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Reports

Emergent stability in a large, free-flowing watershed

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Abstract. While it is widely recognized that financial stock portfolios can be stabilized through diverse investments, it is also possible that certain habitats can function as natural portfolios that stabilize ecosystem processes. Here we propose and examine the hypothesis that free-flowing river networks act as such portfolios and confer stability through their integration of upstream geological, hydrological, and biological diversity. We compiled a spatially (142 sites) and temporally (1980–present) extensive data set on fisheries, water flows, and temperatures, from sites within one of the largest watersheds in the world that remains without dams on its mainstem, the Fraser River, British Columbia, Canada. We found that larger catchments had more stable fisheries catches, water flows, and water temperatures than smaller catchments. These data provide evidence that free-flowing river networks function as hierarchically nested portfolios with stability as an emergent property. Thus, free-flowing river networks can represent a natural system for buffering variation and extreme events.

Key words: biodiversity; dendritic network; Fraser River, British Columbia, Canada; natural defense system; portfolio effect; resilience; salmon; scale; watershed stability hypothesis.

Introduction

There is growing appreciation that specific habitats can buffer people and their infrastructure from perturbations; for instance, mangrove forests and coastal dunes protect shoreline communities from cyclones and sea level rise (Das and Vincent 2009, Arkema et al. 2013). In addition, variability can be dampened through the integration of multiple asynchronous dynamics, also known as the portfolio effect (Markowitz 1952). Human activities can integrate across multiple dynamics to increase stability (Figge 2004, Koellner and Schmitz 2006), whether it is a stock portfolio with a diverse set of investments (Markowitz 1952) or a fishing fleet that moves across space to harvest multiple fish populations (Schindler et al. 2010). It is also possible that some habitats could function as natural portfolios by integrating multiple dynamics, leading to intrinsic stability that has not yet been recognized. Understanding such natural buffers against perturbations could help guide spatial planning to consider these natural stabilization systems.

Here we propose that the structure of free-flowing river networks stabilizes their biotic and abiotic processes through the progressive integration of asynchronous upstream dynamics. We call this the watershed stability hypothesis (Appendix). River networks integrate and propagate water, materials, and organisms downstream through their hierarchical branching structure (Horton 1945, Rodriguez-Iturbe et al. 2009). Trickles drain into creeks, creeks drain into streams, and streams drain into rivers (Frissell et al. 1986, Lowe et al. 2006). Downstream dynamics are thus a function of upstream dynamics (see Plate 1). As tributaries coalesce, their separate dynamics are aggregated. This aggregation of dynamics, according to the statistical averaging that underpins the portfolio effect, should dampen variability (Markowitz 1952, Doak et al. 1998, Yeakel et al. 2014). Stability will generally increase with an increasing number of assets in the portfolio and increasing asynchrony among those assets (Doak et al. 1998). Here, stability is defined by the relative size of fluctuations over time (Doak et al. 1998). If we consider the portfolio of a given location on a river, its assets will be the upstream tributaries and habitats. Our hypothesis is also linked to concepts of hierarchical scales and stability (Levin 1992, Holling 2001, Elmqvist et al. 2003). Specifically, larger areas of observations (e.g., larger plot size) will include more diversity with more stable aggregate processes (Levin 1992). Rivers, in essence, observe upstream dynamics. Thus, the dynamics of a specific location on a river should scale with upstream catchment size. That is, free-flowing river networks should function as hierarchically nested portfolios. More downstream sites with larger catchment size will integrate more diversity, which we predict will lead to higher stability.

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The principles of the watershed stability hypothesis could be generally applicable to geological, hydrological, and ecological watershed processes that are driven by directional water flow. Furthermore, for harvest of migratory species that swim upstream, such as anadromous salmon, similar principles apply, where downstream habitats temporarily contain an aggregate of upstream groups. If so, stability may be an emergent property of rivers that arises from their directionality and branching network structure.

