

The spatial organization of ecosystem services in river-floodplains

STEPHANIE A. TOMSCHA^D,¹,[†] SARAH E. GERGEL,¹ AND MATTHEW J. TOMLINSON²

¹Forest and Conservation Sciences, Faculty of Forestry, UBC, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4 Canada ²National Capital Commission, 202–40 Elgin Street, Ottawa, Ontario K1P 1C7 Canada

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Abstract. River-floodplains are hotspots for many ecosystem services (ES), and thus, understanding how these services are spatially organized along river systems is essential. General principles from river-floodplain ecology may provide guidance for understanding these spatial patterns, yet such concepts have rarely been incorporated into spatial assessments of ES. Using a lens of riverine concepts, we contrasted how floodplain ES capacity and diversity (orchard production, forage production, carbon storage, paddle route quality, fish capacity) vary with longitudinal river-floodplain position. High spatial resolution aerial photography (2006) facilitated detection of floodplain features contributing to the production of ES. We also determined how river reach types are linked to production of ES. We found that ES capacity varied considerably with longitudinal position and reach type. Agricultural capacity was concentrated in lower reaches, high-quality paddle routes in middle-lower reaches, and fish capacity and carbon storage in upper reaches. Furthermore, the highest diversity of ES was concentrated in the lowland floodplain reaches. Our results suggest river-floodplain concepts can improve spatial assessments of ES, increase our understanding of the relationships among biological features and ES, and thus help us better manage some of the key ES trade-offs.

Key words: aerial photography; agriculture; carbon storage; fish habitat; fluvial geomorphology; landscape position; River Continuum Concept; Washington State; Wenatchee River.

Received 10 August 2016; revised 11 January 2017; accepted 17 January 2017. Corresponding Editor: Ryan R. Sponseller. **Copyright:** © 2017 Tomscha et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited. † **E-mail:** stephanie.tomscha@gmail.com

INTRODUCTION

The benefits people receive from ecosystems, known as ecosystem services (ES), are foundational to human well-being. ES include tangible benefits such as the provisioning of food and freshwater as well as less tangible benefits including carbon sequestration for climate stabilization and quality environments for recreation. To better manage and maintain ES, understanding their spatial arrangement has been a fundamental aim of ES research since the concept was established (Naidoo et al. 2008). Widespread and ongoing efforts toward understanding ES spatial patterns have included broad-scale mapping of ES and identifying clusters of ES (Raudsepp-Hearne et al.

2010). Special attention has been given to spatial concordance among ES for identifying win-win scenarios for conservation planning (Chan et al. 2006, Anderson et al. 2009, Egoh et al. 2009). ES co-occurrence has also been used to indicate ES interactions (i.e., trade-offs and synergies; Raudsepp-Hearne et al. 2010), which can vary across space (Qiu and Turner 2013). In order to improve our understanding of the spatial distribution of ES, more nuanced spatial approaches and perspectives are needed (Qiu and Turner 2013). A vast body of literature has synthesized concepts of spatial patterns in river-floodplains, and here, we draw on this literature to bring a novel perspective to ES configuration in river-floodplains (Thorp et al. 2006).

River-floodplains are among the world's most highly modified ecosystems, reflecting their disproportionate importance for ES (Tockner and Stanford 2002). Occupying < 1.4% of global surface area, floodplains provide more than 25% of terrestrial ES (Tockner and Stanford 2002). Floodplains generate a wide range of ES such as fertile soils for agriculture, habitat for fish, and carbon storage (Tockner and Stanford 2002). Riverfloodplains also encompass some of society's most challenging trade-offs in that our endeavors to enhance the provisioning of terrestrial ES often have negative consequences for aquatic ES. As a result, aquatic ES (such as water quality, fish habitats) have diminished in many watersheds due to urbanization, agriculture, and hydropower development (Sweeney et al. 2004, Foley et al. 2005, Eigenbrod et al. 2011).

While efforts to understand spatial trends of floodplain-specific ES have increased in recent years (Felipe-Lucia et al. 2014), ES research has generally ignored the biophysical template of river-floodplains where much of the world's agricultural and urban development occurs. The biophysical template of river-floodplains results from the interactions of geomorphic, hydrologic, and biological processes to form channel patterns and valley shapes, and concepts from these disciplines have been developed to understand and predict floodplain dynamics. ES in floodplains likely have unique spatial structures characterized by such hydro-geomorphic processes but have yet to be articulated and incorporated into many ES assessments. Furthermore, organizing principles from river-floodplain research can help guide testable hypotheses about ES change over space and time. Thus, spatial assessments of ES sorely need better approaches to incorporate fundamental river-floodplain processes.

Linking river-floodplain concepts to ecosystem services

River-floodplain landscapes are the templates upon which many ES interactions occur. Thus, our understanding of ES may benefit greatly from drawing on classic river-floodplain principles which recognize both longitudinal and lateral connectivity. Such principles, derived from the fusion of landscape ecology, riverine ecology, and fluvial geomorphology, have led to a deeper understanding of spatial organization of organisms and processes in river-floodplains (Ward et al. 2002, Wiens 2002). Longitudinal patterns are emphasized in with the River Continuum Concept (RCC), which despite some caveats, was the first framework to emphasize the upstream-downstream ecological organization of river corridors (Vannote et al. 1980). The Serial Discontinuity Concept, highlighting human-driven disruptions pervasive in regulated streams and rivers, also emphasized longitudinal physical and biological patterns (Ward and Stanford 1983). Lateral patterns have been elucidated by the Flood Pulse Concept, which proposes that flood pulses vary in frequency and severity with stream order and structure aquatic-terrestrial linkages (Junk et al. 1989). Riverine spatial configurations have been further explored with the Network Dynamics Hypothesis, which expands longitudinal concepts to include the entire river network hierarchy, characterizing abrupt and predictable changes at river confluences (Benda et al. 2004). Physical network structure and its importance in structuring ecological communities have also been highlighted (Grant et al. 2007). Further synthesis draws on landscape ecology principles and explores the longitudinal distribution of hydro-geomorphic patches. Such patches form unique ecological process zones rather than a continuous gradient of ecological conditions (Thorp et al. 2006).

