















Riverscape approaches in practice: perspectives and applications

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ABSTRACT

Landscape perspectives in riverine ecology have been undertaken increasingly in the last 30 years, leading aquatic ecologists to develop a diverse set of approaches for conceptualizing, mapping and understanding ‘riverscapes’. Spatiotemporally explicit perspectives of rivers and their biota nested within the socio-ecological landscape now provide guiding principles and approaches in inland fisheries and watershed management. During the last two decades, scientific literature on riverscapes has increased rapidly, indicating that the term and associated approaches are serving an important purpose in freshwater science and management. We trace the origins and theoretical foundations of riverscape perspectives and approaches and examine trends in the published literature to assess the state of the science and demonstrate how they are being applied to address recent challenges in the management of riverine ecosystems. We focus on approaches for studying and visualizing rivers and streams with remote sensing, modelling and sampling designs that enable pattern detection as seen from above (e.g. river channel, floodplain, and riparian areas) but also into the water itself (e.g. aquatic organisms and the aqueous environment). Key concepts from landscape ecology that are central to riverscape approaches are heterogeneity, scale (resolution, extent and scope) and connectivity (structural and functional), which underpin spatial and temporal aspects of study design, data collection and analysis. Mapping of physical and biological characteristics of rivers and floodplains with high-resolution, spatially intensive techniques improves understanding of the causes and ecological consequences of spatial patterns at multiple scales. This information is crucial for managing river ecosystems, especially for the successful implementation of conservation, restoration and monitoring programs. Recent advances in remote sensing, field-sampling approaches and geospatial technology are making it increasingly feasible to collect high-resolution data over larger scales in space and time. We highlight challenges and opportunities and discuss

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future avenues of research with emerging tools that can potentially help to overcome obstacles to collecting, analysing and displaying these data. This synthesis is intended to help researchers and resource managers understand and apply these concepts and approaches to address real-world problems in freshwater management.

Key words: rivers, streams, landscape ecology, heterogeneity, scale, connectivity, spatial, temporal, patterns, management

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“Advances in our ability to map riverscapes...have transformed the ways in which rivers can be read and interpreted. These techniques have matured and revolutionized what is possible to resolve and quantify” (Wheaton *et al.*, 2017, p. 22); “we can now measure variability across multiple scales ranging from metric to kilometric and, thus, take the riverscape concept from the realm of theory and into the realm of practice and reality”. (Carbonneau *et al.*, 2012, p. 75)

I INTRODUCTION

Pressures of human population growth and global change have generated a critical need to understand river systems and their response to land and water management over a broad range of scales (Vörösmarty *et al.*, 2010). Because the effects of changing river conditions on freshwater fauna are highly variable across landscapes, it is increasingly important to adopt spatially explicit approaches in freshwater management (Sabo, 2014). River management frameworks that aim to assess and restore the condition of river systems now

consider rivers and their biota as ‘riverscapes’ nested within a socio-ecological landscape (Peipoch *et al.*, 2015; Rieman *et al.*, 2015; Voulvoulis, Arpon & Giakoumis, 2017; Dunham *et al.*, 2018). This perspective is widely accepted as a guiding principle in fisheries and watershed management (Hand *et al.*, 2018), but views on what actually constitutes a ‘riverscape’ approach vary considerably among and within disciplines. The idea of riverscapes is not new (Aldrich, 1966; Leopold & O’Brien Marchand, 1968) but gained momentum in freshwater science and management at the end of the 20th century after principles of landscape ecology had been incorporated into riverine science [see Wang *et al.* (2014) for an historical account].

Nearly two decades after the proliferation of riverscape approaches at the turn of the 21st century, it is time to evaluate how they have been operationalized, particularly in the sense proposed by Fausch *et al.* (2002) as a way to bridge the gap between research and management. For example, how are scientists and managers applying these approaches and at what spatial scales? In this review, we provide perspectives on questions about riverscape approaches in practice:

what are they and how are they being used to address real-world challenges faced by fisheries and watershed managers? What are the costs and benefits of these approaches? Is it logistically feasible for managers to collect and analyse the vast amount of data needed for such a “continuous view...of the entire spatially heterogeneous scene of the river environment, the *riverscape*, unfolding through time” (*sensu* Fausch *et al.*, 2002, p. 483)? Specifically, we (i) trace the origins of the term ‘riverscape’ and trends in the use of riverscape approaches, (ii) explain key concepts and approaches, (iii) provide examples of applications, (iv) highlight future directions and new frontiers, and (v) discuss ways to envision and communicate results.

II ORIGINS AND TRENDS

The word ‘riverscape’ evokes different images for different people because it involves human perception of a visual scene from a specific viewpoint (Meinig, 1979). Like ‘landscape’ and other words built on the combining form ‘-scape’ (e.g. seascape, cityscape, moonscape, soundscape), ‘riverscape’ was originally used in an artistic context as “A picturesque view or prospect of a river. Also: the environment of a river” (OED, 2018a). Riverscapes were mentioned in this context in the 19th century, but over the years, the word has been increasingly used across varied contexts from art to science as the morpheme ‘scape’ has become more common to add to words to denote a view, picture or ‘landscape’ of a given phenomenon (Aldrich, 1966; OED, 2018b). Moreover, in the last several decades, recognition of the gestalt of the watershed in terms of human influence, physical and biological processes, as well as aesthetics, has broadened the usage of ‘riverscape’ (Haslam, 2008; Junker & Buchecker, 2008; Stanford, Alexander & Whited, 2017). In freshwater ecology, recent interest in riverscapes, stygoscapescapes (Ward, Malard & Tockner, 2002), soundscapes (Pijanowski *et al.*, 2011; Kacem *et al.*, 2020), behaviourscapes (White, Giannico & Li, 2014), thermalscapes (Isaak *et al.*, 2015), isoscapes (Brennan *et al.*, 2016) and other ‘scapes’ has been influenced strongly by the key concepts in landscape ecology of heterogeneity, scale, pattern, process, connectivity and hierarchy (Wu, 2013), all of which are linked to a view, picture or landscape in some kind of visual, auditory or other form of space (*sensu* OED, 2018b).

Riverscape approaches developed based on a foundation of perspectives that conceptualized how streams and their biota are linked to landscapes longitudinally, laterally, vertically and temporally (e.g. Hynes, 1975; Vannote *et al.*, 1980; Junk, Bayley & Sparks, 1989; Ward, 1989; Schlosser, 1991; Stanford & Ward, 1993). However, the capacity actually to collect and analyse data to visualize the physical and biological properties of rivers and floodplains at a high spatial resolution over many kilometres was only made possible by the increasing availability of computerized mapping and remote sensing (RS) technology (Torgersen *et al.*, 1999; Malard, Tockner & Ward, 2000; Poole, 2002). The term ‘riverscape’ has been employed in a variety of ways: (i) a contraction of ‘river’ and

‘landscape’ (*sensu* Leopold & O’Brien Marchand, 1968; OED, 2018a), (ii) an abbreviation of ‘riverine landscape’ (Ward, 1998; Wiens, 2002; Stanford *et al.*, 2017), and (iii) a ‘scene of the river environment’ and floodplain above and below the water surface (Fausch *et al.*, 2002; Carbonneau *et al.*, 2012; Wheaton *et al.*, 2017). Some perspectives emphasized the effects of the entire catchment on streams (*sensu* Allan, 2004; Stanford *et al.*, 2017), whereas others (e.g. Fausch *et al.*, 2002; Wiens, 2002; Erős & Lowe, 2019) addressed pattern–process relationships more explicitly and incorporated the central tenets of landscape ecology, including hierarchy and context dependency (Frissell *et al.*, 1986), patch dynamics and disturbance (Pringle *et al.*, 1988), heterogeneity and scale (Cooper *et al.*, 1997) and connectivity and movement (Schlosser, 1995). These different perspectives of the term ‘riverscape’ are not mutually exclusive, nor are they restricted to broad spatial extents of tens to hundreds of kilometres. For example, the principles and approaches of landscape ecology also can be applied over much smaller spatial extents such as a streambed landscape, or ‘benthiscapes’, for macroinvertebrates at scales of meters (Palmer *et al.*, 2000; Monroe, Poff & Thorp, 2005; Olden, 2007).

References to riverscapes in the scientific literature have increased rapidly over the last two decades, and nuances have developed in interpretations and perspectives. Citation rates of articles with the term ‘riverscape’ or ‘riverscapes’ increased from 19 citations/year in 2002 to almost 1400 citations/year by the end of 2019 (see bibliometric analysis in online Supporting Information, Appendices S1 and S2, Figs S1 and S2; WOS, 2021). The term is often used in a broad-scale conceptual sense when referring to “an expansive view of a stream or river and its catchment, including natural and cultural attributes and interactions”, which considers longitudinal, lateral and vertical (i.e. subsurface pathways) dimensions and how they change over time (Stanford *et al.*, 2017, p. 3). The term is also used in a complementary but more applied context that emphasizes the importance of high-resolution data collected over many kilometres for mapping and visualizing actual abiotic and biotic spatial patterns in the river and riparian or floodplain environment (*sensu* Fausch *et al.*, 2002; Carbonneau *et al.*, 2012). Fausch *et al.* (2002) applied this approach primarily in a spatial context for understanding and managing stream fishes, whereas Carbonneau *et al.* (2012) focused on using RS to map fluvial characteristics (e.g. depth, gradient, substrate particle size) in rivers and floodplains. Both papers emphasized the importance of moving beyond traditional, stratified-random sampling of discrete reaches to collecting more spatially continuous observational data that represent the heterogeneity of physical and biological properties better in river systems.

Riverscape approaches that involve spatially intensive data and the analysis of multiscale patterns (*sensu* Fausch *et al.*, 2002; Carbonneau *et al.*, 2012) developed independently but in parallel with the recently formalized science of ‘seascape ecology’, which explicitly draws from the principles of terrestrial landscape ecology to understand causes and

ecological consequences of spatial patterning in marine environments (Pittman, 2017). Stream ecologists have long recognized the potential value of adapting the methods and mapping technologies employed by oceanographers to provide a more complete picture of river environments (Hynes, 1989), but now there are even more opportunities for cross-fertilization with seascape ecology. Here, we illustrate how such approaches can be used to operationalize concepts of heterogeneity, scale and connectivity in rivers. Our discussion and examples are largely oriented to fish and their habitat, in part because there are many applications in this area, but also because fish are often of direct management concern. However, there are notable examples where riverscape approaches are contributing to the understanding of ecological communities, linked water–land food webs and ecosystem processes, and we have highlighted these studies to show this important area of application.