Previous studies from a diversity of fields support predictions of the watershed stability hypothesis. Classic work by Leopold and others (Leopold and Maddock 1953) introduced the search for scaling patterns in river systems. Indeed, classic studies of riverine temperature (Vannote et al. 1980, Vannote and Sweeney 1980) and hydrology (Woods et al. 1995) have observed scaling patterns of variability across watershed locations that support predictions of the watershed stability hypothesis (Appendix: Table A1). However, to what extent the watershed structure of rivers impacts biotic and abiotic stability is not well understood. Integrative watershed theories (Vannote et al. 1980, Rodríguez-Iturbe and Rinaldo 2001, Campbell Grant et al. 2007) have yet to explore patterns of stability. Our contribution is to integrate across these disciplines, introduce this general hypothesis, and examine patterns in a large watershed for key abiotic and biotic river dynamics.

River networks provide the fundamental structure of flowing water ecosystems (Rodríguez-Iturbe and Rinaldo 2001, Campbell Grant et al. 2007). The branching structure of river networks is often dendritic and fractal and follows scaling relationships, evidenced by predictable distributions of river attributes such as stream size, spacing of ridges and valleys, and branching probability (Horton 1945, Rodríguez-Iturbe and Rinaldo 2001). These networks shape and are shaped by landscapes and control the distribution of river physical characteristics such as sediment size and average water flow (Rodríguez-Iturbe and Rinaldo 2001, Benda et al. 2004). There is also growing appreciation that river network structure influences biology, such as the spatial distribution of biodiversity (Campbell Grant et al. 2007, Muneepeerakul et al. 2008) and dynamics of metapopulations (Mari et al. 2014, Yeakel et al. 2014).

Here, our aim is to examine predictions from the watershed stability hypothesis within a large, free-flowing watershed. However, large, free-flowing watersheds are increasingly rare; the vast majority are now severed by large dams (Nilsson et al. 2005). The Fraser River, British Columbia, Canada, provides an opportunity to examine the watershed stability hypothesis within one of the largest remaining free-flowing rivers in the world. Data on multiple watershed processes, ranging from biological to physical processes, provide insight into the potential generality of the hypothesis. Thus, we compiled data to examine the stability of water flows, water temperatures, and First Nations fisheries for chinook salmon (*Oncorhynchus tshawytscha*) from sites throughout the Fraser watershed. Stability of these three watershed processes is critical to the cultural well-being, biodiversity, and economic security of this region (Fraser Basin Council 2010). We treat upstream catchment area as a proxy for the amount of diversity that is integrated by a given sampling site (Appendix). With increasing catchment area, the number of tributaries will increase (Horton 1945, Rodríguez-Iturbe and Rinaldo 2001), and their dynamics should be generally more asynchronous, as asynchrony often increases with distance (Moran 1953). We calculated variability as both the magnitude of fluctuations (Doak et al. 1998) and as the frequency of events that exceed critical magnitude for each site. Sites range from high in the watershed with catchments of only 20 km^2 to sites on the lower Fraser that integrate all 229 840 km^2 of the basin and all of its tributary, climatic, geologic, and biological diversity. Sites therefore range from rather simple portfolios to ones that are extraordinarily diversified. Across response variables, we predicted that streams with larger catchments that integrate more dynamics will be more stable on average than smaller catchments.

Materials and Methods

We compiled a spatially and temporally extensive data set on First Nations catch, water flow, and water temperature from sites within the Fraser River watershed. Approximately the size of the United Kingdom, the Fraser River watershed is the second-largest watershed without dams on its mainstem in North America (Appendix: Fig A1). It discharges approximately 112 km^3 of water each year into the Pacific Ocean adjacent to the city of Vancouver, British Columbia and sustains annual migrations of millions of anadromous Pacific salmon and their associated commercial, recreational, and First Nations fisheries (Fraser Basin Council 2010).

