The Role of Discharge Variation in Scaling of Drainage Area and Food Chain Length in Rivers

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The Role of Discharge Variation in Scaling of Drainage Area and Food Chain Length in Rivers

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Food chain length (FCL) is a fundamental component of food web structure. Studies in a variety of ecosystems suggest that FCL is determined by energy supply, environmental stability, and/or ecosystem size, but the nature of the relationship between environmental stability and FCL, and the mechanism linking ecosystem size to FCL, remain unclear. Here we show that FCL increases with drainage area and decreases with hydrologic variability and intermittency across 36 North American rivers. Our analysis further suggests that hydrologic variability is the mechanism underlying the correlation between ecosystem size and FCL in rivers. Ecosystem size lengthens river food chains by integrating and attenuating discharge variation through stream networks, thereby enhancing environmental stability in larger river systems.

Food chain length (FCL) is a key measure of the vertical structure of food webs (*1*, *2*) that determines energy flow through ecosystems (*3*), carbon exchange between freshwater ecosystems and the atmosphere (*4*), and nutrient cycling (*5*). FCL is also important to human health, influencing the bioaccumulation of contaminants in top predators consumed by humans (*6*). Ecological theory suggests that FCL should increase with energy supply (*7*, *8*), the available energy pool (*9*), and environmental stability (*8*). In contrast, empirical studies have revealed weak effects of energy supply (*10*–*12*) and contradictory reports of negative, positive, or null effects of environmental variation on FCL (*10*, *12*). Recent studies show a strong effect of ecosystem size on FCL in lakes and on oceanic islands (*11*, *13*), but the mechanisms underlying this relationship remain unclear (*12*, *14*).

In river ecosystems, climate change and human appropriation of fresh water are altering discharge variability and the frequency of intermittency across the globe (*15*). These hydrologic alterations have implications for the structure of river food webs. FCL in rivers may vary with the stability of the environment [for example., $\propto$ 1/(flow variation)], ecosystem size (such as drainage area), and energy supply. All three are correlated because the magnitude of high flows, channel geometry, and the relative supply of aquatic and terrestrial energy sources (such as algae and leaf litter from riparian trees, respectively) vary with drainage area (*16*–*18*). Thus, flow variation and other putative controls of FCL may scale with drainage area and mechanistically link ecosystem size to FCL. To date, no single study has addressed the simultaneous effects of energy supply, environmental variation, and ecosystem size—and correlations among these drivers—on the length of food chains in rivers or any other ecosystem.

We tested the role of ecosystem size, environmental stability, and energy supply on FCL in 36 rivers in North America. We define FCL as the maximum trophic position of stream-dwelling consumers measured via a stable isotope approach, which can accommodate omnivory and non-integer values of FCL (*19*). Our analysis expands on previous work on FCL in three ways. First, our study sites include a comprehensive range of values for all putative controls of FCL (*20*): a variation of >6 orders of magnitude in ecosystem size [drainage area (A_d) = 0.35 to 10^6 km^2], a variation of >3 orders of magnitude in energy supply [gross primary production (GPP) = 0.06 to 18.9 g of O_2 m^{-2} day^{-1}], and high-flow variation [σ_{HF} (*21*) = 0.03 to 12.9]. Our study sites also include both perennial and intermittent rivers, providing us with an opportunity to quantify how river drying affects riverine food web structure. Second, we used a hybrid of spectral and extreme event statistics to quantify environmental variation [($\propto$ 1/(environmental stability)], which provides a quantitative measure of discharge variation with reference to long-term discharge patterns (*21*). Third, we used path analysis to quantify and compare the path coefficients of drainage area→FCL and drainage area→flow variation→FCL relationships. In doing this, we asked whether ecosystem size has direct effects on FCL, or whether these effects are indirect and mediated via scaling between drainage area and flow variability (*22*).

We found that FCL increased with ecosystem size and decreased with σ_{HF} but was unrelated to energy supply (Fig. 1), which is consistent with previous findings (*23*–*25*). Ecosystem size had similar effects on FCL when measured as drainage area or cross-sectional area (fig. S1). Food chain length ranged from ~3 (predator) to nearly 5 (tertiary predator), matching the largest range of variation in FCL of any ecosystem (*10*, *11*). Top predators in 32 streams were fish, and these taxa were sufficiently large to be piscivorous in 29 sites (table S1). In intermittent streams, the top predator was consistently an invertebrate or an insectivorous fish.

