Appendix A

Applying portfolio theory to river networks

In this manuscript, we propose and examine the watershed stability hypothesis. There are multiple uses of the word "stability" that are somewhat interconnected (McCann 2000, Ives and Carpenter 2007, Donohue et al. 2013). Here we focus on stability in a statistical sense, the lack of variability through time, following Doak et al. (1998). This statistical stability provides an index of the ability of the system to absorb unmeasured and stochastic perturbations. As noted by Doak et al. (1998), the principles we outline below also apply to the stability of responses to known perturbations (in other words, resilience). A common metric of this type of stability is the coefficient of variation (CV), where variance is normalized by the mean. Higher CV indicates lower stability. However, for dynamics that are the result of mixtures (e.g., temperatures), then standard deviation is a more appropriate index of variability.

There is an enormous body of literature on the importance of diversity to stability of ecosystems (McCann 2000). Pioneering work (Odum 1953, MacArthur 1955) suggested that communities with many species were more resistant and resilient to perturbations. Doak et al. (1998) illustrated that stability was a "statistical inevitability" resulting from the statistical averaging of asynchronous dynamics. Tilman et al. (1998) agreed that diversity can confer stability, but noted that it will depend on the scaling between variance and the mean. Ecological studies such as these have increasingly adopted insights from economics (Figge 2004, Koellner and Schmitz 2006), where it has long been realized that diverse portfolios can be more stable (Markowitz 1952).

Portfolio theory provides a quantitative basis to predict variance throughout river networks. Specifically, the variance can be predicted throughout the watershed by knowing the proportional contribution, variance, and covariation among tributaries. The variance of the river (σ_R^2) can be predicted as the average of the variances (σ^2) of *n* upstream tributaries or river sections plus the covariance among upstream units (COV_{jk}), weighted by the proportional contribution (X_j) of each unit:

$$\sigma_R^2 = \sum_{j=1}^{n} X^2 \sigma_j^2 + \sum_{j=1}^{n} \sum_{\substack{k=1 \\ k \neq j}}^{n} X_j X_k COV_{jk}$$

To compare the variances, variance is often normalized by the mean (μ_R) to estimate the coefficient of variation (*CV*):

$$CV = \sigma_R^2 / \mu_R$$

As shown by Doak et al. (1998), as *n* increases, the CV decreases. In addition, as the covariation decreases among assets (increased asynchrony), the CV decreases (Doak et al. 1998). Applying this to rivers, sites with more upstream tributaries are predicted to be more stable (Yeakel et al. 2014). Furthermore, sites that integrate tributaries with more asynchronous dynamics (lower correlation coefficient) are predicted to be more stable. Not surprisingly, relatively smaller

tributaries are predicted to influence downstream dynamics less than larger tributaries. The number of tributaries scales positively to catchment area (Horton 1945, Rodríguez-Iturbe and Rinaldo 2001). Asynchrony generally increases as distance increases (Moran 1953). Thus, both the number of "assets" and the asynchrony among "assets" should increase with increasing catchment area. Therefore, here we use catchment area as our metric of watershed diversity. We recently illustrated the mathematical theory that links watershed structure, such as the branching probability and location in the river network, to metapopulation stability (Yeakel et al. 2014).

The watershed stability hypothesis builds on past work on watershed structure and aquatic processes. The River Continuum Concept (Vannote et al. 1980) examines how carbon cycling in river systems changes from their headwaters to their outlets due to progressive shifts in carbon sources and processing. As flows transport materials downstream and as river size increases, there are predictable shifts in the primary sources of carbon and the communities that rely on that carbon. Benda et al. (2004) highlighted the importance of tributary junctions as dynamic regions that add complexity to river systems and vary predictably across watersheds. Recent research on fisheries stability has appreciated the importance of scale of aggregation--sockeye salmon life-history variation and associated asynchronous population dynamics has led to remarkably stable catches of sockeye salmon over 100+ years of commercial fishing (Hilborn et al. 2003, Schindler et al. 2010). Studies of river science have long appreciated scaling patterns in river dynamics (Rodríguez-Iturbe and Rinaldo 2001, Singh 2003), such as for water temperature as well as flow variability (Vannote and Sweeney 1980) or flashiness (Woods et al. 1995).