Of these concepts, the RCC has been the most foundational and influential within river science, inspiring decades of research exploring spatial and temporal dynamics of river-floodplain ecosystems (Vannote et al. 1980, Thorp et al. 2006). The concept suggests that stream flow, organisms, and ecological communities change in a relatively predictable manner from upstream to downstream (Vannote et al. 1980), including attributes such as the ratio of organisms (shredders, grazers, predators, collectors, microbes), ecosystem process rates, and physical variables (stream flow and temperature; Vannote et al. 1980). While the specific predictions from this concept have been debated for decades, the RCC has been instrumental in advancing understanding of spatiotemporal variability in river-floodplains ecosystems (Statzner and Higler 1985, Thorp et al. 2006). Here, we explore the longitudinal patterns in ES from the RCC's simple, yet spatially explicitly perspective.

Another well-appreciated spatial driver in riverfloodplains is the geophysical template and associated fluvial-geomorphic characteristics which vary from local and regional scales (Montgomery 1999). Regionally, climate, geology, and topography govern stream flow, sediment supply, and ultimately, the physical shape of streams (Montgomery 1999). Locally, valley width and slope, channel width and depth, bank resistance, and channel roughness and channel slope interact to influence channel morphology. Such channelforming processes are linked to ecological communities. Interacting fluvial-geomorphic processes underlie ecological habitat formation and destruction in river-floodplains (Fryirs and Brierley 2012) and create different reach types (e.g., islandbraided, meandering) with associated ecological communities. As such, channel types are fundamental in understanding ecological patterns in river-floodplains (Beechie et al. 2006).

Reach types vary considerably in structure and function; thus, the distinct floodplain habitats created by fluvial-geomorphic processes most certainly influence and constrain ES. For example, some fish species prefer pool/riffle habitats for spawning over step pool reaches (Moir et al. 2004); thus, reach characteristics clearly contribute to the recreational fishing capacity of rivers. Wide valley bottoms of meandering rivers accumulate fine substrates deposited by rivers over millennia creating fertile soils for agriculture. Despite these linkages, basic relationships among ES and reach types are not well articulated, and even the very basic fundamentals of fluvial geomorphology are not routinely considered in ES assessments.

High-resolution approaches needed for detecting river-floodplain ecosystem services

Many ES (e.g., habitat for salmonids, fruit production) and pressures driving their decline (e.g., urban expansion) are linked to fine-scale features of landscapes. As such, high spatial resolution mapping approaches are necessary to map many river-floodplain features and their associated ES capacity (Gergel et al. 2007, Tomlinson et al. 2011). Most ES mapping efforts use a combination of land-cover indicators derived from moderate-resolution imagery (e.g., Landsat), census information, or modeling (Crossman et al. 2013). Yet moderate- or coarse-scale imagery, such as Landsat and MODIS (Muller 1997), may be inadequate for mapping fine-scale heterogeneity when narrow riparian features are indiscernible. In contrast, high spatial resolution aerial photography (as well as satellite imagery from Quick-Bird or RAPIDEYE) can provide detailed information to discern floodplain ES (Wulder et al. 2004, Gergel et al. 2007, Morgan et al. 2010, Tomlinson et al. 2011). High spatial resolution mapping of ES is uncommon, however, likely because it can be time-consuming and requires specialized expertise, such as aerial photograph interpretation (Morgan et al. 2010). Nonetheless, such high-resolution approaches are particularly germane for characterizing river-floodplain complexity and the associated diversity of ES (Large and Gilvear 2015).

In light of ideas from the RCC and fluvial geomorphology, we hypothesized that the capacity of floodplains to provide ES varies with upstreamdownstream position in drainage networks. Here, we extend these ideas to explore longitudinal distributions and fluvial-geomorphic characteristics of ES. The RCC's simple, yet spatially explicit premise, and the visible structures of fluvialgeomorphic characteristics are easily amenable to ES mapping. We use high spatial resolution aerial photography to map ES capacity in a highly modified floodplain and summarize ES capacity at the scale of localized reaches. In our exploratory study, we assess the spatial position of recreation, agriculture, fish production, and carbon storage and ask: Along a river-floodplain, how do ES capacity and diversity vary with longitudinal position and reach type? Because the biophysical characteristics of rivers vary along a river-floodplain gradient and reach types reflect a suite of biophysical characteristics, we hypothesized that the distribution of individual ES, as well as their diversity, would vary with longitudinal position as well as with reach type.

METHODS

Study site

The Wenatchee River watershed (3440 km²) is a sub-watershed of the Columbia River Basin draining the eastern side of the Cascade mountain range (Fig. 1). Its diverse topography, vegetation, and strong precipitation gradient make it ideal for studying variability in ES capacity along



Fig. 1. The Wenatchee watershed in central Washington State where the floodplains of the Chiwawa River, White River, Little Wenatchee River, Nason Creek, and the Wenatchee main stem comprise the Wenatchee system floodplains examined in this work.

a river-floodplain gradient. The region is a popular destination for regional tourists who visit for paddling (canoeing, kayaking, white water rafting) and agritourism. This river-floodplain has been rapidly urbanizing since the mid-20th century (Tomlinson et al. 2011). While the floodplain of the Wenatchee mainstem has been largely converted to orchards, tributary floodplains remain forested yet are traversed by extensive road networks (Fig. 2). We focus on the floodplain portions of the Wenatchee River system (210 km² of floodplain, composed of the Chiwawa River, White River, Little Wenatchee, Nason Creek, and the Wenatchee mainstem floodplains; Fig. 1).