Our results suggest that the strong effect of ecosystem size on FCL arises in part from a relationship between drainage area and flow variation and strong control of FCL by high- and low-flow events. σ_{HF} scaled with drainage area (Fig. 2A), but the power of the scaling relationship was significantly less steep and the mean σ_{HF} value was significantly higher in intermittent than in perennial rivers. Significant negative powers in both cases indicate that flow variation declines with drainage area. Attenuation of discharge variation results from spatial averaging in larger basins of asynchronous precipitation and high flows occurring in upstream portions of the drainage network. FCL increased

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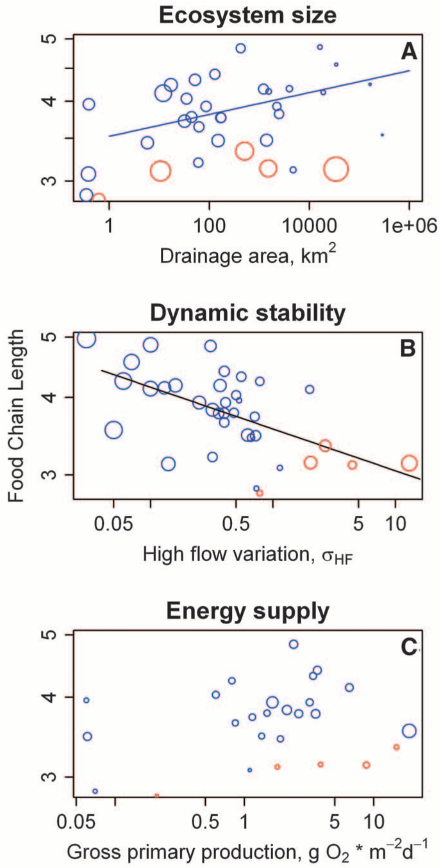

Fig. 1. Test of the effect of ecosystem size, environmental variation, and energy supply on FCL. (**A**) Relationship between drainage area (A_d in km^2) and maximum realized FCL (*20*) for streams with perennial (blue circles) and intermittent (red circles) flow. Data are shown on a double log plot. Circle diameter is proportional to σ_{HF}. A univariate mixed-effects linear model was used for the entire data set: $F = 10.58$, df = 1,29, $P < 0.005$, $R^2_{LR} = 0.48$ R^2_{LR}, coefficient of determination estimated via the likelihood ratio, LR. Regression parameters for FCL versus A_d did not differ between perennial and intermittent streams. (**B**) Relationship between σ_{HF} (*21*) and maximum realized FCL. Data are shown on a double log plot, with color as in (A). Circle diameter is proportional to drainage area. Mixed effects linear model: $F = 16.75$, df = 1, 29, $P < 0.001$, $R^2_{LR} = 0.44$. (**C**) Nonsignificant relationship between energy supply (GPP) and maximum realized FCL. Circle diameter is proportional to cross-sectional area. Mixed-effects linear model: $F = 1.37$, df = 1,20, $P > 0.25$.