Predicted stability should match observed stability if downstream reaches are an aggregate of upstream reaches. However, in many cases, river dynamics are likely more controlled by internal processes. The watershed stability hypothesis may not apply to these scenarios. We hope that the quantitative basis for the watershed stability hypothesis will serve as a null model to compare against data. Theory can lend insights when predictions are not met, thereby quantifying processes that are not captured in a simplified framework such as this. Through comparing expected to observed, one can investigate whether rivers are more or less stable than predicted based on the simple rules outlined above. If downstream habitats are more variable than predicted, this deviance can illuminate the magnitude of internal variation that is generated. For instance, deviation from expected sediment supply dynamics might illuminate the transition to a deposition zone. In essence, this null approach can reveal the degree to which rivers are a function of local versus upstream dynamics. We anticipate that some response variables, scales, and watersheds will not exhibit the predicted patterns of watershed stability. Specifically, when local sources of variation swamp upstream sources of variation, then upstream catchment may have little influence on downstream stability. Highlighting and identifying these exceptions could lead to new insights about how watersheds function. Furthermore, such a null model could be useful in management applications to examine how specific land use changes alter patterns of watershed stability, either through changing the covariance (COV_{jk}) or the variance (σ_j^2). Explicit testing of such a watershed variance model necessitates a shift in study design to examine patterns of stability in watersheds.

LITERATURE CITED

Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock. 2004. The
network dynamics hypothesis: how channel networks structure riverine habitats. BioScience
54:413.

Doak, D. F., D. Bigger, E. K. Harding, M. A. Marvier, R. E. O. Malley, and D. Thomson. 1998.
The statistical inevitability of stability-diversity relationships in community ecology. The
American Naturalist 151:264–276.

Donohue, I., O. L. Petchey, J. M. Montoya, A. L. Jackson, L. McNally, M. Viana, K. Healy, M.
Lurgi, N. E. O'Connor, and M. C. Emmerson. 2013. On the dimensionality of ecological
stability. Ecology Letters 16:421–429.

Figge, F. 2004. Bio-folio: applying portfolio theory to biodiversity. Biodiversity and
Conservation 13:827–849.

Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries
sustainability. Proceedings of the National Academy of Sciences 100:6564–6568.

Horton, R. E. 1945. Erosional development of streams and their drainage basins; hydrophysical
approach to quantitative morphology. Geological Society of America Bulletin 56:275–370.

Ives, A. R., and S. R. Carpenter. 2007. Stability and diversity of ecosystems. Science 317:58–62.

Koellner, T., and O. J. Schmitz. 2006. Biodiversity , ecosystem function, and investment risk.
BioScience 56:977–986.

MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. Ecology 36:533–536.

Markowitz, H. 1952. Portfolio selection. The Journal of Finance 7:77–91.

McCann, K. S. 2000. The diversity–stability debate. Nature 405:228–233.

Moran, P. A. P. 1953. The statistical analysis of the Canadian lynx cycle II. synchronization and meteorology. Australian Journal of Zoology 1::291–298.

Odum, E. P. 1953. Fundamentals of Ecology. Pages 1–387. W. B. Saunders Co., London, England.

Rodríguez-Iturbe, I., and A. Rinaldo. 2001. Fractal river basins: chance and self-organization. Page 564. Cambridge University Press.

Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609–12.

Singh, V. P. 2003. On the theories of hydraulic geometry. International Journal of Sediment Research 18:196–218.

Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity-stability relationships: statistical inevitability or ecological consequence? The American Naturalist 151:277–282.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The

river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Vannote, R. L., and B. W. Sweeney. 1980. Geographic analysis of thermal equilibria: a

conceptual model for evaluating the effect of natural and modified thermal regimes on

aquatic insect communities. The American Naturalist 115:667–695.

Woods, R., M. Sivapalan, and M. Duncan. 1995. Investigating the representative elementary area

concept based on field data. Hydrological Processes 9:291–312.