III CONCEPTS AND APPROACHES

Rivers and streams are directional, dendritic, patchy and hierarchically organized systems (Poole, 2002). This heterogeneity is expressed longitudinally, laterally, vertically and temporally and constitutes the mosaic of habitats that may be connected or disconnected depending on the structural and functional attributes of the river ecosystem (Ward, 1989; Ward *et al.*, 2002). Hydrological connectivity is closely associated with heterogeneity because the direction and quantity of water flow influences the shape, size and location of patches, gradients and barriers that affect the exchange of nutrients and energy and

the movement of aquatic organisms in river networks (Fullerton *et al.*, 2010; Erős & Lowe, 2019). The degree to which a river system is perceived as heterogeneous, homogeneous, connected or disconnected is determined by the scale of observation, which underpins study design, data collection and analysis.

(1) Scale: extent, resolution and scope

Defining the scale(s) of interest in terms of extent and resolution is a critical first step in detecting spatiotemporal patterns and investigating their reciprocal effects on ecological processes (Wiens, 1989). Extent refers to the area within which data are collected and establishes the context and range of ecological gradients over which finer-scale measurements are made. Resolution refers to the smallest feature discernible in observations or measurements. Examples of spatial resolution and extent in rivers are illustrated in Fig. 1, but the principles of extent and resolution apply similarly in time. Temporal extent is the duration or time of data collection (e.g. day *versus* night, seasons, drought *versus* flood period), and temporal resolution is the interval between measurements.

Pattern detection in space or time is a function of both extent and resolution (Wiens, 1989). Thus, the representation of heterogeneity (biological, physical, chemical) across multiple spatial scales in rivers generally requires high-resolution data collected over a relatively large extent (Fig. 1B). This ability to detect patterns at multiple scales is called the ‘scope’, which is the ratio of extent to resolution and can be used to compare sampling designs (Schneider, 1994). A strength of high-scope approaches is that they may

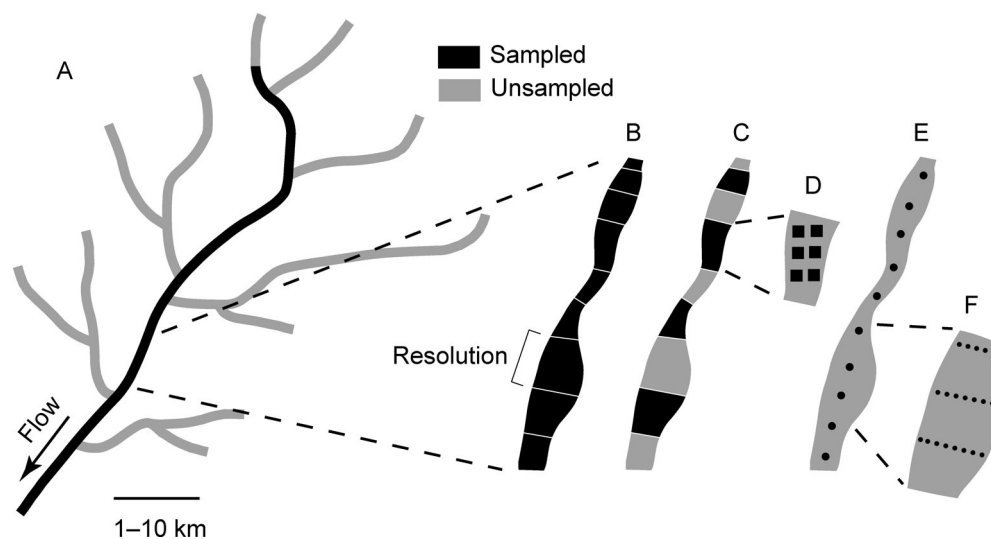


Fig 1. Spatial extent, resolution and intensity of mapping and sampling approaches in rivers and streams. The black (sampled) sections of the stream network indicate the spatial extent (A) within which sampling is conducted. Area-based approaches include (B) contiguous survey at the resolution of channel units (e.g. pools and riffles), (C) subsampling of channel units, (D) nested sampling, (E) spatially intensive, systematic point sampling (e.g. water temperature or point abundance electrofishing) and (F) transects. Surveys and sampling of these types are conducted throughout the entire spatial extent of interest (e.g. the section shown in black in A) in an upstream direction in wadable streams, or in a downstream direction in floatable streams.

increase the likelihood of quantifying and evaluating the relationships between stream organisms and their environment in a manner that better reflects their actual modes of perceiving and responding to environmental heterogeneity, rather than assuming that these organisms detect and respond to such heterogeneity as defined at scales that match those aligned with humans. High-scope data derived from a complete census or spatially continuous data collection is not often achievable or cost effective. However, alternative methods can be developed that are still higher in scope than traditional methods of measurement. For example, intensive fractional or nested stratified designs incorporating subsampling, point sampling and transects can be used (Fig. 1C–F). Non-contiguous sampling and nested designs may have a high resolution and a broad spatial extent, but their capacity to quantify spatial heterogeneity depends on the spacing of samples over a given distance or area (i.e. sampling density or intensity). Fausch *et al.* (2002) emphasized the importance of high-scope data collected over ‘intermediate’ extents of 10^3 – 10^5 m and 1–10 years, at which many processes critical to fish populations and communities occur. However, such approaches also can be applied over smaller extents and time durations (e.g. for smaller organisms) if the resolution is sufficiently high to quantify patterns (Palmer *et al.*, 2000).

Rivers and stream networks present scaling challenges that are unique to their linear and network structures. Two- (2D) and three-dimensional (3D) representations (e.g. aerial images and maps) of rivers and floodplains are desirable because they can depict lateral, longitudinal and vertical heterogeneity. However, to scale up and view spatial patterns over tens of kilometres and across entire stream networks it may be necessary to convert higher-dimensional data to points, line segments or 1D profiles, so they can be displayed cartographically or plotted graphically (Fonstad & Marcus, 2010; Duffin *et al.*, 2021). In reviewing riverscape approaches, we focus on longitudinal patterns (e.g. points, lines and graphical profiles) because this level of dimensionality reduction is generally required to display high-scope data collected over broad spatial scales.

(2) Hydrological and functional connectivity

Connectivity is a central concept in river ecology because it determines how energy and organisms move throughout riverine ecosystems and between land and water (Hynes, 1975; Stanford & Ward, 1993). The characterization of heterogeneity enables the identification of patches (i.e. a spatial unit of habitat determined by a given organism or process of interest) and their spatial arrangement, providing a template for analysis of their use by organisms that can only exist in the water, such as stream fishes (Pringle *et al.*, 1988; Fullerton *et al.*, 2010). This information is critical to quantify the degree of resistance, permeability or fragmentation among patches needed to address conservation and management issues (Schlosser, 1995; Fagan & Calabrese, 2006; Le Pichon *et al.*, 2006). The concepts of hydrological and functional connectivity for fishes (Fig. 2) can be applied explicitly with a riverscape approach (Roy & Le Pichon, 2017). Hydrological

connectivity is determined by physical structure (e.g. shape, size and distribution of habitat patches and barriers) and water flow, whereas functional connectivity takes into account the capacity of aquatic organisms to move among patches depending on their swimming capacities, dispersal behaviour, energy costs, mortality risks and hydrological connectivity.

Flow regime, climatic drivers and life cycles govern the spatiotemporal dynamics of connectivity in rivers. For example, at low flow, barriers and the relative size and arrangement of unfavourable habitats (Fig. 2A) impede movement of fish based on their dispersal abilities, behaviour and environmental tolerances (Fig. 2B). Depending on flow, the shifting mosaic of habitats (Stanford, Lorang & Hauer, 2005) may favour the movement of individuals of one species at one time and place, and a different species at another (Fig. 2B). Upstream or downstream movements may also depend on discharge thresholds or temporal fluctuations in flow. To quantify such changes in structural and functional connectivity, measurements of the physical environment and associated biological responses (e.g. movement or distribution of fishes) must be made at scales consistent with the magnitude of spatial and temporal variations (White *et al.*, 2014).

Connectivity needs to be thought of very differently for aquatic insects. Not only do aquatic insects perceive and respond to environmental heterogeneity very differently than large-bodied fishes (e.g. Monroe *et al.*, 2005; Olden, 2007; Tonkin *et al.*, 2018), their life cycle (which for many includes a winged, air-breathing adult phase) means that a feature that might be impermeable to fishes, is not necessarily so for an insect. Moreover, there are many aquatic organisms – including aquatic invertebrates, aquatic plants and micro-organisms – that do not ‘swim’ like fishes.

(3) Study design, data acquisition and analysis

Spatially intensive data collection over relatively large spatial extents is key to revealing new patterns and elucidating complex relationships in river ecosystems (Tetzlaff *et al.*, 2007; Carbonneau *et al.*, 2012). Putting this approach into practice can be accomplished with a framework of steps that flow from study design through data collection and analysis. Implementation is guided and informed by the overarching concepts of scale and connectivity. In particular, the scope (i.e. the ratio of the extent to the resolution) of a study is considered explicitly during study design, data acquisition and data analysis (Fig. 3). In the design phase, trade-offs are weighed among three factors: (i) addressing clear and well-defined scientific objectives and management questions, (ii) considering the biological and physicochemical context, and (iii) identifying logistical constraints. These three factors in the design triangle (Step 1 in Fig. 3) inform decisions about the type(s) of data acquisition (Step 2 in Fig. 3) that will be targeted for study and thus establish analytical and field project workloads. The design triangle therefore entails describing the types of data that are needed and assessing whether such data exist and are of sufficient spatiotemporal scope. The