Aerial photographs and floodplain delineation

Ecosystem services capacities were mapped using aerial photography so that relevant finescale floodplain-specific features could be discerned. Geodata from our previous work in the Wenatchee floodplain were utilized (Tomlinson et al. 2011), including an orthomosaic from July 2006 (1:40,000) acquired from United States Department of Agriculture National Agricultural Imagery Program (USDA 2006). We broadly defined the floodplain as areas of low topographic relief adjacent to a river which included geologically ancient floodplain terraces in order to capture a broader range of benefits from fluvial landscapes, especially the fertile soils suited for agriculture. We mapped ES capacity only within the extent of floodplain valley bottom which was manually digitized using a hillshade derived from USGS 10 m DEM and 1:24,000 topoquads (Tomlinson et al. 2011). ES capacities were summarized at the reach scale, an ecologically meaningful unit for floodplain analysis, digitized as 10–20 times local stream width (Tomlinson et al. 2011). Floodplain width ranged from 84 m in the most confined headwater floodplains to 2905 m at its widest point.

Reach type identification

Fluvial-geomorphic characteristics vary considerably along river-floodplains. We draw on reach types identified in Tomlinson et al. (2011) to determine whether different reach types were associated with different ES (Table 1). Defined by confinement, sinuosity, gradient, and visual characteristics, five reach types were distinguished (straight, meandering, island-braided, pool/riffle, and plane-bed; Tomlinson et al. 2011). Reaches were mapped at the 1:4000–1:5000 scale. Unconfined reaches included straight, meandering, and



Fig. 2. The total area of different land covers within each floodplain. The Wenatchee River main stem floodplain shows the most modification. Tributary floodplains are largely forested.

island-braided reaches. Straight reaches include those with a single thread and low sinuosity <1.5. Meandering reaches also had a single thread, but a sinuosity >1.5. Island-braided reaches contained multiple threads and islands with permanent vegetation. Confined reaches mapped included plane-bed reaches (gradient = 1.1–3.0%, with relative featureless bed) and pool/riffle reaches (gradient ≤1.0%, with undulating bed creating bars, pools, and riffles; Tomlinson et al. 2011).

Longitudinal river-floodplain position

We used these reach distance rankings to determine how ES varied with river-floodplain position. Reaches were ranked based on distance to the Wenatchee River's mouth on the Columbia River (rank = 1 at the confluence and rank = 164 farthest upstream). Of the 424 reaches, 98 were tied with at least one other reach. We used this ranking approach (rather than a classic stream order approach) because many of the first- and second-order streams did not have floodplains. Furthermore, while other variables (such as contributing area) could be considered in future work, our straightforward reach-ranking approach is useful as it is applicable in locations where highresolution digital elevation models, required for watershed modeling, are unavailable.

Land-cover classification

Using high-resolution air photographs from the USDA National Agricultural Imagery program (July 2006, 1-m color orthophotos captured at 1:40,000 for Chelan County; Tomlinson et al. 2011), we classified land cover into five main categories: orchard, field, urban, forest, and water. To

Table 1. Criteria used to define different reach types (Tomlinson et al. 2011).

Confinement	Reach type	Other criteria		
Unconfined: floodplain width/ channel width >3.8%	Island-braided	Multiple threads and islands with permanent vegetation		
	Meandering	Single thread, sinuosity >1.5		
	Straight	Single thread, sinuosity <1.5		
Confined: floodplain width/	Plane-bed	Gradient of 1.1–3.0%, relatively featureless bed		
channel widtĥ ≤3.8%	Pool/riffle	Undulating bed bars, pools, and riffles; gravel substrate, gradient $\leq 1.0\%$		

do so, we used details of agricultural cover types such as regularly spaced trees, dark green color, and coarse textures which helped distinguish orchards from yellow/green, smooth-textured fields at the 1:4000 scale. We distinguished detailed vegetation classes (mostly conifer, mixed conifer and broadleaf, wet shrub, scrub, rock-snow) and density classes for vegetation (high, moderate, and low). These land-cover types were used as proxies for a variety of ES capacity, linking them to indices described in the *Mapping ES capacity* section.

Mapping ES capacity

Land-cover classes derived from aerial photography were combined with other geospatial data to quantify ES capacity. This approach is especially useful in river-floodplains as data sources often used in ES research (i.e., census data) are unavailable at high resolutions. ES indicators useful for river-floodplains can be somewhat studysite specific as a wide diversity of ES exist at the terrestrial and aquatic interface, can vary with the spatial extent over which they are measured, and may not be directly and quantitatively transported to another floodplain system. However, our approach improves upon the benefits transfer approach, a method where ES values are assigned to land-cover types and multiplied across entire landscapes on an areal basis (Nelson et al. 2009). We mapped capacity for five ES (orchard production, forage production, carbon storage, paddle route quality, and fish capacity). Despite providing different benefits, many ES may be associated with shared landscape characteristics (Bennett et al. 2009, Mouchet et al. 2014).