Yeakel, J. D., J. W. Moore, P. R. Guimarães, and M. A. M. de Aguiar. 2014. Synchronisation

and stability in river metapopulation networks. Ecology Letters 17:273–283.
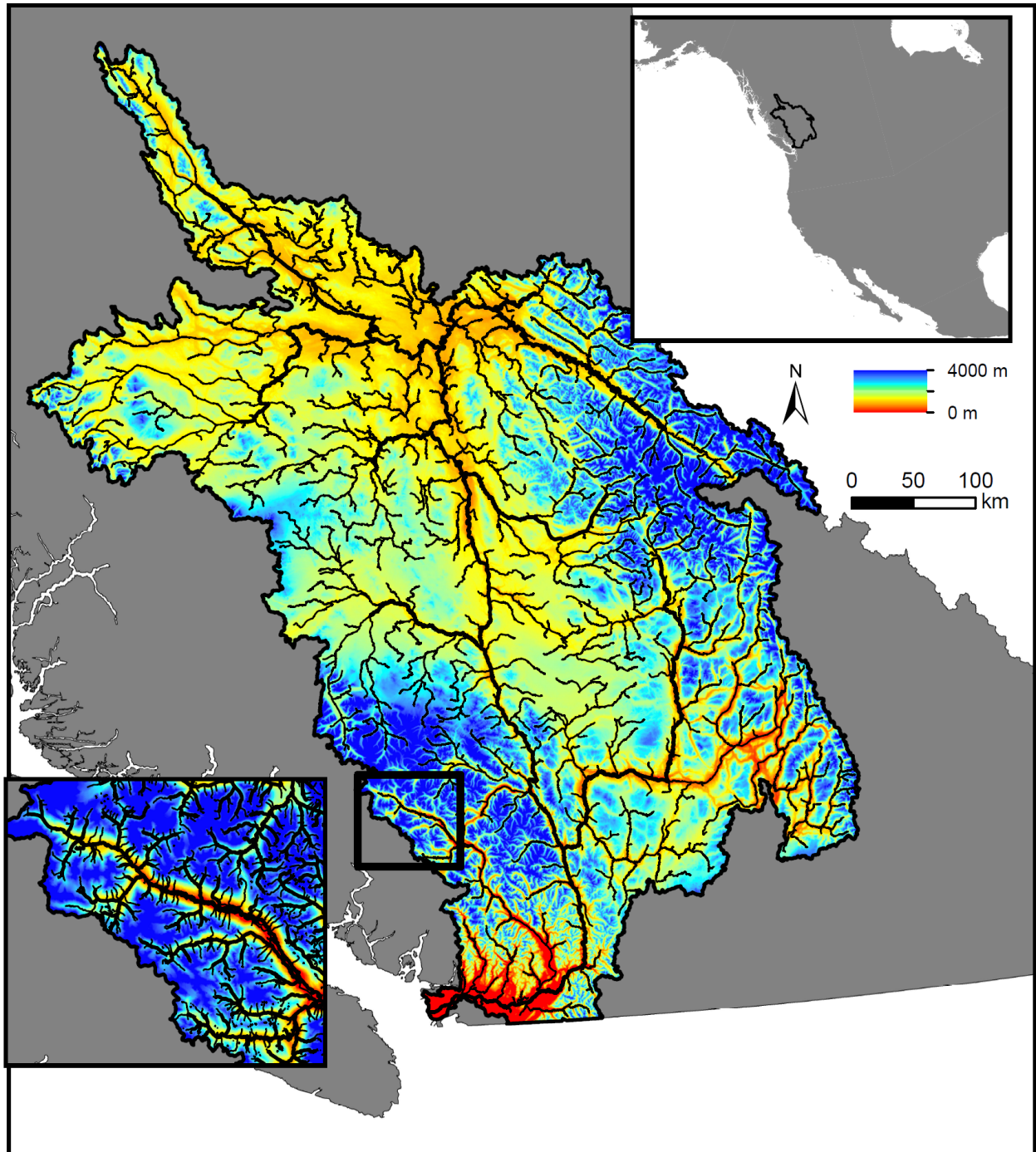
FIG. A1. The vast fractal dendritic river network of the Fraser River. Streams at least fourth order are shown on the primary map, zoomed in inset map shows streams at least second order. Overview map in the upper right shows the location of the watershed in relation to North America. Colour indicates the elevation, highlighting the geomorphic complexity integrated by this catchment.
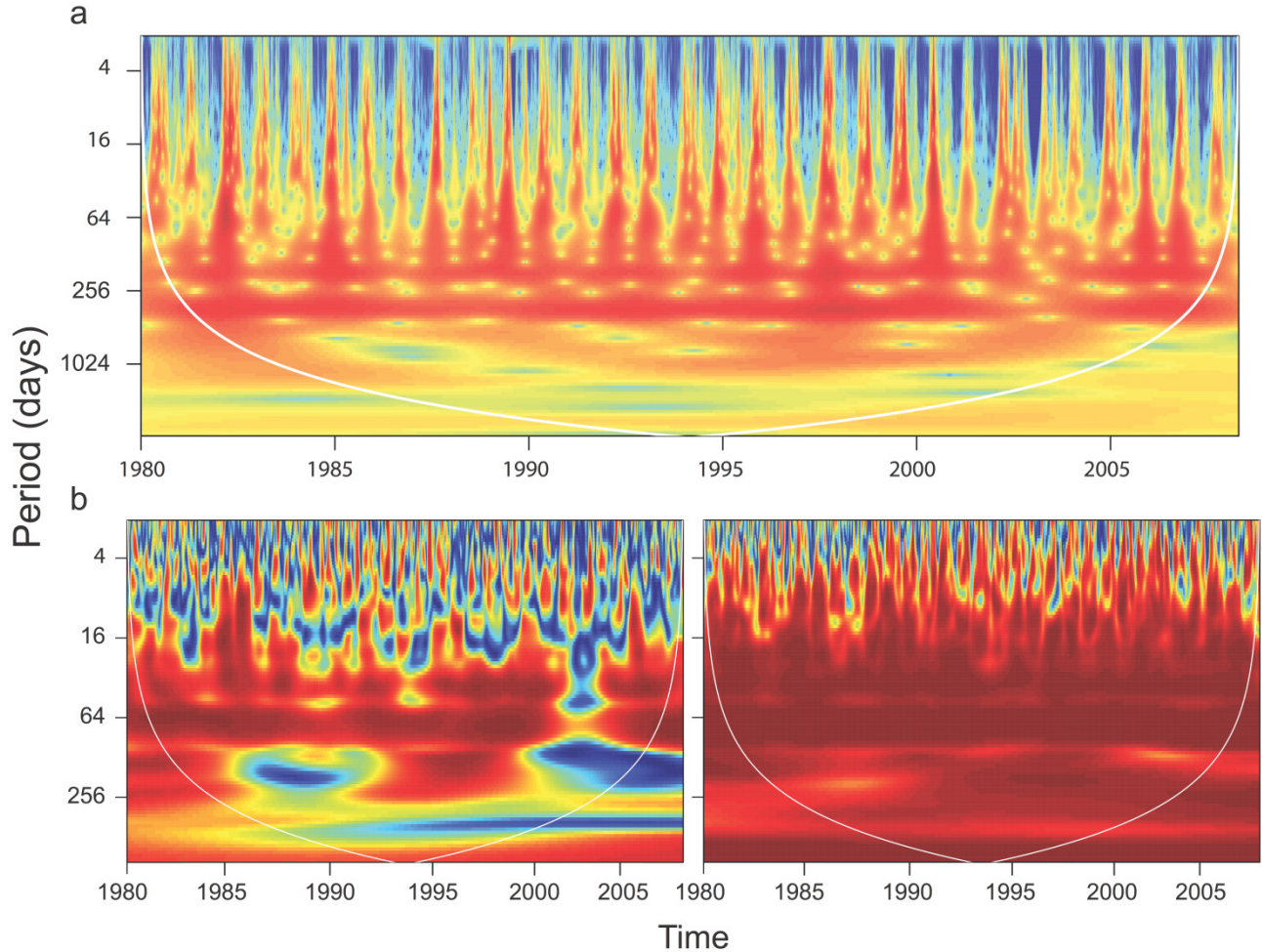
FIG. A2. Frequencies of water flow variability over time and the attenuation of asynchronous dynamics. Wavelet scalogram plot for water flow time-series (m³ s⁻¹) from 1980 to 2010 on the Quesnel River in the Fraser River watershed, highlighting the multiple frequencies of variability (**a**). Colors denote wavelet vector coefficients (warmers colors correspond to larger coefficients and thus greater variability at a given frequency), which scale the relative contribution of different frequencies for flow data as a function of time. Wavelet coherency between two upriver flow stations and the downstream confluence flow station (**b**). Wavelet coherence measures the correlation between the spectra of the up- and downstream stations; warmer colors denote greater correlation (on a scale from 0 to 1). Left panel is the coherence between the Quesnel River and downstream Fraser River site, right panel is the coherence of the Fraser River above and below the confluence. Blue colors indicate low correlation of up- and downstream flow at a given frequency and time, highlighting the attenuation of short-term (high frequency) variability in both cases, and long-term (low frequency) variability in the case of the smaller Quesnel River. White lines denote regions susceptible to edge effects (cone of influence).