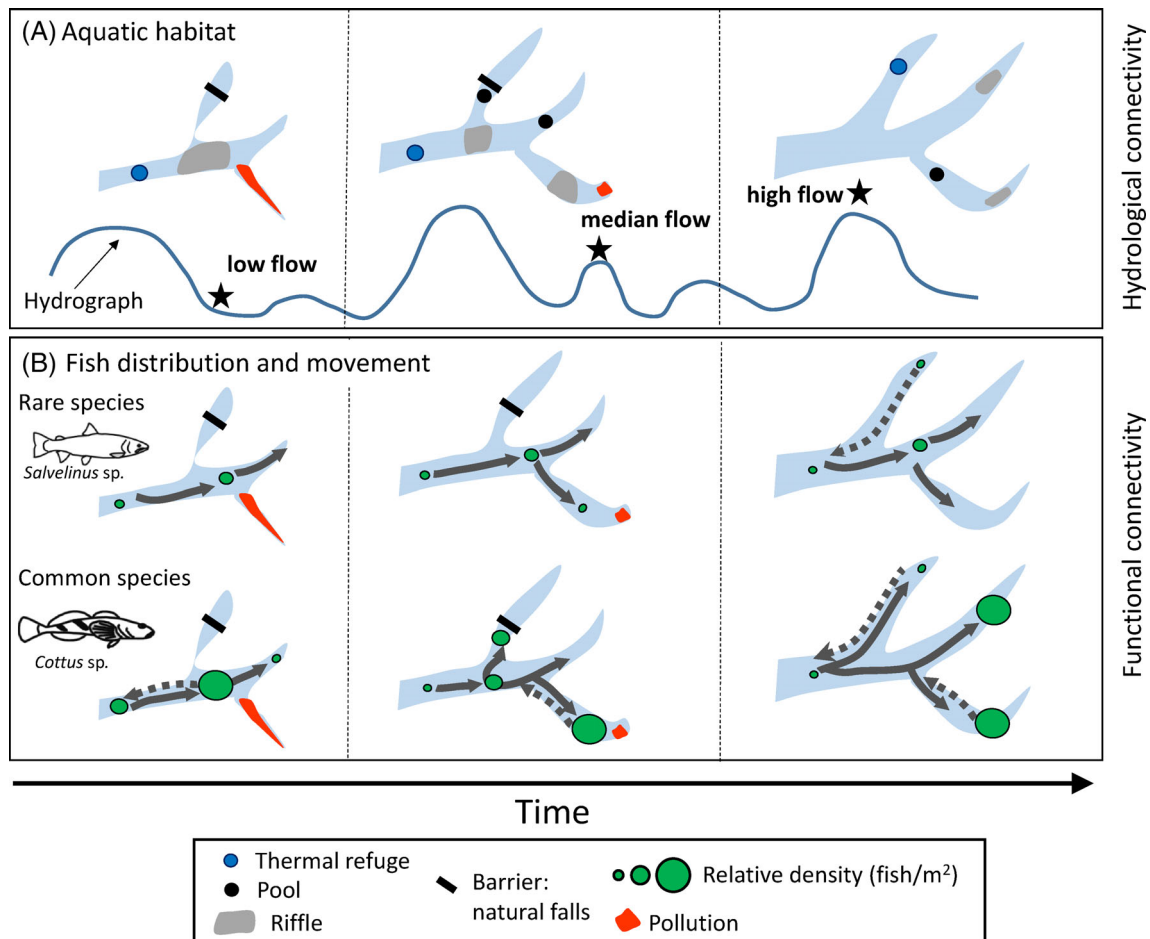


Fig 2. Hydrological and functional connectivity for fish in a river network over time. Changes in flow influence (A) hydrological connectivity and (B) the ability of an organism (e.g. fish) to move throughout the river to use preferred habitat and avoid unfavourable habitat; dark grey arrows on the blue stream channel indicate the direction (dotted line: downstream; solid line: upstream) and spatial extent of movement. Star symbols on the hydrograph indicate flows of different magnitudes. Hydrological connectivity and functional connectivity increase at higher flows, e.g. passive drift of fish larvae and macroinvertebrates downstream or active migration of fish upstream. The spatial distribution of barriers, pollution sources, thermal refuges and habitat (e.g. pools and riffles) change over time with hydrological conditions and control the spatial distribution of organisms.

analysis phase (Step 3 in Fig. 3) is important because large, spatially referenced data sets and sophisticated software for visualization and statistical analysis pose unique challenges for practitioners who may need to gain skills or hire staff with appropriate expertise. As with the two preceding phases (design and data), ecological interpretation in the analysis phase also requires explicit consideration of the overarching concepts of scale and connectivity in order to understand patterns and processes in a management context.

(a) Logistics

Riverscape approaches present unique logistical and technical challenges compared to conventional studies. Depending on the geographical context and the spatiotemporal scope of the study, the expense of conducting high-scope surveys can

be high because data acquisition requires time-intensive field logistics and labour, travel and the use of specialist equipment (e.g. RS, *in-situ* sensors, aircraft). The study design must be placed within the context of timing, accessibility and safety. It is not uncommon to have multiple field crews simultaneously collecting data, potentially requiring a large number of trained personnel. When sampling long and continuous river stretches, finding properly spaced access points along the river and ensuring that crews can safely complete their work during daylight can be challenging. Logistical planning is key and typically focuses on safety, assigning daily sampling schedules to align workload with starting and ending sites, and if necessary, obtaining legal permission to access multiple study sites. These logistical constraints mean that technical and financial trade-offs are generally necessary. Such trade-offs may include changes to resolution or scope or may involve supplementing empirical data with

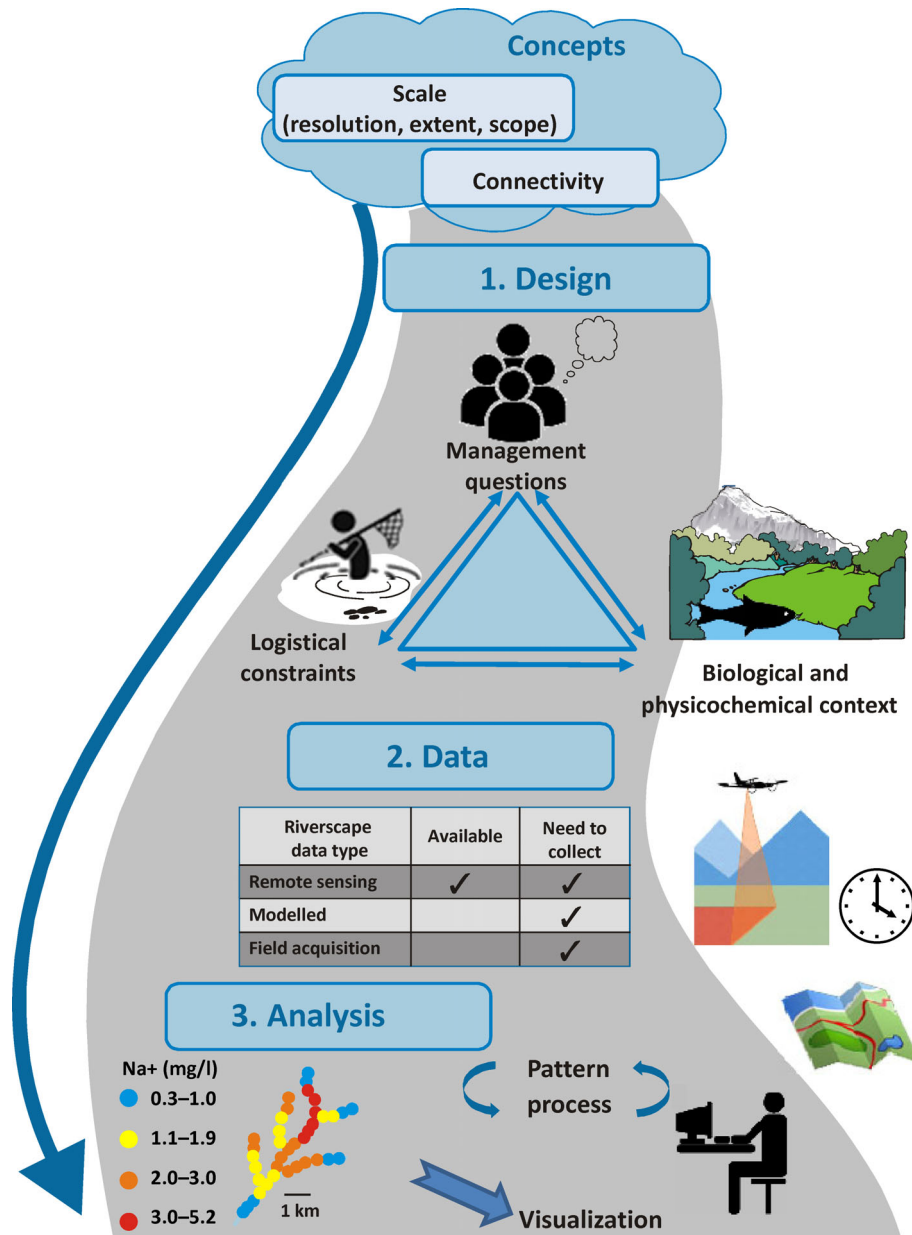


Fig 3. Framework and flow of steps for applying a riverscape approach in practice. The overarching concepts of scale (resolution and extent) and connectivity (structural and functional) are guiding principles in the design, data acquisition and analysis phases. In the design phase (Step 1), trade-offs among management questions, logistical constraints and biological and physicochemical context are illustrated with bidirectional arrows between vertices of the triangle.

modelled data where it would be otherwise too difficult or expensive to collect.

(b) Remote sensing

RS methods entail the use of airborne sensors to record continuous or quasi-continuous river habitat data in one, two or three dimensions (longitudinally, laterally, vertically). To date, RS has been used to map most physical habitat variables commonly required by river scientists and managers, including substrate

size (Carbonneau, Bergeron & Lane, 2005; Scholl *et al.*, 2021), biotope (Woodget *et al.*, 2016), suspended sediment and water quality (Pavelsky & Smith, 2009), channel bathymetry (Dietrich, 2017), water temperature (Torgersen *et al.*, 2001), submerged aquatic vegetation (Flynn & Chapra, 2014), woody debris (MacVicar *et al.*, 2009), riparian buffer characteristics (Loicq *et al.*, 2018) and river-ice cover (Emond *et al.*, 2011; O’Sullivan, Linnansaari & Curry, 2019). Although flow state variables (e.g. discharge, velocity) have traditionally been more difficult to measure using RS approaches, recent advances

indicate that the retrieval of these metrics is possible (Durand *et al.*, 2016; Detert, Johnson & Weitbrecht, 2017). As with all RS approaches, data quality is a key consideration when working with these derived (as opposed to field-measured) variables, and remote observations of river habitat variables must be accompanied by a thorough understanding of the limitations and accuracy of the methodology used, often employing validation procedures with field calibration. However, the reduction in accuracy that RS approaches often entail is generally considered an acceptable trade-off given the improvement in spatial or temporal scope.

(c) Modelling

Increases in computing power and improved quantitative tools, coupled with process understanding, have led to development of modelling approaches capable of simulating river habitats in remote or data-poor regions. Models are particularly useful for extending observations into the temporal domain, where RS and field surveys are less feasible or more expensive. Indeed, hydrological models are increasingly able to generate detailed simulations of surface or subsurface flow over entire river basins at resolutions of 10^2 m or finer (Melsen *et al.*, 2016) and at sub-hourly time steps. Similarly, physically based hydraulic and hydrodynamic models can generate spatially explicit maps of water depth, flow velocity and related 'second-order' variables (e.g. shear stress, stream power) at metric or decametric resolutions across whole-river extents (Altenau *et al.*, 2017; Fryirs *et al.*, 2019) and multiple dimensions. These advances in process-based modelling also extend to water quality parameters such as temperature (Dugdale, Hannah & Malcolm, 2017) and water chemistry (Nguyen *et al.*, 2019). Broad-scale, high-resolution interpolated data from spatial stream network (SSN) models are often publicly available for downloading and provide valuable perspectives on spatial variability in stream temperature and fish density (Isaak *et al.*, 2017a,b). However, as with all numerical modelling approaches, care must be taken to acknowledge that models are simplified versions of reality and thus are susceptible to bias and inaccuracy that require validation. For example, predictions from models that involve interpolation or extrapolation have higher standard errors where field-based data are lacking.