For each site, we estimated catchment area upstream of the site with a digital elevation model (100-m^2 resolution) and the hydrology toolbox in ArcGIS 10.1 (ESRI, Redlands, California, USA). This catchment area is a proxy for the amount of geological, biological, and hydrological diversity integrated by each site (Appendix). We focused on the period 1980–present, as it has higher-quality data and includes better spatial coverage. Temperature and flow were aggregated to daily averages and fisheries catches were aggregated to annual total catches. The analyzed data set had a total of 142 sites (19, 86, and 37 sites for fisheries, flow, and temperature, respectively) and a total of 891 176 measurements went into estimates of variability. We calculated variability at each of these sites with these empirical data. The number of measurements that comprised estimates of variability for flow ranged from 366 to 11 688 (mean = 9982) depending on site. Sample sizes for each site for temperature ranged from 260 to 2106 (mean = 876). Sample sizes for each site for

fisheries ranged from nine to 30 (mean = 18). The sample sizes for each site were not significantly associated with catchment size for any of the response variables ($P > 0.05$). For dynamics that are measured on interval scales (and can be below zero), namely temperature, we calculated variability as the standard deviation (SD). For additive dynamics, namely flow and fisheries catches, we calculated variability as the coefficient of variation (CV). In order to examine aspects of variability that are less abstract and to avoid assumptions regarding symmetry of variability, we also calculated the frequency of events of critical magnitude. We define events of critical magnitude as when the value of the response variable crosses a threshold value, specific to each response variable.

Fisheries

First Nations communities are located along the Fraser River and have food, social, and ceremonial (FSC) rights to fish for returning adult migratory salmon throughout the watershed. While salmon migrate upstream, counter to the downstream flow of water, the principles of the watershed stability hypothesis should apply; downstream fisheries integrate more diversity than upstream fisheries. Given that locally adapted salmon populations spawn through the watershed, downstream fisheries would thus aggregate across more populations than upstream fisheries. We focus on the annual stability of First Nations catches of chinook salmon, the largest and most valuable of the salmon. Within the Fraser River, there are numerous populations of chinook salmon that are locally adapted and spawn in different locations throughout the watersheds, exhibiting a diversity of life histories, behaviors, and asynchronous population dynamics (Parken et al. 2008). There are also several chinook salmon hatcheries within the watershed that contribute to fisheries, but returns to these hatcheries are not more stable than returns to wild populations and thus do not bias results (data not shown). FSC rights have priority over commercial and recreational fisheries. We compiled Fraser River FSC catch reports from publicly available online sources and through requests to Fisheries and Oceans Canada (Ottawa, Ontario, Canada). For each FSC management region along the Fraser River, we acquired yearly catch totals from 1983 to 2012. Adjacent management regions were consolidated if they were grouped in some years and not in others. We used the downstream point of each management region to estimate the catchment area of the fishery. Data were restricted to sites with average annual catches that were >20 fish and had data for >9 years, leaving a total of 19 sites that integrated catchment sizes ranging from 3691 to 229 841 km^2. For fisheries, an event of critical magnitude was a year with poor catch, defined as when the annual catch was less than 50% of the average catch for that site. More stable FSC fisheries indicate more consistent fulfilment of this culturally important harvest.

Water discharge

The Fraser River flows through the greater urban area of Vancouver, including approximately 2.6 million people and 13×10^9 Canadian dollars (CN$) of structures, much of it located behind dikes that isolate the river from its historic floodplain (Fraser Basin Council 2010). Thus, stability of flows is critical for the people in this watershed. River height data are collected by hydrometric gauges continuously or hourly and then are converted to discharges based on stage–discharge relationships by the Water Survey of Canada (WSC; Environment Canada, Gatineau, Quebec, Canada). Data were extracted from WSC's publically available HYDAT database (version 1.0). Discharge data were aggregated to daily averages. The catchment areas of flow sites ranged from 19.8 to 227 643 km^2. We used the 1948 Hope flood of the lower Fraser River as a reference for an extreme high-flow event which caused approximately CN$20 million in damage (in 1948 dollars) and flooded one-third of the lower watershed (Ministry of Environment and Northwest Hydraulic Consultants 2008). Given that the discharge during this flood was 5.8 times the long-term average flow at the lower Fraser River, we considered an extreme high-flow event to be when the flow was at least 5.8 times greater than the average daily discharge of a site, our index of an event of critical magnitude.

