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Ecosystem Structure Emerges as a Strong Determinant of Food-Chain Length in Linked Stream–Riparian Ecosystems

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Abstract

Environmental determinants of fluvial food-chain length (FCL) remain unresolved, with predominant hypotheses pointing to productivity, disturbance, and/or ecosystem size. However, drainage configuration (for example, drainage density, and stream length)—in spite of recent advances demonstrating the significance of catchment structure to habitat and biodiversity of fluvial systems—has yet to be explored in relation to FCL. In this study, we quantified the relative influences of ecosystem size and structure on FCL for linked stream–riparian food webs. At 19 stream reaches distributed within three mountain catchments of northern Idaho, USA, we sampled aquatic and riparian consumers and determined FCL using the naturally abundant stable isotopes ^{13}C and ^{15}N. Food-chain length was then related to reach measures of size and structure using an information-theoretic model selection approach. Model selection was followed by exploratory linear regression of FCL with purported mechanistic factors (that is, resource availability and disturbance regime). FCL ranged from 2.6 to 4.4 across study reaches and was best explained by catchment structure such as number of tributary junctions and distance to nearest downstream confluence. Regression analyses suggested that disturbance regime may mechanistically link number of tributary junctions and FCL, as well as drainage area and FCL. Our results introduce novel evidence that ecosystem structure may integrate the effects of several mechanistic factors and thus be an important predictor of food-web structure.

Key words: ecosystem size; ecosystem structure; food-chain length; food webs; stream–riparian ecosystems; tributary junctions.

Introduction

Food-chain length (FCL) represents an important measure of food-web structure and exerts strong influences on community composition, species diversity, and ecosystem function (Post and Takimoto 2007; reviewed in Sabo and others 2009). Multiple studies have shed light on the relationships between natural variation in FCL and environmental variables (Vander Zanden and Rasmussen 1999; Post and others 2000; Post

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Author contributions SMP Sullivan conceived and designed the study. SMP Sullivan collected the data with contributions from CM Cianfrani. K Hossler analyzed the data with contributions from SMP Sullivan. All authors contributed to preparation of the manuscript.

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2002b). Realized FCL, the number of energy transfers leading to a single species in a food web, is thought to be influenced by several factors, broadly categorized as resource availability, natural disturbance regime, and ecosystem size (Sabo and others 2009; Takimoto and others 2012). The resource availability hypothesis states that FCL is limited by available energy sources because energy is lost with each trophic transfer (Hutchinson 1959). The dynamical stability hypothesis (Pimm and Lawton 1977; Pimm 1982) predicts that ecosystems affected by frequent or intense disturbance should have shorter FCL as a result of either longer food chains that are less resilient to environmental perturbations than shorter food chains (Pimm and Lawton 1977) or the disproportionately strong effect of disturbance on top predators (Jenkins and others 1992). Ecosystem size is implicated as an environmental determinant of FCL (Post and others 2000) because larger ecosystems are predicted to support greater habitat heterogeneity (Persson and others 1992) and more compartmentalized food webs (Krause and others 2003). Ecosystem size may also integrate both resource availability (for example, through support of more basal resources; Cohen and Newman 1991; Sabo and others 2010) and disturbance regime (for example, by attenuating disturbance effects via spatial averaging, such as downstream reduction in flow variation within a river network through averaging of upstream heterogeneous precipitation events; Sabo and others 2010), although commonly ecosystem size is treated independently (but see Sabo and others 2010).

Whereas several studies have explored the impacts of resource availability, natural disturbance regime, and ecosystem size on FCL in streams and rivers, controls on FCL within these quintessentially dynamic systems (varying in resources, disturbance regimes, and size even within a single catchment) remain equivocal (see reviews in Sabo and others 2009; Warfe and others 2013). Ecosystem size, for instance, had a significant positive effect on FCL for 18 streams in New Zealand (R^2 = 0.18; Thompson and Townsend 2005) and 36 streams in North America (R^2 = 0.48; Sabo and others 2010), but no significant effect on FCL across 46 global streams and rivers (Vander Zanden and Fetzer 2007) or 66 reaches in northern Australia (Warfe and others 2013). Resource availability had a positive effect on FCL in the New Zealand study (assessed as algal productivity, R^2 = 0.54; Thompson and Townsend 2005), but no effect on FCL in either the North American (assessed as gross primary productivity; Sabo and others 2010) or Australian studies (assessed as total dissolved nitrogen and phosphorus; Warfe and others 2013). Likewise, FCL exhibited a significant negative relationship with disturbance regime in the North American streams (assessed as flow variation, R^2 = 0.44; Sabo and others 2010), but was not significantly affected by disturbance in the Australian streams (assessed as hydrological isolation; Warfe and others 2013).