(d) In-situ data collection

Field data collection is necessary when it is not possible or desired to measure the variable of interest with RS or modelling. However, high-scope data from RS and modelling may be used to complement, supplement or guide *in-situ* surveys and sampling. Physical variables at the mesohabitat scale can be mapped in the field by foot or boat (Dauwalter, Fisher & Belt, 2006; Le Pichon *et al.*, 2006), whereas water-quality data can be recorded with data loggers or high-resolution water samplers towed in a streamwise direction (Vaccaro & Maloy, 2006). Such approaches are relatively field-intensive and generally better suited for small- and medium-sized rivers, but they allow

detection of physical or biogeochemical patterns (Torgersen, Gresswell & Bateman, 2004; Gresswell *et al.*, 2006; McGuire *et al.*, 2014; Le Pichon *et al.*, 2017b), including discontinuities, not easily identified with RS data. Although extensive field-based physical habitat data collection is achievable from shore or watercraft, the acquisition of spatially continuous data on riverine taxa is challenging due to the mobile nature of many organisms and the difficulty and expense of sampling them at high resolution. Nevertheless, study designs with spatially intensive sampling strategies (i.e. closely spaced samples) can provide the necessary resolution to describe spatiotemporal heterogeneity and reveal discontinuities in stream organism distribution (Baxter, 2002; Bateman, Gresswell & Torgersen, 2005; Le Pichon *et al.*, 2017b).

Direct observation of fishes and other stream biota by snorkelling is one sampling method often applied in small- to medium-sized rivers to evaluate species distribution at scales of 10^0 – 10^2 km (Torgersen *et al.*, 2006; Lawrence, Olden & Torgersen, 2012; Plichard *et al.*, 2016). Snorkelling provides reliable estimates of species abundance and community composition, particularly in remote locations and in rivers that are too large and deep for electrofishing (Brenkman *et al.*, 2012; Chamberland, Lanthier & Boisclair, 2014). However, snorkelling may not be appropriate in shallow, high velocity or turbid streams and can be ineffective for detecting cryptic species (Macnaughton *et al.*, 2014; Plichard *et al.*, 2016). As the presence of a human observer may disrupt natural behaviour, snorkelling can sometimes be combined with airborne (Isaak *et al.*, 2007) or shore-based (White & Rahel, 2008) visual estimation methods.

Sampling by electrofishing can be cost-effective over long river segments, especially when using systematic or random sampling designs. For instance, single-pass backpack electrofishing can highlight fish 'hotspots' or fish–habitat relationships (Kruse, Hubert & Rahel, 1998; Bateman *et al.*, 2005; Reid & Haxton, 2017). Nested or spatially intensive electrofishing can also quantify patterns in single-species abundance (Torgersen & Close, 2004) or community-level metrics (Le Pichon *et al.*, 2017b) at multiple scales. Similarly, biotelemetry approaches are useful for quantifying how fish and other mobile organisms use and move among habitats (Cooke *et al.*, 2013). Fish tagged with passive integrated transponders (PITs), radio tags or acoustic tags are detected when they pass stationary receivers (Keefe *et al.*, 2015; Dugdale *et al.*, 2016) and can be tracked actively using mobile antennas. These techniques can monitor the movement of riverine organisms in two or three dimensions (Johnston *et al.*, 2009; Capra *et al.*, 2017).

(e) Data analysis and visualization

Technological and methodological advances have made many riverscape approaches achievable, but the analysis of these data may be challenging. Considerable time may be required to process the spatial data before it is accessible in tabular and graphical form. Furthermore, consultation with landscape ecologists and spatial ecologists may be necessary

to relate complex patterns in heterogeneous data sets to ecological processes and drivers of population and ecosystem dynamics. The complexities of data analysis can be divided into data management (storage and georeferencing), visualization and processing (e.g. filtering, reduction and manipulation). RS data sets containing high-resolution, spatially and temporally explicit data over tens of river kilometres can comprise hundreds to thousands of gigabytes. Although geospatial software capable of managing data sets of this size are increasingly common, conventional geographical information system (GIS) software is often unsuited to examining spatial patterns in stream networks owing to their curvilinear, branched nature. Instead, the analysis of data in linear networks requires the contextualization of river variables and their spatial relationships in terms of their lateral, longitudinal and directional components (Ganio, Torgersen & Gresswell, 2005; Legleiter & Kyriakidis, 2006). The proliferation of scientific computing packages (e.g. R, Python, MATLAB) has made these longitudinal, or ‘channel-centred’, coordinate systems (e.g. distance upstream) increasingly accessible (Carbonneau & Piégay, 2012); however, it is often necessary to use or develop bespoke solutions to

visualize and interrogate these data (see Table S1 for examples of computing tools with descriptions of their features and functions).

Data visualization is the process of adapting the mode and scale(s) of graphical display to the questions of interest and is required to explore data longitudinally (Welty *et al.*, 2015). Depending on the variable(s), it may be more effective to (i) plot data longitudinally (Fig. 4A, B), (ii) create a map (Fig. 4C) or (iii) use more sophisticated modelling and graphical visualization techniques to quantify heterogeneity in space (Fig. 4D, E) and time (Fig. 4F). Each of these depictions of heterogeneity constitutes a visual perspective of some biological, physical or chemical property of the river. Owing to the self-organized nature of many riverine processes, it is often advantageous to analyse data at nested scales and quantify spatial autocorrelation (Ganio *et al.*, 2005). Advances in hyperscale graphing (Fonstad & Marcus, 2010) or wavelet decomposition (Steel & Lange, 2007; Le Pichon *et al.*, 2017b) may be useful for highlighting spatiotemporal patterning in data.

The intricacies of river environments have also necessitated the development and implementation of new methods for

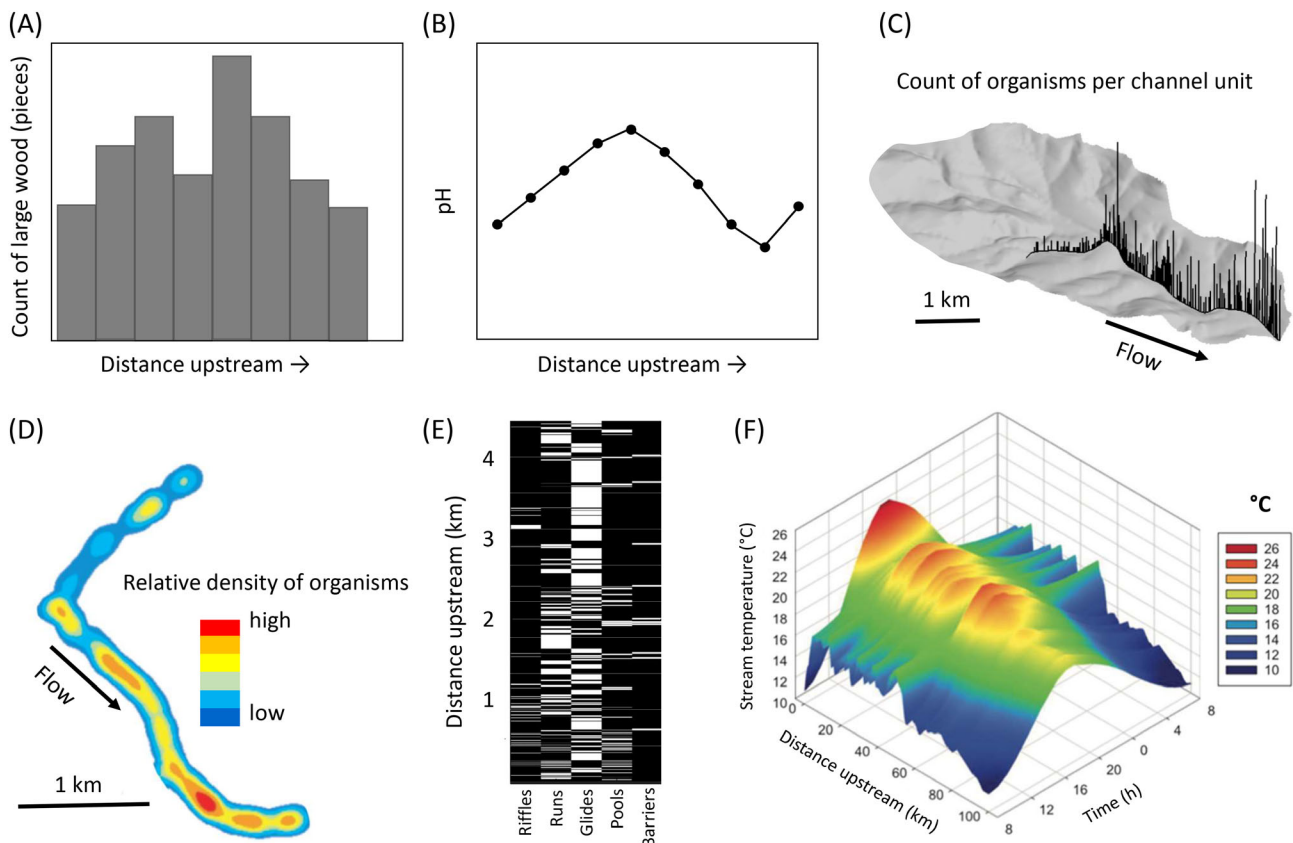


Fig 4. Graphical approaches for visualizing longitudinal heterogeneity in rivers and streams. (A) Bar graphs of habitat characteristics (e.g. counts of large wood in equal-length reaches), (B) point and line plots of water quality (pH), (C) maps of counts of organisms (e.g. fish, mussels, crayfish) (modified after Gresswell *et al.*, 2006), (D) relative density of organisms (modified after Gresswell *et al.*, 2006), (E) strip maps of habitat type (modified after Roy & Le Pichon, 2017) and (F) space–time variation in stream temperature (modified after Vatland *et al.*, 2015).

detecting patterns and relationships. Recent developments in statistical analysis that are designed for strongly autocorrelated data, such as SSNs (Peterson *et al.*, 2013; Isaak *et al.*, 2014; McGuire *et al.*, 2014; Brennan *et al.*, 2016), are uniquely suited for exploring patterns using spatially continuous data sets throughout stream networks (Zimmerman & Ver Hoef, 2017). Such methods of analysis provide the context within which patterns can be detected that would not have been evident with more traditional statistical approaches, such as analysis of variance (ANOVA) and comparisons of means and medians. Statistical approaches that account for serial autocorrelation and combine linear, non-linear, parametric and non-parametric processes are particularly powerful for assessing complex linkages between river habitats and ecosystems that arise from spatiotemporal variability and non-normal distributions (Malcolm *et al.*, 2019). These methods are powerful for relating spatial patterns to ecological processes and drivers of population, community and ecosystem dynamics.