Water temperature

The Fraser River has warmed 1.5°C over the last five decades, and these temperatures are starting to adversely impact key native species such as sockeye salmon (*O. nerka*) (Patterson et al. 2007, Macdonald et al. 2010). Thus, stability of temperature is important for the freshwater biodiversity of this watershed. We focused our temperature analyses on the summer months when adult salmon migrate (June, July, August), and restricted analyses to sites with at least 250 d of data—three summers of data. Water temperature data were primarily collected by the Department of Fisheries and Oceans Canada (DFO) with support from WSC and were extracted from DFO's Environmental Watch Program internally managed database. Temperature data were collected from temperature stations and included both continuous and hourly measurements, depending on site; temperature data were aggregated to daily averages. The catchment areas of temperature sites ranged from 56 to 229 684 km^2. Given that temperatures are the result of mixing temperatures (not adding temperatures) and are on an interval scale, we calculated the SD as an index of magnitude of variation. We considered an extreme warm water temperature day to be when the daily temperature was 30% higher than the average temperature of the site during the summer period from

1980 to 2012, our metric of an event of critical magnitude.

Results

Mapping stability on the dendritic river network of the Fraser River revealed striking watershed-scale patterns of emergent stability (Fig. 1). All high-variability sites, across response variables, occurred in the smaller catchments (Fig. 1). The few small-catchment sites with low variation for water flow and water temperature were typically downstream of a lake. From fish catches to water flows to water temperatures, the highest stability (lowest CV or SD) was consistently found in the sites that integrated the largest catchments. Thus, the whole catchment is more stable than its component catchments, a pattern that was consistent across these diverse response variables.

Fisheries that integrated the largest catchments and thus the most salmon population diversity were 2.6 times as stable (average CV = 0.48) as those in the smallest catchments (average CV = 1.26; Fig. 2a). The probability of a poor catch year (less than one-half of average annual catch) also decreased with increasing catchment area (Fig. 2d). Poor catches occurred every other year in the smallest catchments, but only once every seven years in the largest catchments. Thus, watershed structure is connected to stability of First Nations fisheries and cultures (Lepofsky et al. 2005).

Flows of rivers in the largest catchments were 2.2 times more stable than those in smallest catchments. Specifically, the CV of daily flow averaged 1.52 for the smallest catchments, but was variable, and then rapidly decreased with increasing catchment area, approaching a CV of 0.70 in catchments that exceeded 50 000 km^2 (Fig. 2b). This remaining variation represents the flood pulse of the predictable seasonal pattern of water flow (Bayley 1995). The probability of extreme high-flow events was also attenuated in larger catchments (Fig. 2e). Streams with the smallest catchments had extreme high flows on average every one in seven days (averaged over the time series). In contrast, extreme high flows only occurred one time at most in the biggest catchments during the 11 000-day (30-year) time series. In other words, small streams on average have >1000 times more extreme high-flow events than the lower Fraser River. Thus, larger basins are buffered from extreme flows, which supports previous work (Woods et al. 1995).

Water temperature also showed greater stability as upstream catchment area increased. Summer water temperatures in the smallest catchments were 1.5 times more variable on average than the largest catchments (Fig. 2c). In addition, extreme warm water temperatures (when the temperature was at least 30% higher than the average daily temperature of the site for the summer period) were less frequent in sites with larger catchments (Fig. 2f). Elevated water temperatures negatively impact the freshwater biodiversity of this watershed, and historically, elevated temperatures are associated with