In addition, ES estimates are often aggregated (at a county, township, or country level). Here, we aggregated ES at the scale of a river reach. ES capacity was then normalized by reach area to account for differing reach sizes and to ensure better representation of local ES hotspots (i.e., without normalizing by reach area, ES importance would simply be a function of reach size). While the entire suite of ES provided by a floodplain are not represented here for practical reasons including data non-availability, the ES we chose represent regulating, cultural and provisioning ES, including recreation, orchard production, forage production, carbon storage, and fish capacity, capturing key ES categories identified by the Millennium Ecosystem Assessment (cultural, provisioning, and regulating; MA 2005, Tomscha and Gergel 2016). We integrate multiple landscape characteristics, which have been empirically associated with ES, as described below.

Orchard and forage production

Orchard production capacity was estimated based on area (ha) classified as orchard in our land-cover maps. Reaches most important for orchard production were those with the largest area of orchards normalized by the reach area. Similarly, forage production capacity, grasses and hay generally used for horses and cattle, was estimated based on area in fields using landcover maps and normalized by reach area.

Aboveground carbon storage

We assigned aboveground carbon storage values according to forest cover composition and density and land-cover types using estimates from local FIA (forest inventory and analysis) plots and COLE (Carbon OnLine Estimator; O'Connell et al. 2014, Van Deusen and Heath 2014). Using all FIA conifer plots within the Wenatchee watershed (weighted by the number of plots in each species class), we used the upper third quartile of carbon storage value for dense conifer forests and the lower first quartile carbon storage value for moderately dense conifer forests. For mixed conifer-broadleaf forests, we assumed a 50% conifer and 50% broadleaf composition. Because there is only one hardwood FIA plot in our study area, we incorporated hardwood plots found in Chelan County to estimate hardwood carbon storage. Replicating our approach for conifer stands, we used the upper third quartile value for dense, mixed coniferbroadleaf, and the lower first quartile value for moderately dense mixed conifer-broadleaf. Aboveground carbon storage values for other land-cover types (including orchards, urban, fields, and shrubs) were derived from published estimates (Table 2). Carbon storage was totaled, normalized by reach area, and reported in tC/ha, thus distinguishing reaches with the highest areal carbon storage. While large reaches might store more total carbon, normalizing (on a per hectare basis) accounts for local hotspots of carbon storage. Although belowground carbon storage is likely important (and highly variable) in

Table 2. Aboveground carbon storage for different land-cover types.

Land cover	Aboveground carbon storage (tC/ha)	Source
Urban	25.1	Nowak and Crane (2002)
Orchard	63.0	Penman et al. (2003) (IPCC)
Field	5.0	Ruesch and Gibbs (2008) (IPCC)
Water	0	Not applicable
Conifer forest-dense	136.9	COLE (Van Deusen and Heath 2014)
Conifer forest-moderately dense	93.0	COLE (Van Deusen and Heath 2014)
Mixed conifer-broadleaf-dense	132.8	COLE (Van Deusen and Heath 2014)
Mixed conifer-broadleaf-moderately dense	67.4	COLE (Van Deusen and Heath 2014)
Shrub (wet shrub and dry scrub)	7.4	Ruesch and Gibbs (2008) (IPCC)
Rock/snow	0	Not applicable

our study area, we did not include belowground carbon storage in the analysis, in part because relevant soil characteristics are challenging to distinguish using aerial photography.

Paddle routes

Quality paddle routes are influenced by multiple landscape characteristics, which can be seen in aerial photography and supplemented by other data. Documented paddle routes were identified using American Whitewater, a popular website for paddlers (http://www.americanwhite water.org/), and then manually digitized. If no paddle routes were noted on a reach, this portion was considered unsuitable for paddling. Most parts of the river contained documented paddle routes with the exception of the upper reaches which likely are inaccessible or have water levels too low for paddling.

To map quality of paddle routes, we identified the natural vegetation and land-cover types (including forests, shrubs, wetlands, rock/snow), flanking the paddle routes in each reach. While aesthetic preferences in recreational landscapes are complex and vary among cultural, occupational, and user groups (Gomez-Limon and de Lucio Fernandez 1999), European and American adults generally prefer natural land cover to urban covers (Ulrich 1986). Forested and natural cover are also preferred to intensified agricultural cover (Arriaza et al. 2004), yet agricultural land, particularly traditional agricultural land, has also been shown to be aesthetically appealing (Bergstrom et al. 1985, Brady 2006). Thus, we considered documented paddle routes with the highest percentage of natural cover to be "highquality" paddle routes, followed by agricultural cover types and then by urban, which were considered of lower quality from an aesthetic perspective. Longer river pathways were incorporated into our index by multiplying percentage cover by paddle route length, accounting for the greater amount of travel/paddle time spent in longer sinuous reaches. The following equation shows how we integrated multiple landscape characteristics contributing to paddle route quality, which were normalized by reach area:

Paddle route quality = Paddle route

$$\begin{pmatrix} (\% \text{Natural Cover} + 0.5(\% \text{Agriculture})) \\ \times \text{Channel length} \\ \hline \\ \hline \\ \text{Reach area} \end{pmatrix} (1)$$
Paddle route =
$$\begin{cases} 1 & \text{for Paddle route} \\ 0 & \text{for No paddle route} \end{cases}$$

Fish capacity index

We mapped a suite of ecological characteristics important to fisheries to estimate the capacity of each reach to provide fish habitat. The landscape characteristics important for fish and macroinvertebrates include the provision of wood for habitat formation, wetlands/ponds, and slow/ stagnant channels. The rationale for each of these characteristics is explained next, in further detail.