IV APPLICATIONS IN RESEARCH AND MANAGEMENT

Riverscape approaches are providing researchers and managers with novel types of information relevant to riverine resources. We provide examples from a growing body of literature and from additional insights gained during an informal survey conducted in May 2016 among scientists who have published journal articles on this topic (see Appendix S3). These studies had operational goals of describing spatial patterns of habitat and biota in riverine systems consistent with approaches described by Fausch *et al.* (2002) and Carbonneau *et al.* (2012) (see Table S2 for examples of studies with their associated measured variables and spatial and temporal characteristics). Although the focus in the majority of our examples is on spatial heterogeneity, we emphasize that examining these patterns over time is important. Therefore, we have included information on temporal aspects of studies when available. The examples are drawn from applications ranging from the general areas of freshwater conservation, restoration and monitoring to very specific management objectives, such as reducing habitat degradation, and increasing species viability by enhancing habitat connectivity.

(1) Mapping and quantifying spatial patterns

Decades of applying riverscape approaches to the analysis of aquatic habitats provide examples of their utility for detecting unexpected patterns and understanding rivers and their biota. Ecological ‘surprises’ – outside of initial ideas or hypotheses – can lead to fundamental shifts in ecological paradigms and have been recognized as crucial for advancing ecology (Lindenmayer *et al.*, 2010). When repeated through time, spatially intensive field surveys are powerful tools for detecting important patterns, characteristics and dynamics of physicochemical habitats in stream networks (Gabbud, Robinson & Lane, 2019). For example, a spatially intensive

sampling of water chemistry in a fifth-order catchment showed how spatial heterogeneity of chemical constituents was influenced by network topology and land–water interactions (McGuire *et al.*, 2014), and another study described seasonal dynamics in spatial heterogeneity of water chemistry (i.e. low during winter but high in spring and summer) (Malard *et al.*, 2000). A similar high-scope, spatial synoptic sampling campaign was used to identify non-point sources of pollutants throughout an entire watershed (Ishida *et al.*, 2019).

Because spatially intensive field surveys do not always provide full continuous habitat description, RS technologies and platforms have been a particularly important complement to *in-situ* data (Carbonneau & Piégay, 2012; Piégay *et al.*, 2020). For example, accurate 2D maps of in-stream channel morphology display depth variability (as illustrated in Fig. 5G, H) and can inform the relevant locations of stream restoration actions (Wheaton *et al.*, 2019). RS is also a powerful tool for watershed-wide mapping of riparian vegetation (Fernandes, Aguiar & Ferreira, 2011) and woody debris (Marcus *et al.*, 2003), both of which play a crucial role in the hydromorphological and biological functioning of river channels (Gurnell, Gregory & Petts, 1995). The ability to analyse riparian vegetation pattern and functioning can provide riparian status indicators to address management and policy initiatives, for instance in Mediterranean-climate river ecosystems (Stella *et al.*, 2013).

The analysis of spatiotemporal patterns in the distributions of species can highlight patterns not detectable with traditional methods. Spatially intensive sampling (see Table S2 for examples) can identify local hot spots of high species richness, consistently occupied locations (core areas), richness of specific guilds, abundance of particular life stages and presence of risks such as predation and non-native species (Fig. 5A–D). For instance, prior to dam removal in the Elwha River (USA), two annual 65-km spatially continuous snorkel surveys highlighted biological hotspots, revealing that that most federally protected bull trout (*Salvelinus confluentus*) occurred near two dams slated for removal (Brenkman *et al.*, 2012). The information was used to target fish rescue and relocation efforts during dam removal. In coastal Oregon watersheds, spatiotemporally intensive snorkel surveys showed that interannual distribution of juvenile coho salmon (*Oncorhynchus kisutch*) expanded and contracted around core habitats, depending on annual adult abundance (Flitcroft *et al.*, 2014).

High-scope spatial information about species distribution is often used to inform management decisions and conservation priorities. Spatially intensive sampling enabled detection of concomitant hotspots of adult and juvenile freshwater mussels and highlighted mussel beds (Ries *et al.*, 2016) and rare federally protected species in rivers of the southern USA (Levine *et al.*, 2018). Le Pichon *et al.* (2015) used spatially intensive electrofishing to identify all potential feeding habitat patches at dawn and dusk to learn how two uncommon cyprinids were spatially distributed. Conducted over long distances, spatially intensive sampling may allow

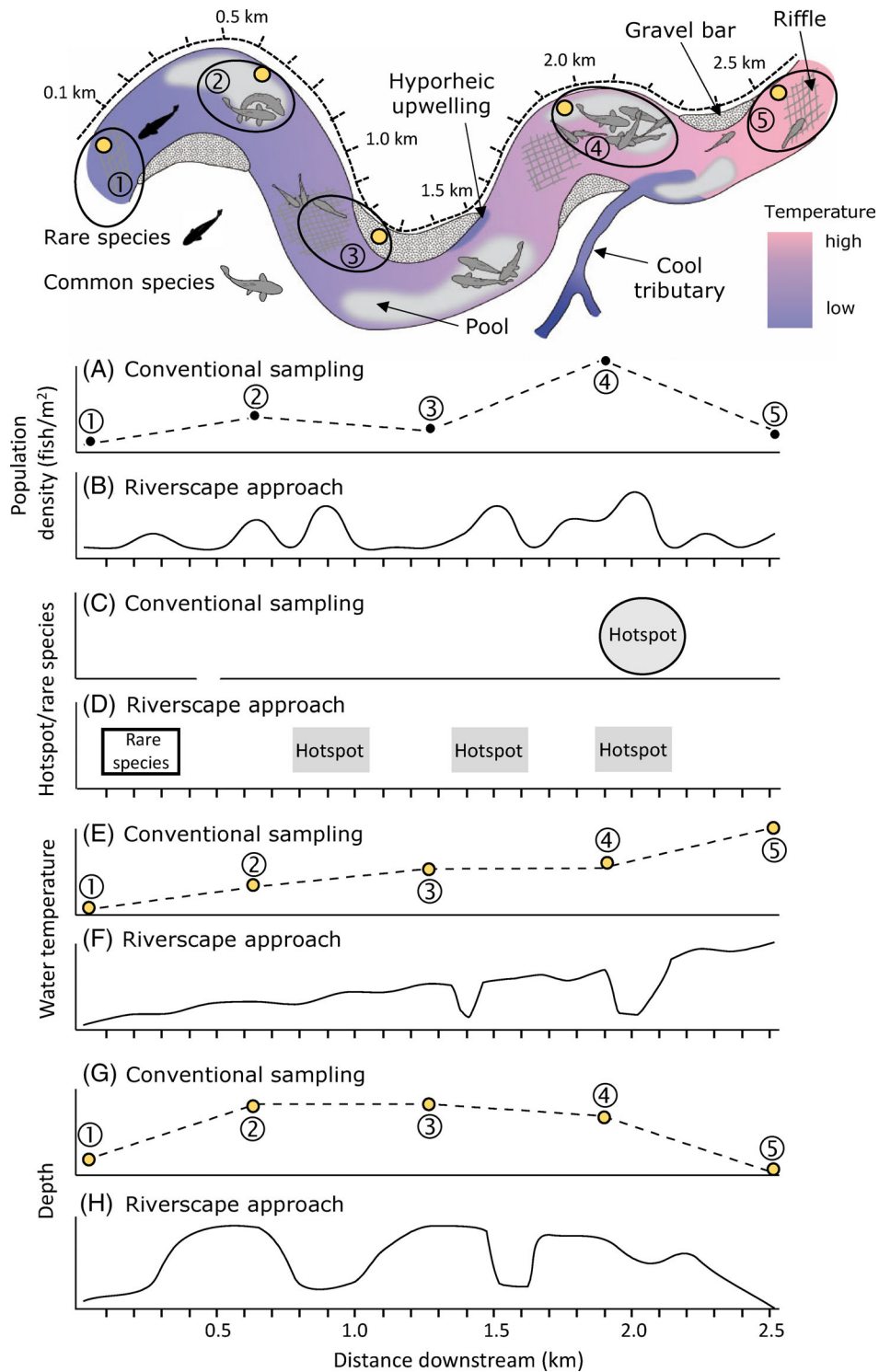


Fig 5. Comparison of data acquired using conventional (i.e. at discrete locations) (A, C, E and G) versus riverscape (i.e. spatially intensive) sampling approaches (B, D, F and H). The hypothetical stream at the top of the figure flows from left to right, and longitudinal locations are indicated with circled numbers and river distance (km) markers. Stacked panels show data from conventional versus riverscape approaches plotted with respect to distance downstream (x -axis). Data types depicted include relative abundance of fish (population density; presence of rare species; locally high abundance or ‘hotspots’) (A–D), water temperature (E and F) and water depth (G and H). On the drawing of the stream, black ellipses demarcate sampling areas for fish, and yellow dots indicate point locations where temperature and depth are measured. Note that a conventional approach may not be sufficient to detect spatial heterogeneity in fish abundance and habitat due to the scope (ratio of extent to resolution), intensity and continuity of data collection.

quantification of the colonization limit imposed by physical or chemical obstacles or the invasion front of species (Brenkman *et al.*, 2012; Rubenson & Olden, 2017). After restoration of longitudinal connectivity, spatially intensive sampling can document long-term, unassisted recolonization of newly available habitat (Kiffney *et al.*, 2006). Spatially intensive sampling can also provide information at a spatial resolution and extent that enables detection of unexpected patterns in the distribution and abundance of species. For instance, scales of periodicity, trends at different scales and discontinuities in fish species distributions were detected using empirical variograms and wavelet analysis (Torgersen *et al.*, 2004; Steel & Lange, 2007; Le Pichon *et al.*, 2017b). Citizen science and monitoring programs provide another kind of data that can be spatially and temporally intensive due to the large number of participants. For example, a citizen-science effort provided exceptionally high-scope data on aquatic insect emergence along the Colorado River that would have been cost prohibitive for typical research and management teams (Kennedy *et al.*, 2016). This unique data set has led to new adaptive management experiments regarding the management of Glen Canyon Dam on the Colorado River (USA).