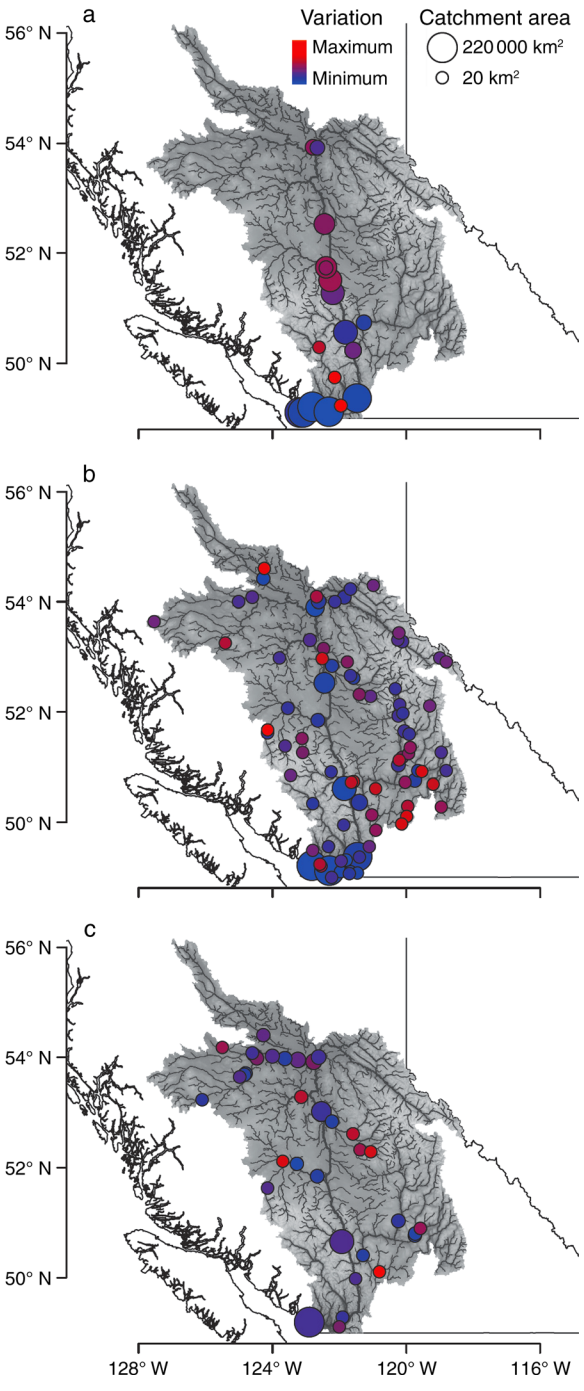

Fig. 1. Mapping stability (variation) of processes within the watershed of the Fraser River, British Columbia, Canada, of (a) First Nations fisheries, (b) water flows, and (c) water temperatures. The Fraser River watershed is shown as the gray region, with lighter colors indicating higher elevations. Dark gray lines indicate streams that are at least fourth order. Each point represents a sampling site used in analyses. The size of the points scales to the catchment area of each sampling site, with larger circles indicating a larger catchment area. Color scales to the range of variability observed in each variable, with red indicating more variability (higher coefficient of variation [CV] or standard deviation [SD]) and blue indicating more stability (lower CV or SD).