Normalized wood importance index

Wood in streams is associated with formation of habitat for both fish and microinvertebrates. For example, higher volumes of wood have been linked with greater numbers of juvenile salmonids in winter (Murphy et al. 1984, Beechie and Sibley 1997). Invertebrates rely on woody debris for habitat and biofilms which form on woody surfaces (Benke and Wallace 2003). A suite of forest and geomorphic factors influence the ability of a reach to contribute large wood including tree species, channel confinement, and channel sinuosity. For example, more decay-resistant coniferous wood remains in stream longer than deciduous wood (Hyatt and Naiman 2001). We combined a suite of factors including forest type, percentage of forest area, and stream sinuosity to account for differences among reaches in their capacity to produce large wood. We used a multiplier to account for faster rate of decay (and shorter instream residence time) for deciduous tree species. These factors form the basis of our wood importance index for each reach.

The capacity to contribute wood for habitat formation was estimated by using forested area within 75 m of streams (flanking both banks of the river, without exceeding the outer floodplain boundary). This distance (75 m) is the minimum buffer width required by the Washington State Department of Ecology (Water Quality Program's Financial Management Section 2013) for eastern Washington for surface waters in agricultural land. Forested land-cover types (both mostly conifer and mixed conifer and broadleaf) were considered important for contributing wood. Sinuous channels are disproportionately important for wood production (Nakumura and Swanson 1994), so we multiplied importance value by stream sinuosity to account for this key riverine attribute.

Wood importance index =

(%Conifer + 0.75(%Mixed conifer broadleaf)) (2) × Sinuousity

Longer reaches (in the lower portions of the floodplain) with wider channels require larger trees and wood volume for geomorphic effects (Gurnell and Pie 2002). Thus, from a habitat formation perspective, large vs. small reaches are comparable even though total area in forest might greater in larger reaches. We accounted for this by using percentage of forest cover within the 75-m buffer in each reach. Percent forest cover allows us to account for differing reach areas. We normalize wood importance (see Eq. 2) from 0 to 1 based on the maximum observed value to create a normalized wood importance index.

Fish habitat

Fish reared in floodplain habitats (such as slow/stagnant channels) can have higher growth and survival rates than those in the main channel (Sommer et al. 2001, Jeffres et al. 2008). Ponds and wetlands are critical refugia during times of low flow (Robinson et al. 2002). Mapping specific habitat features allows us to identify key locations for habitat. Habitat characteristics important for salmonids, such as ponds/wetlands and slow/stagnant channels, were digitized at each time frame (Tomlinson et al. 2011). The importance of each habitat feature was found by dividing the habitat area by reach area (e.g., area dry channel/reach area); this value was scaled from 0 to 1. These habitat characteristics were combined into a (unitless) fish capacity index, which was calculated as follows. The final values of the index ranged from 0 to 1.12 with a maximum possible of 4.00 (Eq. 3).

Fish capacity index = Normalized wetland importance + Normalized slow and stagnant channel (3) importance + Normalized dry channel importance + Normalized wood importance

ES quintiles for comparing floodplain positions of individual ES

For comparing the longitudinal river-floodplain positions of individual ES, we separated ES capacity values into quintiles-each composed of an equal 20% of reaches-to analyze the importance of each reach for an ES. Quintiles are breaks that divide data distributions, such as our individual ES capacity values, into five equal parts. This approach also accounted for differences in the shape of the distributions among different ES (e.g., normal vs. skewed; Fig. 3) which were not well characterized by mean/median ES values. Similar approaches have been used to determine covariance of important locations for ES (e.g., Schulp et al. 2014). Each reach was assigned a quintile value for each ES. In practice, for reaches where a particular ES was not present, we assigned a value of 0. For reaches where an ES was present, the lowest quintile reaches (reaches with ES capacity values in the lowest 20%) were assigned value of 1, while reaches in the second quintile were assigned a value of 2,



Fig. 3. Histograms of ecosystem services (ES) found at the reach level. Quintiles (labeled Q-n), which divide each distribution into five equal parts, are helpful in comparing ES with distributions of different shapes (e.g., skewed vs. normal distributions). Orchard and forage production as well as paddle routes did not occur throughout the floodplain, while fish habitat and carbon storage occurred in some capacity in all reaches.

etc. Finally, reaches in the highest quintile (reaches with ES capacity values in the highest 20%) were given a value of 5. Such quintiles were used to analyze the differences in longitudinal spatial distributions of ES. We mapped ES capacities across the Wenatchee system floodplain to visualize their longitudinal variability using quintiles as well (Fig. 4).

Statistical analyses

We compared patterns of individual ES as well as ES diversity longitudinally as well as by reach position. All calculations and analyses were performed in R version 3.3.0 (R Core Team 2015). We assessed individual services using ES quintiles (Fig. 3). Weighted mean river position for each ES

was determined, by multiplying ES quintile values by river reach ranking. To determine whether the occurrence of ES differed with longitudinal position, we used a Friedman's test due to nonnormality of ES and unequal variances. From there, we used a pairwise Wilcoxon rank-sum test with Bonferroni corrections to determine which specific pairs of services differed with river-floodplain position. To determine whether individual ES varied with fluvial-geomorphic reach type, we used a Kruskal-Wallis rank-sum test followed by post hoc, pairwise Wilcoxon rank-sum test with Bonferroni corrections. We fit both models in the mgcv library in R version 3.3.0 (Oksanen et al. 2016). Exploring ES diversity in floodplain reaches is not without limitations. In



Fig. 4. Longitudinal patterns in ecosystem services (ES) capacity across the Wenatchee system floodplain in 2006, highlighting variability in ES through maps of ES quintiles. The highest (5th) quintile (in black) shows locations with the highest 20% ES capacity, the most important location for these ecosystem services. In contrast, locations in white show reaches lacking a service. The lightest gray shows locations where the lowest 20% of values for an ES are present. Our maps support the hypothesis that ES capacity varies along the river continuum.