Recent advances in water temperature data collection and modelling (Dugdale *et al.*, 2017) have enabled new insights about the patterns and drivers of thermal heterogeneity (Tonolla *et al.*, 2010; Fullerton *et al.*, 2015; Steel *et al.*, 2017). The use of thermal infrared (TIR) RS of rivers to implement management scenarios of water temperature is an example of how approaches are transitioning from theory to applied technology. By describing variability in thermal patterns and refuges (e.g. Fig. 5E, F), conservation and restoration actions can be better targeted, ultimately increasing the effectiveness of management. A more continuous perspective on riverine thermal heterogeneity and fish habitat use has led to improved contextual understanding of salmonid–habitat relationships and enhanced management (Torgersen *et al.*, 1999; Frechette *et al.*, 2018). For example, Torgersen, Ebersole & Keenan (2012) developed a primer for state, tribal and federal fisheries and watershed managers that illustrates how to identify cold-water refuges for salmonids using high-resolution thermal RS and spatially intensive *in-situ* thermal mapping. These approaches are being applied to protect and restore thermal diversity in riverine landscapes across North America and Europe (Dugdale, 2016).

(2) Assessing connectivity and movement

Structural hydrological connectivity in rivers (Fig. 2A) is dynamic and influenced by the complex interplay of flows, geomorphic variables, habitat patchiness and discontinuities. One-dimensional maps of modelled or classified flows identify watershed-scale patterns of hydrological connectivity and can locate sub-basins susceptible to low flows or intermittency. Mapping discontinuities within entire river networks is also critical for managers, not only because of the potential effect of a single discontinuity on the whole segment, but also

the cumulative effect of several discontinuities. To capture all potential physical and chemical discontinuities that influence stream hydromorphology and physicochemistry, spatially exhaustive surveys are required to be compared with the habitats needed by species at particular times and locations. Discontinuities may be related to tributary confluences (Kiffney *et al.*, 2006; Torgersen *et al.*, 2008), the presence of lateral waterbodies and connected ponds, local groundwater inflows or physical barriers. Longitudinal connectivity analyses of the spatial structure of physical habitat, based on graph or network theory, provide a topological representation of the interconnections between habitat patches within large river networks (Erős *et al.*, 2012; Saunders *et al.*, 2016). A graph-theory approach integrating structural connectivity and habitat suitability was used to predict the historical loss of functional connectivity caused by construction (Segurado *et al.*, 2015) and removal of large dams (Branco *et al.*, 2014). Whereas 1D longitudinal connectivity analyses provide insights at a network scale (O’Hanley *et al.*, 2013; McKay *et al.*, 2017), a 2D raster-based analysis of connectivity is particularly useful for describing potential functional connectivity in large rivers, riverine lakes and estuaries with connected waterbodies (Foubert *et al.*, 2019; Alp & Le Pichon, 2020).

Functional habitat maps provide a basis to model functional connectivity and create easy-to-read maps of habitat accessible to lotic organisms like fishes. River connectivity analyses, predominantly driven by methods focused on prioritizing barrier removal or improvement, are increasingly incorporating information about species behaviour. Placing georeferenced environmental variables into organism-centred maps of functional habitats at specific aquatic life stages is a powerful application. An organism-centred perspective improves contextual understanding about the river structure by describing and quantifying both the configuration of functional habitats (i.e. proximity, fragmentation) and their spatial ecological relationships (Dunning, Danielson & Pulliam, 1992). Mapping the spatiotemporal availability of complementary habitat(s) needed during particular life stages elucidates spatial relationships (Le Pichon *et al.*, 2009) that clarify conservation needs, such as reducing fragmentation or protecting rare habitat types. For instance, the relative spatial distribution of salmon holding pools, spawning beds and parr habitats highlighted potentially productive areas in a watershed and improved the estimation of the population carrying capacity (Kim & Lapointe, 2011). Flitcroft *et al.* (2014) modelled the ‘intrinsic potential’ of streams to support quality rearing habitat for coho salmon. Spatially explicit information produced by these approaches can be useful for managing recreational fishing opportunities and for establishing strategies that meet conservation objectives.

Combining biotelemetry and mapping has revealed previously unknown details of fish movement, behaviour and ‘core’ habitat use. Specific examples include the use of thermal habitats by fish (Hillyard & Keeley, 2012; Frechette *et al.*, 2018) or the importance of complementary intertidal habitats during high tide and subtidal refuges during low tides (Le Pichon *et al.*, 2017a). Considering the

‘behaviourscape’ of fish can improve predictions of fish responses to anthropogenic impacts such as habitat degradation, hydropeaking, landscape fragmentation and climate change (White *et al.*, 2014).

(3) Establishing a spatial context for management actions

Riverscape approaches to mapping, sampling and modelling set the context for management actions, ensuring effective project implementation and monitoring (*sensu* Bell, Fonseca & Motten, 1997). Scientists and managers have known for decades that conservation and restoration efforts aimed at streams and rivers require a perspective on the watershed as context, including at multiple scales (Frissell *et al.*, 1986; Doppelt *et al.*, 1993; Hand *et al.*, 2018). The challenge in realizing this charge has been to have information and understanding that provides just such a continuous and multi-scale context – this is what riverscape approaches are increasingly providing (Wheaton *et al.*, 2019). Continuous or spatially intensive data present a potential solution for targeting (i) critical habitats, rare species or hotspots for protection and conservation, (ii) degraded habitats or species populations to be restored, (iii) structural and functional connectivity enhancement opportunities, and (iv) the locations of monitoring sites. Given limited budgets, the spatial prioritization of management and monitoring actions is essential for successful restoration programs (Roni *et al.*, 2018), and for garnering public support. Identification of strong relationships between habitats and aquatic organism distribution and movement can be used to prioritize and implement preservation and restoration actions.

High-resolution data over broad spatial extents can be harnessed to determine conservation actions for spatially structured populations. In particular, this applies to cases of rare species, highly specialized habitat use and hot spots of productivity. For example, mapping of 2D interconnected aquatic and terrestrial features revealed that bedforms are a primary control of salmon spawning site distribution, whereas the local pool–riffle scale determines the location of redds (McKean, Isaak & Wright, 2008). Knowledge of complexity in channel morphology and sediment composition at multiple scales was crucial for designing efficient Pacific lamprey (*Lampetra tridentata*) conservation efforts (Torgersen & Close, 2004). In collaboration with local stream managers, hot spots of Atlantic salmon (*Salmo salar*) spawning were found to be consistently located just downstream from the centre of ‘sedimentary links’ (Davey & Lapointe, 2007; Lapointe, 2012).

In intermittent streams and rivers, high-scope survey approaches are especially important given the need to characterize patchiness and discontinuities resulting from stream drying. Long-term flow permanence drives invertebrate communities, and connectivity metrics derived from continuously collected data can improve understanding of critical ecological processes and guide management in highly heterogeneous aquatic environments (Datry *et al.*, 2016). Recent

applications of high-scope mapping of stream water chemistry illustrate the power of such approaches for quantifying spatial connectivity and influences of streamflow intermittence on stream biogeochemical processes (Hale & Godsey, 2019; MacNeille *et al.*, 2020).

Over broad spatial extents, riverscape approaches can help identify watersheds, river segments or biological reserves for focused conservation and restoration. For example, in Maryland (USA), Weber & Allen (2010) defined a conservation network of high-quality habitats as including ‘core streams’ that provide suitable habitat for fish, mussels and benthic macroinvertebrates. Functional connectivity modelling identified high-potential northern pike (*Esox lucius*) habitats and connectivity corridors with high return frequency as priority areas for conservation by regional agencies (Le Pichon *et al.*, 2018). Restoring functional connectivity mainly involves (i) prioritizing barrier removal or improvement to increase fish migration (see review in McKay *et al.*, 2017) and (ii) restoring a network of core habitats and corridors (Wheaton *et al.*, 2019).

Emerging spatially explicit, high-resolution mapping and modelling approaches allow consideration of multiple riverine functions when prioritizing which reaches within a river network to restore (Benda, Miller & Barquín, 2011). Using conservation-planning software adapted for rivers, Hermoso *et al.* (2015) developed a holistic approach for identifying restoration strategies that benefit both freshwater biodiversity and ecosystem services. Optimization modelling offers a more robust approach for efficiently prioritizing decision making in river restoration planning, allowing decision makers to account for key uncertainties and effectively to balance multiple, possibly competing, environmental and socioeconomic goals and constraints (Kemp & O’Hanley, 2010). To assist salmon conservation better around the North Pacific Rim, Whited *et al.* (2012) summarized metrics of freshwater habitat from satellite imagery and provided this information online as a ‘riverscape analysis’ tool. When key habitat features are altered or population declines are observed, restoration actions are typically prescribed and could benefit from the knowledge provided by high-resolution spatially comprehensive surveys and modelling (Macfarlane *et al.*, 2017; Wheaton *et al.*, 2019). Recent regional river temperature models (Isaak *et al.*, 2017b; Jackson *et al.*, 2018) or TIR imagery (Dugdale, 2016) could be used to identify reaches that are consistently warmer than other locations or areas influenced by thermal pollution (e.g. from water abstraction, industrial water discharge or river regulation) and inform precisely targeted restoration activities (Kurylyk *et al.*, 2015).

Knowledge of habitat patterns and structure, barriers, species hotspots and locations of source populations across a broad range of scales makes it possible to optimize site-based monitoring and sampling effort. More extensive biological monitoring is essential to increase understanding and improve the design of strategies, including site selection, that will best support successful restoration (Pretty *et al.*, 2003). Spatial heterogeneity patterns can inform long-term

monitoring programs by helping to decide where to focus more detailed *in-situ* investigations, and where extrapolation may be warranted. ‘Focal patch’ studies – sampling potential functional habitat patches previously mapped based on environmental variables – allow optimized sampling effort across scales (Brennan *et al.*, 2002). High-scope surveys of spawning habitat provide information on the relative influence of local habitat characteristics and spatial processes to inform the selection of index reaches that can be sampled to evaluate long-term trends in population size (Isaak *et al.*, 2007; Duffin *et al.*, 2021).