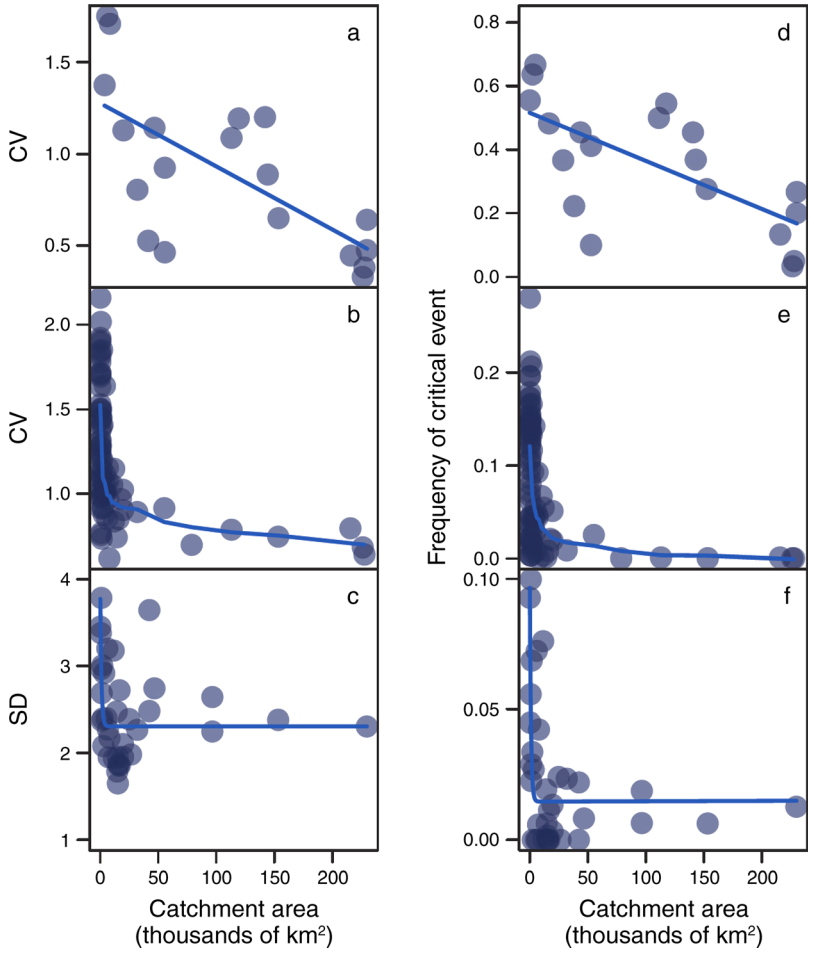

FIG. 2. Relationships between catchment area of sites within the Fraser River watershed and stability. The left column shows the magnitude of variability, as quantified by the coefficient of variation for the additive processes (a) annual chinook salmon catch by First Nations and (b) daily water flow, and the standard deviation for the averaging process (c) daily summer temperature. The right column shows the frequency (measured as the proportion of measurements of critical events given the total number of observations; for catches it is the proportion of years while the other variables have different time scales) of events of critical magnitude: (d) poor annual chinook salmon catch (blue line shows linear fit), (e) extreme high water flows that are relatively higher than the 1948 Hope flood (blue lines shows lowess fit), and (f) extreme warm daily water temperatures relative to site averages (blue lines shows exponential fit). See *Materials and methods* for more details.

massive die-offs of migrating sockeye salmon (Patterson et al. 2007, Macdonald et al. 2010).

DISCUSSION

We found consistently strong patterns of watershed stability in the expansive free-flowing Fraser River watershed, Canada. Specifically, larger catchments exhibited less variability, including fewer extreme events, than the average smaller catchments, from First Nations fishery catches to water temperatures to water flows. These data provide evidence that stability may be an emergent property of river networks, illustrated from one of the few remaining relatively intact large river networks in the world.

Observed patterns of watershed stability are likely due to progressive integration of asynchronous upstream dynamics, but may depend on scale. Quesnel River, as an example of a major tributary on the Fraser River, exhibits intense water flow variability at periods of several months that represent the seasonal patterns of runoff, short-term variability representing specific storm events, and multi-year variability likely driven by longer-term climatic forcing (Appendix: Fig. A2). The coalescence of the Quesnel River and Fraser River absorbs variability. We observed this effect by measuring the normalized correlation between the non-stationary frequency spectra of the upstream and downstream time series data, calculated as wavelet coherency (Cazelles et al. 2008). High coherence indicates that the upstream and downstream flow data are linearly correlated at a given time and for a given frequency (Appendix: Fig. A2). For the Quesnel River example, tributary coalescence does not dampen the underlying seasonal flood pulse (Bayley 1995) but both higher (week to day)

PLATE 1. Aerial view of a stream network in the headwaters of a large free-flowing river in British Columbia, Canada. Through integrating upstream dynamics from their tributaries, rivers may act as a natural portfolio that stabilizes dynamics. Photo credit: J. W. Moore.

frequency and lower (year) frequency variability is attenuated (Appendix: Fig. A2). By contrast, the upstream branch of the Fraser River with the majority of the flow is strongly correlated with the downstream reach, except at high frequencies (Appendix: Fig. A2, right panel). Thus, two branches coming together aggregate and stabilize dynamics, but this depends on temporal scale.