		Differences in mean longitudinal position (<i>P</i> -values)					
Weighted mean longitudinal position	Ecosystem service	Orchard production	Forage production	Carbon storage	Paddle routes		
12.3	Orchard production						
43.8	Forage production	0.002					
98.3	Carbon storage	< 0.01	< 0.01				
82.0	Paddle routes	< 0.01	< 0.01	< 0.01			
91.9	Fish capacity	<0.01	<0.01	1.00	< 0.01		

Table 3. Ecosystem services according to longitudinal position.

Notes: Weighted mean landscape position for each ecosystem service (2006) is in the first column. Orchards have the lowest mean longitudinal position with the most downstream positions being most important, while fish capacity has the highest weighted mean longitudinal position. In columns 3–6, boldface indicates the mean longitudinal position differs among pairs of services (significance of pairwise Wilcoxon rank-sum test). All ecosystem services have different longitudinal positions with the exception of carbon storage and fish capacity.

ES research, using different-sized plots to explore ES diversity is common, largely because data are generally summarized by different-sized watersheds or political units (Raudsepp-Hearne et al. 2010). Here, we normalized ES by area to minimize this issue.

Because our data did not meet the assumptions of linear regression and could not be improved by variable transformation, we used a GAM (generalized additive model) approach with mixed effects to estimate whether reach type and longitudinal position affected ES diversity. Semi-parametric models, GAMs are more robust to violations of the assumption of homogeneity of variance. We considered reach type a random effect due to differences in variances in ES diversity among reach types, likely a result of differences in sample size (Gelman and Hill 2007). We compared two GAMs both fit using Gaussian distributions, one with reach type as a random effect and one without reach type using a chi-square test (Zuur et al. 2007). We fit both models in the mgcv library in R version 3.3.0 (Wood 2006). To determine the amount of variation explained by our fixed and random effects, we also fit a null model and two reduced models (one including only the fixed effect and one including only the random effect). For each reduced model, we subtracted the deviance of the reduced model from the deviance of the full model and divided it by a null model, keeping smooth factors the same as the full model. This gave us the variation explained by longitudinal position and reach type.

Results

Individual ES vary with longitudinal position

Locations important for ES capacity differed for each ES (Fig. 4). Median longitudinal position differed among services (Friedman's $X^2 = 904.96$, df = 4, P < 0.01). Pairwise comparisons showed nine of the 10 ES pairs occurred in significantly different locations (P < 0.05) (Table 3). Relative to other ES, carbon storage and fish capacity were both widespread throughout the floodplain. Carbon storage and fish capacity did not differ significantly in longitudinal position from each other, yet all other ES differed from each other (Fig. 4, Table 3). The most important locations for carbon storage and fish capacity were concentrated in upper reaches, while the lowermiddle reaches were important for high-quality paddling (Fig. 4). Mean longitudinal position of orchard and forage production was lower than every other ES.

Individual ES vary with reach type

We found differences in ES capacity by reach type for all individual ES with the exception of paddle route quality (Tables 4 and 5). Upon further examination of those that differed by reach type, island-braided reaches were significantly higher in orchard production capacity than planebed (P = 0.01) and straight reaches (P = 0.03). For forage production, plane-bed reaches were significantly lower in capacity than island-braided (P < 0.01), meandering (P = 0.01), and straight reaches (P = 0.01). For carbon storage, meandering

Confinement	Reach type	Orchard production	Forage production	Carbon storage	Paddle route quality	Fish capacity
Unconfined	Island-braided	$\textbf{0.65}\pm\textbf{1.511}$	$\textbf{0.675} \pm \textbf{1.289}$	2.7 ± 1.305	1.075 ± 1.185	3.025 ± 1.672
	Meandering	0.094 ± 0.491	0.623 ± 1.376	2.585 ± 1.151	$\textbf{1.774} \pm \textbf{1.825}$	$\textbf{4.17} \pm \textbf{1.139}$
	Straight	0.18 ± 0.773	0.424 ± 1.201	3.128 ± 1.445	1.428 ± 1.753	2.888 ± 1.375
Confined	Plane-bed	0 ± 0	0 ± 0	2.859 ± 1.533	1.352 ± 2.132	2.437 ± 1.204
	Pool/riffle	0 ± 0	0 ± 0	$\textbf{3.9}\pm\textbf{1.101}$	0.4 ± 1.265	3.2 ± 1.033

Table 4. Ecosystem service quintiles by reach type (mean \pm SD), indicating the relative importance of each reach type in supporting each ecosystem service.

Notes: The higher the mean ecosystem service quintile, the more important this reach type is for a particular service. Reach types with the highest mean quintile value for an ES shown in boldface. Island-braided reaches are most important for orchard and forage production, while meandering reaches are most important for paddle routes and fish capacity. Plane-bed reaches are the most important for carbon storage.

reaches were lower in capacity than pool/riffle reaches (P = 0.03). Paddle route quality did not differ with reach type ($X^2 = 8.47$, df = 4, P = 0.08). For fish capacity, island-braided reaches were significantly higher than meandering (P = 0.014) and plane-bed reaches (P = 0.01). Meandering reaches were significantly higher in fish capacity than plane-bed (P < 0.01) and straight reaches (P < 0.01).

Longitudinal patterns of ES diversity

Diversity of ES capacity varied with longitudinal position and reach type. The model with reach type as a random effect was superior to the model without reach type as a random effect (P < 0.01), which suggested including reach type improves the fit of the model. Our selected model explained 35.9% of the variance. Upstream position accounted for 35.9% of the variance in ES diversity, while reach type accounted for <1% of the variance. The highest variability in diversity was found in the middle reaches. Lower portions of the floodplains were most diverse, owing to the presence of agriculture (Fig. 5).