Thus, broad FCL patterns in fluvial systems remain unresolved, suggesting the potential importance of additional or complementary environmental attributes. In particular, the influence of catchment structure on FCL has not been explored, yet represents a dynamic area of research. Early riverine paradigms, for example, have emphasized the importance of longitudinal (that is, upstream–downstream) and lateral (that is, river–floodplain) structure to community composition and trophic dynamics (Vannote and others 1980 and Junk and others 1989, respectively). Longitudinal properties of riverine structure (for example, stream order, distance to confluence) especially would be expected to correlate with FCL, in part because of their associations with ecosystem size: that is, higher stream order and shorter distance to confluence equate to greater habitat capacity and presumably the potential to support more and larger top-level consumers (Vannote and others 1980; Power and Dietrich 2002).

More recently, the potential additional importance of riverine network structure to communities and food webs has emerged (Power and Dietrich 2002; Benda and others 2004; Swan and Brown 2011; Carrara and others 2012; Altermatt and others 2013). For example, the dendritic nature of river systems has been shown to structure channel habitat and strongly influence the biodiversity and population persistence of aquatic communities, whereby areas with greater connectivity [for example, stream confluences as sites with small ecological diameters (that is, more centrally located: the ecological diameter of a site is the average distance between it and all other sites; see for example, Altermatt 2013)] support greater species richness (Benda and others 2004; Carrara and others 2012). Link magnitude (the sum of all first-order streams draining into a given stream segment) and confluence link (the number of confluences downstream of a given stream segment) have emerged as significant predictors of fish assemblage metrics (Osborne and Wiley 1992; Smith and Kraft 2005). Important characteristics of dendritic ecological networks for food-web architecture include the accumulation of resources at nodes (that is, tributary junctions), the transport of

resource subsidies from smaller tributaries to organisms restricted to larger systems, and spatial heterogeneity in predation pressure and resource availability via spatially repeating yet indirectly linked tributaries (reviewed in Grant and others 2007). We might also expect areas with greater connectivity to support longer food chains because of the addition of top or intermediate consumers in association with the increase in diversity (Cohen and Newman 1991; Post and Takimoto 2007; McHugh and others 2010).

Thus, we explored the influence of structural catchment elements—used as measures of connectedness within the drainage network—on FCL using the naturally abundant stable isotopes ^{13}C and ^{15}N at 19 study reaches in three Idaho, USA catchments. To account for the tight linkages between streams and their adjacent riparian zones (reviewed in Baxter and others 2005; Sullivan and Rodewald 2012)—as well as the importance of lateral connectivity to trophic dynamics (for example, Junk and others 1989)—we adopted a broad food-web approach, including both traditional aquatic (aquatic macroinvertebrates and fish) as well as semi-aquatic and riparian (riparian arthropods, aquatic and riparian birds) consumers. To our knowledge, this is the first stream-based study on FCL to adopt such an approach.

In addition to ecosystem size, we considered structural catchment elements related to the longitudinal, lateral, and network organization of subcatchment features. We were particularly interested in the importance of riverine ''connectedness'' to FCL, which could be manifest in two primary ways: (1) more connected sites (that is, sites downstream of more tributary junctions) were expected to support greater species richness and have higher FCL through greater resource availability and a natural disturbance regime characterized by greater predictability/less variability (Benda and others 2004), and (2) more connected sites (that is, sites with smaller ecological diameters) were expected to support greater species richness and have higher FCL through dispersal/network effects (Altermatt and others 2013). Two structural elements describing anthropogenic impacts in the region were also included (that is, road length and road density).

To our knowledge, ecosystem structure has not been considered in relation to FCL, and we thus developed this study largely within an exploratory framework. To do this, we used an information–theoretic model selection approach based on Akaike's information criterion (AIC) (Burnham and Anderson 2004) to evaluate the relative strength of evidence supporting ecosystem size and structure in determining FCL. We also considered resource availability and disturbance regime as potential mechanisms linking ecosystem size and structure to FCL through post hoc regression analysis.

Methods

Study Area Description

We conducted this study at 19 sites (that is, stream reaches) distributed across three catchments of northern Idaho: Beaver Creek Catchment (BCC, $n = 7$), Elk Creek Catchment (ECC, $n = 5$), and Mica Creek Catchment (MCC, $n = 7$; Figure 1). All catchments are located in the Northern Rockies Ecoregion and are mountainous with rugged topography and a maritime-influenced climate. We defined reaches as arbitrary units equal to 15–20× bankfull width (Harrelson and others 1994; Kondolf and Micheli 1995) and subsequently used breaks in geomorphic types to more precisely delineate reach boundaries. All study reaches were steep (≥ 0.002 m m^{-1}), confined channels dominated by gravel, cobble, and boulder substrates with limited floodplains, thereby meeting the criteria of mountain stream channels as outlined by Wohl and Merritt (2008).

