, 2012
Geomorphology	Topographic signature of river bed morphology	Airborne lidar and photographs, ground observations of riparian woodland canopy height and structure	59, 2011
Geomorphology, Sedimentology	Signatures of past damming and drainage of large pro-glacial lakes	Sedimentological and morphological data from contemorary river systems	60, 2011
Ecology	Signatures of tree range expansion and erosion	Inventory of species abundance in >100,000 plots across the USA	61, 2010
Climatology, Geomorphology, Remote Sensing	Climatic signature of incised meanders	Morphology and planform data extracted from SRTM DEM, geological map data, rainfall data from climatological stations	62, 2010
Remote Sensing	Thermal signatures of river-floodplain habitats	Multi-temporal thermal-infrared imagery	63, 2010
Ecology, Remote Sensing	Signatures of vegetational functional diversity	Classification of spectral information from satellite (Quickbird) data	64, 2008
Hydraulics	Hydraulic habitat signature	Signatures extracted from grids interpolated between field measurements of water depth and average flow velocity within river channels	65, 2007
Geomorphology	Topographic signatures of physical process domains	5 Digital elevation models, digitised river channel networks, field mapping and measurement of morphological features	
Geomorphology	Is there a unique signature of life on Earth?	Reviews published sources regarding the impact of biota on the Earth's surface processes and landforms and considers how the topographic signature of life at various spatial scales might be identified	67, 2006

Ecology	Signature of spatial structure of successional grasslands as a result of environmental heterogeneity, intra- and inter-specific competition, and localised dispersal	Field observations of successional grassland in a series of large-scale experiments compared with predictions from a spatially-explicit model of plant competition in heterogeneous landscapes	68, 2005
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Table 2: The main river-influenced physical processes; their vertical linkages with the atmosphere, vegetation cover, land surface, alluvial sediments and bedrock; their maximum spatial extent; and examples of other (secondary) processes that are affected by the main river-influenced physical processes.

River-Influenced Physical Processes	Vertical Locations of River Influence	Maximum Spatial Extent of River Influence	Examples of Other (Secondary) Processes Affected by River Influence
Atmospheric circulation patterns induced by river valley morphology	Atmospere-Land Surface	Valley	Wind speed and circulation patterns. Precipitation regime. Air temperature regime. Aeolian dispersal of fine mineral sediment particles, organic particles, seeds, insects
Near surface turbulence and microclimate induced by valley bottom morphology, surface materials and vegetation cover.	Atmosphere- Vegetation-Land Surface	Valley bottom	Mobilisation and trapping of fine mineral sediment particles, organic particles, seeds. Land surface temperature regime. Atmospheric and microclimate refugia for organisms.
Flood and flow pulses	Vegetation-Land surface-Alluvial Sediments	Floodplain	Magnitude, duration and frequency of inundation depth, flow velocity, sediment erosion-mobilisation-transport-deposition. Physical habitat creation and turnover. Spatially dynamic refugia for mobile organisms. Soil moisture and alluvial aquifer recharge. Production, dispersal, retention of organic material including plant and animal propagules. Nutrient spiralling.
Intermediate and low flows	Alluvial sediments	Floodplain, particularly river margins	Moisture supply to support terrestrial, riparian and hyphoreic organism growth and life cycle stages, biogeochemical processes of organic matter and nutrient processing, soil development.
Flow regime	Land surface- Alluvial sediments(- Bedrock)	Active river channel, particularly low flow channel	Hydraulic and hyphoreic conditions to support organism growth and life cycle stages