Discussion

We examined how river-floodplain concepts relate to ES capacity and found several compelling patterns. Our results suggest that both the spatial

Table 5. The *P*-values for differences in fluvial-geomorphic reach type by individual service (Kruskal–Wallis rank-sum test followed by post hoc, pairwise Wilcoxon rank-sum test with Bonferroni corrections).

	Kruckal Wallie				Reach type			
Ecosystem service	X^2	df	Р	-	Ι	М	РВ	PR
Orchard production	19.43	4	< 0.01	М	0.111			
				PB	< 0.01	0.924		
				PR	1.000	1.000	_	
				S	0.030	1.000	0.263	1.00
Forage production	21.27	4	< 0.01	Μ	1.000			
				PB	< 0.01	< 0.01		
				PR	0.613	1.000	_	
				S	0.334	1.000	< 0.01	1.000
Carbon storage	12.83	4	0.01	Μ	1.000			
				PB	1.000	1.000		
				PR	0.141	0.033	0.426	
				S	0.759	0.117	1.00	1.000
Paddle route quality	16.88	4	0.08					
Fish capacity	48.77	4	< 0.01	М	0.014			
				PB	0.726	< 0.01		
				PR	1.000	0.062	0.636	
				S	1.000	<0.01	0.164	1.00

Notes: I = island-braided; M = meandering; PB = plane-bed; PR = pool/riffle. Significant differences are shown in boldface.



Fig. 5. Diversity patterns for ecosystem services (ES) capacity vary according to river position. Diversity of ES capacity is negatively related to upstream position explaining 35.9% of the variance in ES diversity. Our best model that included reach type suggested reach type explained <1% of the variance in ES diversity. Upstream reaches have lower ES diversity than downstream reaches.

distribution and the diversity of ES along river corridors may be better understood through the lens of classic concepts of riverine science and fluvial geomorphology. We found that ES differed among fluvial-geomorphic reach types. For example, orchard production was more abundant in island-braided reaches than in plane-bed reaches. Upstream longitudinal position explained nearly 36% of the variance in ES diversity, yet reach type accounted for less than 1%. Interestingly, neither fish habitat nor carbon storage differed longitudinally, as both varied more directly with forest cover. These longitudinal and fluvial-geomorphic drivers of ES may have a wide range of implications. Next, we highlight implications for examining concordance between ES and biodiversity in riverfloodplains as well as explore some potential mechanisms driving the patterns of ES distributions we found, and lastly, explore ideas for extending this research to include additional river-floodplain concepts.

Fluvial geomorphology as a driver of ecosystem service distribution

Fluvial geomorphology may play a role both in driving ES capacity and in driving access to ES. Our findings support the idea that different fluvial-geomorphic reach types produce specific ES. For example, hydromorphic and geomorphic characteristics influence locations for fish spawning (Moir et al. 2004) and biomass (Penaluna et al. 2015). Trout biomass can be more sensitive to the geophysical template than to changes in stream temperature, flow, turbidity (Penaluna et al. 2015). Vegetation is also linked to fluvial landforms (Polvi et al. 2011), which in turn could affect ES.

Furthermore, river-floodplains are disproportionally important for ES access, largely due to their geomorphic suitability for roads and railways, yet access and infrastructure development can differ with floodplain position (Tomscha and Gergel 2015). Infrastructure is an important

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driver of ES access, yet the nuances of infrastructural development within floodplains and links to multiple ES remain poorly understood. Understanding and comparing ES provided in developed vs. pristine rivers is an important next direction of river-floodplain ES research.

Understanding concordance among ES and river-floodplain biodiversity

Characterizing biological patterns of riverfloodplains remains a long-standing, active area of interest (e.g., Dodds et al. 2015, Tornwall et al. 2015). Since publication of Vannote's seminal RCC (Vannote et al. 1980), more than 326 papers have characterized the arrangement of species diversity in river channels (Tornwall et al. 2015). This body of literature has been rich for invertebrates alone. For example, hydrologic connectivity to the main channel is a key predictor of species richness of floodplain invertebrates (Starr et al. 2014), and mid-order streams often have the highest macroinvertebrate diversity (Clarke et al. 2008). Lateral distributions of macroinvertebrates also vary longitudinally forming distinct floodplain communities which change from upper to lower reaches (Arscott et al. 2005, Reese and Batzer 2007). River-floodplain concepts have also been used to explain the spatial distributions of other species groups. Fish communities in lower reaches were more diverse across tropical and temperate rivers (Araújo et al. 2009, Ibañez et al. 2009). Plant diversity was higher immediately downstream of confluences (Osawa et al. 2010), and meandering reaches provide important habitat for rare and threatened species (Osawa et al. 2011). Our results also reflect these relationships with downstream positions exhibiting greater ES diversity, mirroring downstream increases in riparian plant diversity that have been observed along river continua (Kuglerová et al. 2015). Thus, the rich body of literature examining biological patterns of riverfloodplains is highly germane to understanding river-floodplain ES.

Analogous patterns of ES diversity and taxonomic diversity may provide new insights into spatial relationships among biodiversity and ES, a debate that has yielded assorted results (Ricketts et al. 2016). Abundance of common species has been associated with high levels of ES (Winfree et al. 2015). Yet concordance among biodiversity and ES has been found to be strong at some locations (Egoh et al. 2009), but less compelling at others (Naidoo et al. 2008). An ES approach to conservation in freshwater systems in eastern Canada was shown to miss some biodiversity targets in freshwater systems (Cimon-Morin et al. 2016). Thus, conservation planning exercises optimizing either biodiversity or ES may have differing consequences for the other.