TABLE A1. Empirical examples of relationships between watersheds and their biotic and abiotic stability. This is not an all-encompassing literature search, but rather are examples of comparisons of variability of sites from different locations within watersheds, highlighting the potential generality of the watershed stability hypothesis.

Process	Example	Temporal scale	Citations
Abiotic			
Discharge	Variability in total annual discharge is lower in more downstream sites in the Fraser River watershed, British Columbia, Canada.	Annual variation across at least 10 years of data.	(1)
Temperature	Stream temperatures exhibit spatial heterogeneity in a French alpine river basin due to landscape features and stream water sources, and exhibited a trend toward increased stability in temperature in more downstream sites.	Fluctuations in temperature within a day across a summer.	(2)
Sediment transport	Larger watersheds had less time since a debris flow than smaller headwater streams in Oregon, USA.	Variation over centuries, inferred by dendrochronology.	(3)
Particulate organic matter	Particulate organic matter was more stable through time in downstream reaches of Toyo River, Japan	Seasonal variation in a single year.	(4)
Biotic			
Chinook salmon	Chinook salmon productivity was less variable with larger spatial scales of aggregation in rivers in Central Valley, California and in the Snake River watershed, USA.	Annual variation over 5 decades.	(5, 6)
Sockeye salmon	Sockeye salmon returns and productivity were less variable in Bristol Bay, Alaska, USA, when considered across the entire regional stock system than across component rivers populations, and were most variable considered across individual spawning populations.	Annual variation over 5 decades.	(7)

REFERENCES FROM TABLE A1.

1.   Déry SJ, Hernández-Henríquez MA, Owens PN, Parkes MW, Petticrew EL (2012) A century of hydrological variability and trends in the Fraser River Basin. Environmental Research Letters 7:1–10.

2.   Brown LE, Hannah DM (2008) Spatial heterogeneity of water temperature across an alpine river basin. Hydrological Processes 967:954–967.

3.   May CL, Gresswell RE (2004) Spatial and temporal patterns of debris-flow deposition in the Oregon Coast Range, USA. Geomorphology 57:135–149.

4.   Akamatsu F, Kobayashi S, Amano K, Nakanishi S, Oshima Y (2011) Longitudinal and seasonal changes in the origin and quality of transported particulate organic matter along a gravel-bed river. Hydrobiologia 669:183–197.

5.   Carlson SM, Satterthwaite WH (2011) Weakened portfolio effect in a collapsed salmon population complex. Canadian Journal of Fisheries and Aquatic Sciences 68:1579–1589.

6.   Moore JW, McClure M, Rogers LA, Schindler DE (2010) Synchronization and portfolio performance of threatened salmon. Conservation Letters 3:340–348.

7.   Schindler DE et al. (2010) Population diversity and the portfolio effect in an exploited species. Nature 465:609–12.