V FUTURE DIRECTIONS AND NEW FRONTIERS

As riverscape approaches have gained momentum, methods for data collection and analysis have been refined at increasingly reduced costs, allowing exploration of new frontiers in river research and management. In fact, many concepts and theoretical constructs in river science that are explicitly spatial in nature can now be tested empirically and modelled with large data sets as opposed to relying on central tendency and parametric statistics (Carbonneau *et al.*, 2012; Zettler-Mann & Fonstad, 2020). Riverscape approaches have been and are becoming more essential to addressing explicitly and more accurately conceptual constructs important to stream ecology that require a more spatially continuous and spatially explicit approach to evaluate (e.g. Fullerton *et al.*, 2015). For example, two recent studies have used more spatially continuous approaches to detect process domains (Montgomery, 1999) in riverine geomorphology (Scholl *et al.*, 2021) and ecosystem metabolism (Honious *et al.*, 2021). These studies evaluate and extend conceptual frameworks and theory, thus contributing to the progress of the field as a whole, but also address management needs.

With technological progress, novel applications are revolutionizing data-collection techniques for characterizing physical habitats and surveying stream biota. Moreover, increasing awareness of the power of high-scope data is leading researchers and managers to apply established ‘low-tech’ methods (e.g. snorkelling and *in-situ* data collection with citizen science) in creative new ways. In parallel, advances in data analysis provide new ways of combining empirical and modelled data. Another important frontier is the integration of high-scope spatial data over time, a critical requirement for environmental monitoring and adaptive management. Below, we discuss examples that illustrate promising avenues for further application.

(1) Remote sensing and *in-situ* data collection

The recent profusion of remotely piloted aircraft systems (RPAS, popularly known as ‘drones’) equipped with sensors can be deployed quickly, repeatedly and with less effort and expense than ‘conventional’ RS approaches. This makes them an excellent tool to study sudden disturbances such as

floods, droughts or pollution events. Furthermore, when flown at low altitude, RPAS can provide sub-centimetre spatial resolution imagery that can be used to characterize hydromorphological features, bathymetry and substrate granulometry using structure from motion (SfM) photogrammetry techniques (Woodget *et al.*, 2016; Dietrich, 2017). However, their use tends to be restricted to shorter reaches of shallower rivers, and data collection along the banks can be hampered by riparian vegetation and shadows (Kasvi *et al.*, 2019). Alternatively, bathymetric light detection and ranging (lidar), a laser-based active RS, can provide both submerged and ground elevations throughout entire stream networks (Kinzel, Legleiter & Nelson, 2013; Tonina *et al.*, 2019), but management applications are still limited due to its higher costs. However, recent experiments mounting bathymetric lidar on RPAS (Mandlbürger *et al.*, 2016) might set a path for new tools providing increased resolution, versatility and potentially lower operating costs. Simultaneously, progress has been made to allow faster instream RS of depth and velocity (echo sounding and acoustic profilers) in shallow waters and conducting surveys using remote-controlled systems (Flener *et al.*, 2015). Furthermore, survey scope and resolution might be increased in the future by continuous development of autonomous boats (Sanjou & Nagasaka, 2017). Furthermore, modern side-scan sonars can produce high spatial resolution imagery (>0.1 m), providing a continuous bed characterization at increasingly low depths (>0.8 m). The cost of surveys continues to decrease as recreational-grade side-scan sonar now offers low-cost solutions to map habitat features (depth, substrate type, vegetation, woody debris) along river reaches (Kaesler, Litts & Tracy, 2013; Hamill, Buscombe & Wheaton, 2018). Underwater remotely operated vehicles, developed for lentic waterbodies, may also provide fruitful avenues for research.

To capture longitudinal spatial patterns rapidly, Lagrangian sampling methods are emerging as a way forward to understand longitudinal variations in flow–ecology relationships and ecological responses (Larned *et al.*, 2010). Spatially continuous measures of flow velocity, depth, temperature or maps of bedload transport were produced using simultaneous recording of passive and active hydroacoustic data or towed probes while rafting downstream (Vaccaro & Maloy, 2006; Lorang & Tonolla, 2014). Lagrangian sampling can also be used to describe longitudinal patterns in biological data. For instance, particle drift speeds and paths of pallid sturgeon (*Scaphirhynchus albus*) larvae were estimated using high-resolution 3D flow fields, bathymetry and temperature obtained by deploying eight acoustic doppler current profilers (ADCPs) from catamaran rafts over the entire width of the Missouri River for 338 km (Marotz & Lorang, 2018). These data also could be used over tens of kilometres to examine near-spatially continuous changes in flow associated with gaining and losing reaches due to hyporheic exchange. This is a new frontier in hydrologic mapping and analysis that could provide higher-scope data compared to traditional seepage runs (Stanford *et al.*, 2005; Ely *et al.*, 2008) and dense arrays of mini-piezometers (Baxter & Hauer, 2000).

When appropriate, citizen science could become a vital element of river monitoring projects, increasing the involvement of citizens and their understanding of the environment and associated issues. Such approaches could help increase the amount of sampled data, particularly when citizen scientists and collaborators collect simultaneous data on flows, water quality and biodiversity (Nerbonne & Nelson, 2008; Turner & Richter, 2011; Kennedy *et al.*, 2016; Abbott *et al.*, 2018). For example, cellular phone applications are available to anglers for reporting species caught, as well as catch locations that contribute habitat use and species dispersion information (Venturelli, Hyder & Skov, 2017). Datry *et al.* (2016) used citizen-observed flow states to reconstruct spatiotemporal dynamics of 1400 km of intermittent rivers in southwestern France, quantified habitat connectivity for insects and fish and assessed impacts on colonization and extinction processes. Similarly, citizen-collected data were used to map the expansion of an invasive alga in eastern Canada (Gillis, Dugdale & Bergeron, 2018). A barrier-tracking application, where users could photograph, characterize and map barriers, contributed to the prediction of about 1 million river barriers across Europe (Belletti *et al.*, 2020). These examples highlight the untapped potential for citizen science to amass large quantities of data at extents and densities that would be difficult to achieve using conventional approaches.

(2) Linking species distribution to critical habitats

The detection of traces of DNA in environmental samples, known as eDNA (Rees *et al.*, 2014), an alternative to capturing live animals, seems particularly promising for characterizing spatial distributions (McKelvey *et al.*, 2016; Ostberg *et al.*, 2019) and potentially relative abundance of aquatic species (Tillotson *et al.*, 2018). Over the past decade, an increasing number of eDNA studies have assessed the presence, distribution and community composition of invertebrates, amphibians, fish and mammals (Rees *et al.*, 2014; Pedersen *et al.*, 2015). eDNA-based approaches are particularly useful for identifying habitats of rare cryptic or difficult to detect species (Minamoto *et al.*, 2012) or protected species (Bylemans *et al.*, 2019), addressing colonization processes (Yamanaka & Minamoto, 2016; Duda *et al.*, 2021) and tracking invasive species range expansions (Jerde *et al.*, 2011). Nonetheless, detection distance tends to vary with the size of the river (Pont *et al.*, 2018).

Passive acoustic monitoring, used for decades in marine ecosystems and increasingly in terrestrial ecosystems, has recently been proposed as a viable, non-invasive and largely unexplored approach to freshwater continuous ecosystem monitoring (Linke *et al.*, 2018). Soundscape analysis could enhance monitoring of acoustically active macroinvertebrates and fishes in situations where animals are notoriously hard to monitor. Although numerous challenges must be overcome before this approach is operational in freshwater ecosystems, it seems a promising way

to collect high-scope spatial information relevant to pressing conservation issues.

Biotelemetry has revolutionized the study of aquatic animal movement, allowing the characterization of horizontal and vertical movements of individuals and populations over periods of hours to years at broad scales. Advances in tag miniaturization and battery technology are increasingly allowing longer deployment and expanding the number of trackable species and life stages (Hussey *et al.*, 2015). Electronic tags can now be equipped with sensors enabling the quantification of physical parameters such as body temperature, body orientation (de Almeida *et al.*, 2013) and depth (Teo *et al.*, 2013), in addition to 2D position. For example, the use of temperature-sensing acoustic tags implanted in adult Atlantic salmon revealed how fish moved between different habitats to maintain an optimal body temperature (Frechette *et al.*, 2018). Such information is invaluable for designing studies and monitoring programs for thermally sensitive species and for protecting critical habitats. Such approaches may reveal the mechanisms underlying spatial patterns in aquatic habitat. Furthermore, recent advances in telemetry for estimating the energy metabolism of wild fish using accelerometry and electromyogram telemetry might provide further insight on the energy-based trade-offs associated with levels of activity in different habitats or thermal strata (Alexandre *et al.*, 2013; Metcalfe *et al.*, 2016). We foresee this approach as promising for calibrating movement resistance for species and life stages, a crucial parameter for calculating functional connectivity (Beier, Majka & Spencer, 2008). Overall, telemetry could increase the spatial and temporal continuity of direct observations of organisms so these data are more on a par with physical habitat data acquired *via* RS.

(3) Investigating communities and ecosystem processes

A major gap in the holistic application of riverscape approaches is that they generally have not been applied to assemblages of organisms, multi-trophic-level communities or ecosystem processes. Developments in eDNA are making it more feasible to detect the presence of multiple species, but the ‘riverscape ecology’ of food webs and ecosystem processes (e.g. nutrient spiralling and metabolism) is also advancing rapidly. For example, ‘meta-community’, ‘meta-food web’ and ‘meta-ecosystem’ studies are increasingly applied to streams and rivers, and these efforts are leveraging analytical tools like stable isotopes, modelling and spatially intensive empirical sampling to characterize food webs in mosaics and networks (Bellmore *et al.*, 2013; Cross *et al.*, 2013; Bellmore, Baxter & Connolly, 2015). Other techniques and approaches are allowing estimation of stream ecosystem metabolism throughout the year for many locations in a network or along a river (Dodds *et al.*, 2018; Mejia *et al.*, 2019; Honious *et al.*, 2021). Although these studies are still relatively low in spatial scope compared to most riverscape approaches, they are leading towards an understanding

of communities and ecosystem processes that is not possible by focusing narrowly on single organisms or assemblages (e.g. fishes) and their habitats.

(4) Analytical tools and modelling

Geospatial and statistical analysis of rivers relies on computing packages that allow customized scripts or functions to aid data management and mining; however, the skills and knowledge required to use these packages can be prohibitive. Fortunately, recent software for river analysis has emphasized accessibility and usability for non-experts (see Table S1 for examples). This list, although not exhaustive, provides examples that may be useful starting places for those struggling with how to extract meaningful information from high-resolution data.