Interestingly, the greater ES diversity we have detected downstream hints that hotspots of biodiversity and ES diversity may occupy similar positions in floodplain landscapes adding to growing evidence that associations between ES and biodiversity are more nuanced than previously thought (Ricketts et al. 2016). New hypotheses on ES and biodiversity relationships may be needed, incorporating landscape position, especially within river-floodplains. While research on ES interactions has alluded to the importance of landscape position for ES interactions (Qiu and Turner 2013), its influence on biodiversity and ES concordance has yet to be explored explicitly. Our work supports this need for further research on complex biodiversity and ES relationships, as well as a better understanding of the mechanisms driving ES distributions.

Potential mechanisms driving distributions of floodplain ES

Ecosystem services patterns reveal multiple mechanisms that interact, and sometimes constrain, the distribution of ES. Longitudinal patterns of agricultural ES were influenced likely by the location of fertile soils associated with flooddriven deposition of organic matter as well as proximity to navigable sections of the river and unconfined reaches. While orchard production abruptly ended as the Wenatchee main stem became confined, this constraint was less apparent for forage production, which occurred further upstream. Upper reaches were hotspots for carbon storage, inversely related to the extensive urban and agricultural development in downstream reaches (Tomscha and Gergel 2016). In more pristine reaches, patterns of carbon storage hotspots may be more nuanced and linked to soil fertility, which limits carbon sequestration potential in many forests (Oren et al. 2001). For fish capacity, upstream areas were particularly important, likely from lower levels of landscape

modification as well as greater lateral connectivity between the river and its floodplain (Jeffres et al. 2008). Recreational paddling was found in both lower and mid-reaches, yet abruptly ended in upstream reaches, suggesting paddling is tied to the interaction between access and naturalness, while simultaneously being constrained by suitable instream flows. These highly contrasting spatial patterns of individual ES suggest further examination of ES patterns in light of well-established river-floodplain concepts is needed.

Can additional river-floodplain concepts help explain spatial patterns and interactions among ES?

Longitudinal as well as reach-level comparisons revealed distinct patterns of ES. Thus, exploring ES within the context of other riverfloodplain concepts, such as the Flood Pulse, Serial Discontinuity, and Stream Biome Gradients, is also warranted (Junk et al. 1989, Ward and Stanford 1995, Benda et al. 2004, Dodds et al. 2015). Drawing on such concepts may advance spatial predictions of ES distributions and mechanistic relationships among ES. For example, lateral differences in the distributions of ES may be better understood by incorporating principles of the Flood Pulse Concept, which suggests variations in timing, magnitude, and predictability of flooding along a river-floodplain drive interactions among biota (Junk et al. 1989). Alterations in the timing, magnitude, and extent of floods by levees and dams may lead to declines in ES which benefit from floodplain connectivity (such as fish production) as well as impact agricultural land (Gergel et al. 2002, Orr et al. 2012). Further research on the relationship between flood pulses and ES distributions is warranted.

Some classic ES trade-offs in aquatic systems are understood within the lens of the Serial Discontinuity Hypothesis. Fragmentation from roads, dams, and other infrastructure is pervasive in river-floodplains (Blanton and Marcus 2009, Tomscha and Gergel 2015), and the Serial Discontinuity Concept helps incorporate fragmentation into river-floodplains ES studies (Ward and Stanford 1995). Dams can increase certain ES (hydropower) yet cause declines in other ES (fish production; Ziv et al. 2012). Discontinuity (resulting from dams and roads) may contribute to trade-offs through direct displacement of an ES or by interrupting processes required to maintain them. For example, impoundments represent pervasive barriers to longitudinal continuity as the movement of resources and organisms can be impeded (Ward and Stanford 1995). When reservoir creation floods a valley bottom, it may displace agricultural production yet enhance it at other locations (Galipeau et al. 2013). In juxtaposition to these trade-offs, roads and dams may also create synergies, or simultaneous increases in multiple ES. Roads create better access for recreational activities, while dams with reservoirs can provide swimming and boating opportunities. Exploring these interactions in light of the Serial Discontinuity Concept may allow for better comprehension and prediction of interactions among ES.

The Stream Biome Gradient Concept, which suggests that biota vary along precipitation and climatic gradients which create hydrologic and geomorphic differences (Dodds et al. 2015), may also be amenable to exploring even broader, biogeographic-scale patterns of ES. For instance, differences in river form and function in boreal vs. arid river-floodplains may produce different types or amounts of ES, such as greater erosion control in heavily forested boreal rivers than in sparely vegetated arid rivers (Dodds et al. 2015). Incorporating broad-scale precipitation and climatic gradients may allow for better predictions across these gradients (Dodds et al. 2015). Such approaches may also be useful for understanding broad distributions of river-floodplain ES in different bioclimatic zones.

Conclusions

Spatial river-floodplain concepts provide improved opportunities to explore the nuances of spatial variability in ES. We found that ES capacity varied longitudinally along the Wenatchee floodplain system, corresponding to the longitudinal ecological variability described by the RCC. Furthermore, ES capacity varied considerably among fluvial-geomorphic reach types. Such classic river-floodplain concepts may invigorate thinking on ES spatial dynamics as well as shed light on relationships among biodiversity and ES. Future work using these concepts to explore

mechanistic relationships can potentially enhance our understanding of ES interactions. The depth and breadth of river-floodplain concepts provides a rich body of work on which to draw to explore the spatial arrangement of ES and create specific hypothesis regarding ES in river-floodplains.

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