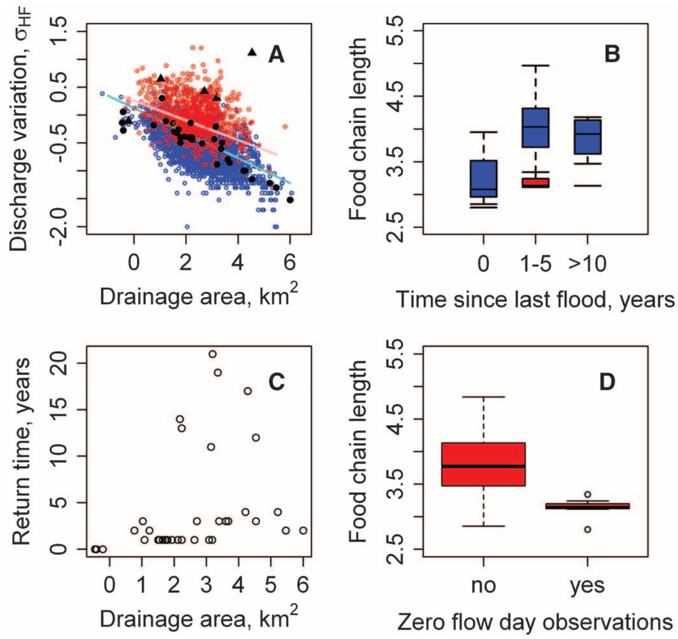

Fig. 2. Hydrologic mechanisms linking ecosystem size to FCL. (**A**) Scaling of σ_{HF} with A_d. Solid black circles and triangles are perennial and intermittent streams, respectively, from our FCL data set ($n = 31$ and 5, respectively). Blue and red open circles are supplementary data for the relationship between A_d and σ_{HF} from 3687 perennial and 866 intermittent rivers from the U.S. Geological Survey National Water Information System (NWIS) database (*20*). Cyan and pink lines are best-fit relationships between drainage area and discharge variation for NWIS data from linear mixed-effects models. Slopes for NWIS data are significantly different in a linear mixed-effects model, with an interaction term between zero flows and drainage area: $F = 50.1$, df = 1,4614, $P < 0.001$. Mean values of σ_{HF} are significantly higher in intermittent streams (linear mixed-effects model: $F = 3483.91$, df = 1,4616, $P < 0.001$). Scaling parameters (and standard errors) from model fits of the power function $\sigma_{HF} = cA_d^n$, are $c = 0.12$ (0.03), 0.25 (0.15), and $n = -0.22$ (0.004), –0.175 (0.012); for perennial and intermittent streams, respectively. The scaling relationships were significant for both stream types (linear mixed-effects model: $F = 3028.28$, df = 1,3665, $P < 0.001$, $R^2_{LR} = 0.55$; $F = 129.2$, df = 1, 865, $P < 0.001$, $R^2_{LR} = 0.33$; for perennial and intermittent streams, respectively). (**B**) Effects of high-flow return time on food chain length in perennial (blue, $n = 31$) and intermittent (red, $n = 5$) systems. Return times on the abscissa are estimated as the number of years since the last anomalous high-flow event (that is, the most recent, average daily discharge observation $>2\sigma_{HF}$). Times are binned as recent (0 years), near-recent (1 to 5 years), and long (10 or >10 years). Return times of 6 to 9 years were not observed in our data set. The effect of return times of anomalous high flows on FCL was significant in perennial rivers ($F = 4.1$, df = 2,22, $P < 0.05$; linear mixed-effects model, with return time and drainage area as fixed effects and basin as a single random effect). FCL was significantly different between recent and near-recent return time categories ($F = 6.97$, df = 1,17, sequential Bonferroni $P < 0.02$) but not for any other pairwise comparisons. The sample size was too low to test the significance of a similar asymptotic relationship between the return time of anomalous high flows and FCL in intermittent rivers. The plot shows the median (dark horizontal line), inner-quartile (box), and 95% (error bars) range of data. (**C**) Relationship between drainage area and return time of anomalous high flows ($n = 36$). The linear mixed-effects model was not significant. (**D**) Categorical effects of the occurrence of zero-flow days (*x* axis) on maximum realized FCL (*y* axis) for streams of similar size ($A_d = 10^{-1}$ to 10^5 km^2). FCL is significantly lower in intermittent streams (linear mixed-effects model: $F = 14.5$, df = 1,29, $P < 0.001$). Two seasonally intermittent streams from the SF Eel River basin without flow gages, but observed to dry during the period of observation for this study, were added to the intermediate flow type category to bolster sample size ($n = 20$, $n = 7$ for streams without and with zero flows, respectively). The plot shows the median (dark horizontal line), inner-quartile (box), and 95% range (error bars) of data and outliers (open circles).

with increasing return times of anomalous high flows (Fig. 2B), and this effect was independent of ecosystem size (Fig. 2C). The relationship between return times and FCL was asymptotic: significantly lower in systems with recent high flows (in the same year) than in systems with events occurring 1 to 5 years before FCL estimation. The shape of the relationship between high-flow return time and FCL did not differ significantly between perennial and intermittent streams, suggesting a similar effect on FCL in spite of significantly lower FCL overall in intermittent rivers. Low-flow events also constitute a form of environmental variation in rivers. Zero flows reduced FCL regardless of ecosystem size (Fig. 2D). The presence of even a single zero-flow event within the 20-year antecedent record reduced FCL by ~2/3 of a trophic level. Not all intermittent streams in our analysis were small or from arid biomes (table S1). Thus, our analyses were not confounded by covariation with other factors that could potentially influence FCL.

Finally, we used path analysis to quantify the relationships between ecosystem size, environmental stability, and FCL (Fig. 3). We applied the same path model to our full data set, including both perennial and intermittent streams and a subset that included only perennial rivers. We hypothesized that the total effect of ecosystem size (A_d) on FCL was dominated by the indirect path linking A_d to FCL via hydrologic variability ($A_d \rightarrow \sigma_{HF} \rightarrow$FCL) and that the direct effect of A_d on FCL was relatively small. For the full data set, path coefficients for the effects of A_d on σ_{HF} and σ_{HF} on FCL were both significant and negative (Fig. 3A). For the perennial subset, the path coefficient for the effect of A_d on σ_{HF} was larger and less variable than in the full data set (Fig. 3B), but the effect of σ_{HF} on FCL was not significant. Path coefficients for the direct effect of A_d on FCL were not significant for either data set; however, the total (direct and indirect) effects of A_d were significant in both analyses. The indirect path