In this review, we present riverscape approaches as primarily empirical. However, data cannot be sampled everywhere simultaneously. Statistical interpolation between *in-situ* data points throughout stream networks provides a powerful alternative to field-based sampling and RS (Peterson *et al.*, 2013; Brennan *et al.*, 2016). Broad-scale, spatially continuous predictions from these models are essential for exploring spatial patterns and developing hypotheses to test with more focused *in-situ* sampling and RS (see Step 2 in Fig. 3). Empirical data and modelled data are not mutually exclusive and can be used in a complementary manner to enhance understanding. A range of studies have demonstrated the utility of combining models with empirical data to infer process or improve predictive power. For example, in a meta-analysis of summertime water temperature for ~60 rivers in the Pacific Northwest (USA), Fullerton *et al.* (2015) found several distinct patterns of downstream warming using empirical data and statistical modelling to associate downstream warming patterns with potential hydroclimatic controls. Similarly, Glover *et al.* (2018) improved their assessment of salmon production in a small Scottish burn by using modelled juvenile capture probability, which avoided bias associated with uncorrected electrofishing data. In these examples, the use of models aided extraction of meaningful process information from field observations.

(5) Importance of the temporal dimension

Heterogeneous spatial habitat patterns unfolding through time provide the environment within which mobile riverine animals live. Limitations in methods or budgets for capturing high-resolution spatial data have limited data sets to one or several discrete times. A recent review by Brady, Chione & Armstrong (2020) describes how “riverscape ecology has embraced space at the expense of time” (p. 2); in their analysis of the literature, they found that 47% of the riverscape studies on stream fishes were biased towards one season (summer). However, with technological advances, repeated surveys are becoming easier to conduct. For instance, Vatland, Gresswell & Poole (2015) combined stream temperature

from a remotely sensed, spatially continuous survey in a large river in Montana (USA) with instream sensors at discrete locations that measured temperature hourly. Through integrating the space and time domains using an innovative statistical model, their approach illustrated how fine-scale spatial temperature patterns varied over time (Fig. 4F). Such an approach demonstrates a potential solution to the ‘snapshot’ nature of surveys with high spatial scope, which typically occur infrequently. Hydrodynamic modelling combined with biotelemetry also offers an effective solution to characterize the temporal dynamics of habitat suitability under rapidly changing environmental conditions, such as in estuaries (Guénard *et al.*, 2020). Furthermore, machine learning algorithms are emerging as a critical tool to extract patterns in very large data sets integrating spatially continuous river data over time (Carbonneau *et al.*, 2020). Detailed information on the temporal characteristics (i.e. frequency and duration) of other studies employing riverscape approaches in a variety of settings is provided in Table S2.

With spatially explicit, more frequent or time-relevant surveys, we can begin to evaluate how the spatial relationships of functional habitats [i.e. complementation and supplementation (Dunning *et al.*, 1992; Schlosser, 1995)] influence life cycles of riverine species. For instance, studies examining the use of habitats needed across ontological periods (foraging, sheltering and spawning) have revealed the relationship between the proximity of functional habitats and fish densities (Kim & Lapointe, 2011; Flitcroft *et al.*, 2012; Le Pichon *et al.*, 2015). Armstrong *et al.* (2013) described how juvenile salmon in Alaska (USA) maximize growth by foraging in cool habitats, while metabolizing their energy-dense meals in warm habitats. As tools have emerged to quantify spatial connectivity among fine-scale habitats (Erős, Schmera & Schick, 2011), the consideration of habitats successively used in time presents a strong potential for management applications. For example, Bergeron *et al.* (2016) proposed a chronological analysis of functional habitats used by Atlantic salmon through its life cycle as an alternative to the more traditional consideration of habitat quality during a single life stage as an indicator of fish productivity. Mapping habitat accessibility creates new opportunities for fisheries and conservation, particularly in highly dynamic environments (Zeigler & Fagan, 2014; Foubert *et al.*, 2019; Alp & Le Pichon, 2020).

VI ENVISIONING AND COMMUNICATING INFORMATION

Over the past two decades, a challenge has been to communicate the need for riverscape approaches and how they can help inform resource-management decisions. Effective visualization of high-scope data and clear terminology will be key to both understanding and communicating the unique benefits of these approaches. Traditional visualization tools such as plots with error bars and boxes and whiskers were designed to convey information about variance for a

statistical sample, but new user-friendly graphical and analytical tools are needed to display information effectively so that variability in the data can be investigated. Maps can be used creatively to display this spatial information in a quantitative way. For example, Torgersen *et al.* (2004) illustrated both spatial distribution and abundance of fish throughout a stream network by overlaying bar plots of fish densities along a stream network in a map that also displayed habitat type (pool, riffle, cascade) and elevation using colour (see Fig. 4C). Researchers are developing new ways to display information-rich ecological outcomes at uncommon scopes. The combination of graphical representation of data in longitudinal profiles paired with high-quality maps and imagery provides cartographic context for interpreting pattern–process relationships (Scholl *et al.*, 2021). Similarly, Steel *et al.* (2017) advocated synthesizing and mapping novel metrics such as ecological facets (i.e. nuanced ecologically relevant elements of interest). Furthermore, animations or videos allow users to take in information in ‘real time’ and get a sense for how spatial patterns can vary over time or across different conditions (Steel *et al.*, 2017). The emerging science of seascape ecology in oceanography offers valuable insights and examples for developing a new vernacular of riverscapes that is based on integrating high-frequency, multiscale and 4D data on variability at broad scales (Kavanaugh *et al.*, 2016).

Communicating results to stakeholders and managers will require an ability to translate complex findings at unfamiliar scopes in straightforward and meaningful ways. More widespread use of these and other visualization techniques will make them more familiar to practitioners and increase the likelihood that riverscape approaches will be adopted into management decision-making. Videos, synthetic maps in easily accessible formats (e.g. Google Earth .kmz) that can be loaded directly into online maps without the need for proprietary software (e.g. GIS) and interactive visualization and data-extraction tools linked to online data repositories are some of the ways that such data can be made more accessible. In addition, methodological and analytical approaches need explicitly to convey the importance of heterogeneity, scale and connectivity. Relevant terminology (e.g. spatially continuous, spatially intensive sampling, high-scope) must be clearly defined to avoid confusion (Fryirs & Brierley, 2018).

As riverscapes continue to be recognized as highly complex, dynamic social–ecological systems (SES) with a long history of human use, emerging applications can lead to stronger integration of social and ecological processes (Dunham *et al.*, 2018; Quintas-Soriano *et al.*, 2021). Mapping and spatial analysis are also important tools of this emerging science (e.g. Alessa, Kliskey & Brown, 2008; Rocha *et al.*, 2020). Riverscape approaches may be of special utility when set in the context of SES science, much of which is place based and increasingly linked to the idea of scientists and communities ‘co-producing’ understanding to guide adaptive management (e.g. Bouleau, 2014; Castro *et al.*, 2018). High-scope mapping of rivers, floodplains and their biota is uniquely attuned to the needs of these place-based, co-production efforts because maps can be a nexus between scientists and community

members (e.g. Baker *et al.*, 2004; Hulse *et al.*, 2009). Maps and imagery are better than scientific plots and data tables in this context because more people have the skills to read and interpret them.

In the context of global change, insights gained from past experience and the knowledge of historical legacies can provide guidelines to formulate preservation and restoration measures (Le Pichon *et al.*, 2020) and adaptive management actions (Haidvogel, Winiwarter & Brumat, 2019). In addition, as human behaviours and societal needs play an increasing role in defining restoration targets and evaluating restoration success, it will be essential to help the general public better to visualize and appreciate the spatially heterogeneous scene of river environments from a birds-eye view of the floodplain and into the water itself. People who live in a place care about and notice environmental heterogeneity at multiple scales, and riverscape approaches embrace the potential value and meaning of such heterogeneity.

VII CONCLUSIONS

- (1) Riverscape approaches highlight the importance of understanding how processes operate across multiple temporal and spatial scales to set the context for riverine ecosystems. Principles of landscape ecology (e.g. heterogeneity, scale, connectivity) provide a foundation for visualizing and understanding rivers as mosaics and networks of habitats and processes driving the distribution and abundance of taxa and variability in ecosystem processes. Despite a rapid expansion of publications on the topic, there have been no reviews assessing the degree of its uptake by practitioners nor how it has developed. In this review, we traced trends in riverscape approaches, illustrated how they can be applied and explored practical considerations and future avenues.
- (2) Key considerations when applying riverscape approaches are (i) the scale(s) of investigation (e.g. extent, resolution and scope) and (ii) the associated methods of data acquisition for describing and visualizing heterogeneity in physicochemical and biological components. Also integral are the concepts of structural and functional connectivity influencing the flow of energy, materials and organisms through the riverine ecosystem. We reviewed study design, data acquisition and data analysis considerations, with particular focus on how to accommodate advances in technology. It is now possible to collect and analyse high-resolution, continuous data across broad spatial extents using intensive field sampling and RS techniques.
- (3) Riverscape approaches have been applied across a spectrum of geographic settings and management questions. By highlighting key management implications, we showed how these approaches have enabled

a more nuanced approach to managing mobile species, such as fish, that use a variety of habitats throughout their life cycle. Other examples were presented that were relevant to monitoring, conservation and restoration of physical stream habitats, as well as emerging applications to food webs, ecosystem processes and even social-ecological phenomena.

- (4) Concurrent advances in computing and statistical modelling have allowed the analysis and visualization of these large, spatially intensive data sets. We identified future directions for development and application, as well as emerging technology for data collection and analysis. Although we focused on improved ways to characterize *spatial* heterogeneity of physical habitats and movements of organisms with RS, modelling and spatially intensive surveys, we emphasize that even more is to be gained from a better incorporation of the *temporal* dimension to enhance understanding about riverine processes over time.
- (5) Novel ways for envisioning and communicating spatio-temporal complexity will make rivers and their biota more accessible to a wide audience. As society continues to face challenges in natural resources management, riverscape approaches will provide innovative avenues for gathering and analysing information to understand, conserve and restore riverine ecosystems.

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X. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Examples of statistical and geographical information system (GIS) tools for organizing, processing and analysing riverscape data.

Table S2. International examples of riverscape approaches with measured variables and methods of data collection.

Appendix S1. Bibliometric analysis of publications and citation rates from a *Web of Science* (WOS) search on the term 'riverscape*'.
Fig. S1. Trends in citation rates in 2002–2019 compiled from the *Web of Science* (WOS) for each of the three most-cited

papers containing the search term ‘riverscape*’, and for all citations of publications containing this term.

Fig. S2. Key word networks for publications that cite the three most-cited papers containing the search term ‘riverscape*’ in 1998–2019.

Appendix S2. Bibliographic database containing 365 references from a *Web of Science* (WOS; accessed on 7 January 2021) search on the term ‘riverscape*’ for 1998–2021.

Appendix S3. Questionnaire and summary of responses from scientists and managers about riverscape approaches in practice.

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