There were also key differences in the patterns among response variables. Variance appeared to asymptote at a nonzero level for both temperature and flow; river networks do not absorb all variability. The asymptote will likely be set by shared environmental forcing that occurs at a spatial scale that exceeds the size of the watershed. For instance, the seasonal synchronous variation of precipitation and snowmelt will be expressed throughout the watershed and thus will not be dampened by river structure, thereby producing the annual rise and fall of the flood pulse that is fundamental to the dynamics and productivity of large rivers (Bayley 1995). Different relationships between catchment area and stability can likely provide information into the spatial extent of environmental forcing. Indeed, the variability of different watershed processes, from physics to fish, is likely expressed on different spatial scales. Further, it is important to note that the different response variables were quantified on different time domains, which likely contributes to observed differences among response variables.

Previous observations from different disciplines support predictions from the watershed stability hypothesis (Appendix: Table A1). For example, analyses of salmon population dynamics show greater stability when the spatial scale of statistical aggregation is larger (Moore et al. 2010, Schindler et al. 2010, Carlson and Satterthwaite 2011). Classic research has noted that variation in water flows scales inversely with river size (Gupta and Waymire 1990, Woods et al. 1995, Chetelat and Pick 2001, Sabo et al. 2010). These examples from a diversity of fields highlight the potential power of our simple hypothesis to synthesize understanding of watershed dynamics across multiple disciplines. It is likely that the watershed stability hypothesis applies to many other response variables that have not yet been examined in a watershed context, but watershed-scale data sets from large, free-flowing watersheds are rare.

Specific watershed habitats can also alter patterns of downstream stability by directly influencing variability as well as their asynchrony. Snowpack, glaciers, lakes, wetlands, and groundwater can store water, thereby attenuating downstream hydrologic variability (Rodriguez-Iturbe et al. 2009). Divergent water flow travel-time

distributions among tributaries can desynchronize dynamics (Rinaldo et al. 1991). Variability of riverine populations will be modulated by their adaptations to river dynamics (Lytle and Poff 2004). In addition, downstream sites with larger catchments will generally have lower elevation and more water volume, which will influence solar heating of water due to thermal inertia and surface-to-volume ratios (Vannote et al. 1980). Downstream fisheries could alter the dynamics of upstream fisheries. The watershed stability hypothesis could provide a heuristic and quantitative framework to examine how these different attributes of watersheds contribute to the stability of watershed processes (Appendix). While our analysis focused on patterns within a large, free-flowing river network, there is an opportunity for future comparisons across and within watersheds to examine how river attributes such as branching structure and size influence patterns of stability.

Freshwater systems are increasingly pressured by climatic variability and anthropogenic change (Postel et al. 1996, Easterling et al. 2000, Milly et al. 2008, Vörösmarty et al. 2010). While river systems are inherently variable and this variability supports their diversity and productivity (Bayley 1995), our research indicates that free-flowing river networks can function as natural portfolios that increase their stability, defending against some aspects of variability, an important but underappreciated ecosystem service (Costanza et al. 1997, Postel and Thompson 2005, Botter et al. 2013). Here, we illustrated that a large, free-flowing river network has stability that emerges from its integration of biological, climatic, and hydrologic diversity.

Given that the watershed stability hypothesis is founded on longitudinal connections in rivers and integration of diversity, human activities that decrease connectivity and diversity could compromise the stability of river processes. Anthropogenic land-use change such as deforestation and urbanization can directly increase variability, and this variability can spread through river networks. Furthermore, anthropogenic change can homogenize watershed dynamics (Moore et al. 2010), and thus weaken portfolio stability. Anthropogenic fragmentation of river networks, such as by dams (Nilsson et al. 2005, Milly et al. 2008), may directly stabilize flows but could also weaken some portfolio processes such as river metapopulation persistence (Fagan 2002, Yeakel et al. 2014). Integrated watershed management and governance could help align scales of management and river processes (Postel and Thompson 2005, Parkes et al. 2010) to conserve the underappreciated stability of watersheds.

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Supplemental Material

Ecological Archives

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