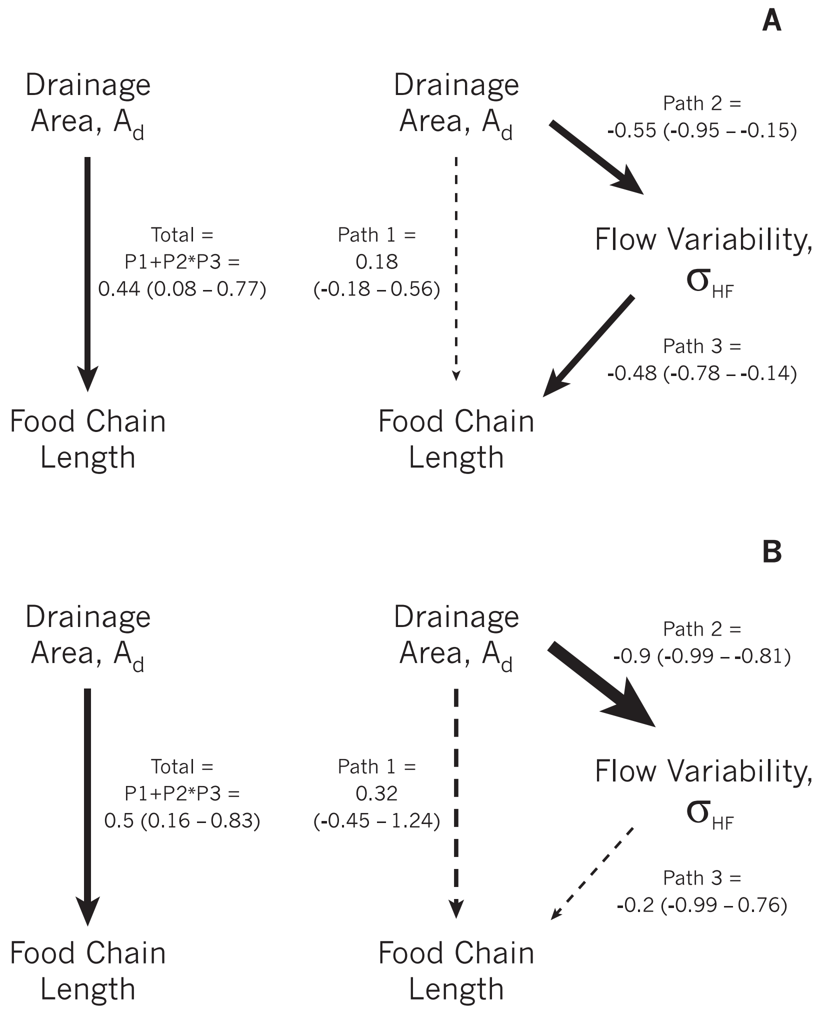

Fig. 3. Path analysis of relationships between ecosystem size (or drainage area), dynamic stability [$\propto$ 1/(flow variability)], and FCL. (**A**) Analysis of the entire data set and of perennial and intermittent streams combined. (**B**) Analysis of a subset of perennial streams. Numbers are path coefficients (mean ± bootstrapped 95% confidence limits).

($A_d \rightarrow \sigma_{HF} \rightarrow$FCL) made up >33% of the total effect of A_d on FCL in perennial streams and >60% of this total effect in all streams.

Flow variation is paramount in determining community structure (*26*, *27*) and trophic dynamics (*28*, *29*) in streams, but its effect on FCL is less clear. Previous work suggests that high flows can either lengthen or shorten food chains (*12*, *23*–*25*). Similarly, droughts increase, decrease, or have no significant effects on FCL (*12*, *30*, *31*). The idea that FCL increases with ecosystem size has support from different ecosystems, including streams (*10*–*13*), but the mechanism(s) underlying this relationship remain elusive. Our path analysis suggests that hydrologic variability is one mechanism potentially linking ecosystem size to FCL in rivers. This conclusion is strengthened by two additional lines of evidence. First, the return time of high-flow events has significant effects on FCL that were independent of drainage area. Second, σ_{HF} is consistently higher in intermittent rivers across a wide range of drainage areas. Thus, anomalous high flows occur with higher frequency in intermittent streams, independent of their size. This property, along with reduced habitat volume during periods of drying, further reduces FCL in intermittent rivers.

Our results have important implications for predicting how river food webs will respond to human- and climate-related changes in hydrology (*32*–*34*). Intermittency can have devastating effects on animal populations via reductions in habitat volume and enhanced σ_{HF}. We found that the top predators were piscivorous fish in perennial rivers, but in even the largest intermittent stream, the top predators were invertebrates or small-bodied fish. Thus, river drying will probably decrease FCL through the loss of large-bodied fishes. More broadly, our results suggest that further human- and climate-related changes in hydrology will have pronounced effects on the structure of river food webs.

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