Catchment Size and Structure

For each of the 19 reaches, we quantified 12 descriptors related to catchment size (drainage area and cross-sectional area) and structure (stream order, elevation, buffer canopy openness, stream length, number of tributary junctions, drainage density, distance to nearest confluence, ecological diameter, and road length and density). We recorded locations of all 19 reaches using a global positioning system (Garmin Rino 120, Olathe, KS, USA) and imported them into a geographic information system (ArcGIS 10, ESRI, Redmond, CA, USA). ArcGIS, along with United States Geological Survey (USGS) digital elevation models (25 m) and the USGS National Hydrography Dataset (NHD; high resolution—1:24,000), was used to delineate catchment boundaries and compute drainage areas. Drainage area was our primary measure of ecosystem size but was complemented with a localized estimate of cross-sectional area (McHugh and others 2010), determined from in-field measurements of bankfull width and depth. To do this, we established ten equidistant lateral transects (across the stream) and one longitudinal transect (bisecting the stream, running down its length) at

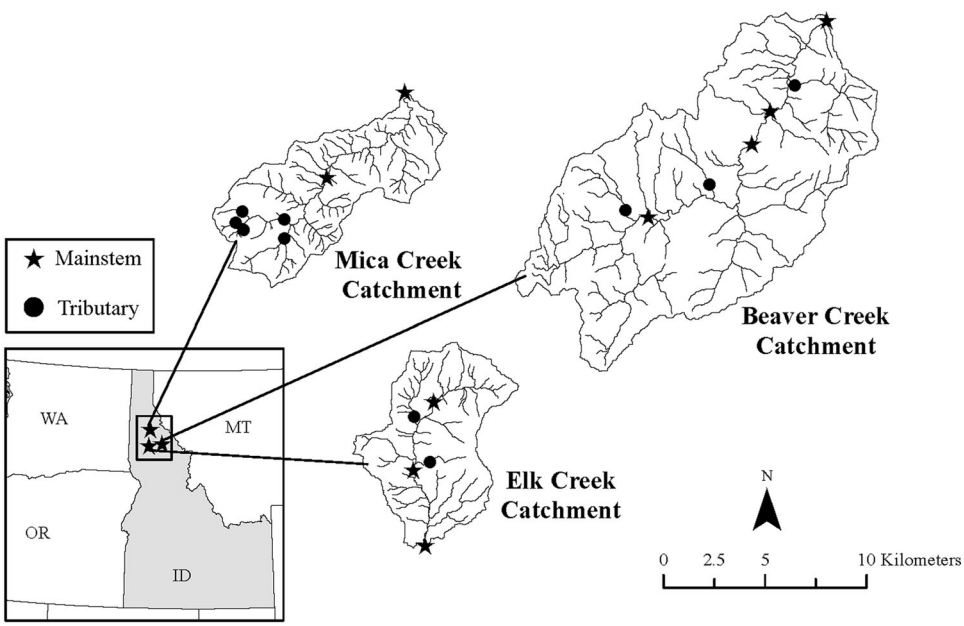

Figure 1. Locations of the three study catchments in northern Idaho, USA: Beaver Creek Catchment (BCC), Elk Creek Catchment (ECC), and Mica Creek Catchment (MCC). Also indicated are the 19 sampled reaches (*star* mainstem reach, *circle* tributary reach): BCC, $n = 7$; ECC, $n = 5$; and MCC, $n = 7$. The study reaches spanned from 46.752° to 47.790° (latitude) and −115.622° to −116.281° (longitude).

each reach. At each transect, we measured bankfull width and depth with a stadia rod, laser level, and measuring tape following Cianfrani and others (2004). From these data, we estimated cross-sectional area (bankfull width × bankfull depth).

Elevation—which can be a driver for species richness (for example, Rahbek 1995; Guo and others 2013) and subsequently might be expected to factor into food-web dynamics—was generated using the USGS (2012) StreamStats program and the 1/3 arc-second National Elevation Dataset (NED). Stream order was manually generated using the NHD and the Strahler method (1952). Total stream length within the subcatchment of each reach was measured using ArcGIS and normalized by catchment area to yield drainage density. Number of upstream junctions was tabulated as all stream intersections occurring upstream of each study reach. Distance to nearest confluence was the measured distance (in ArcGIS) between each study reach and the nearest receiving water body: North Fork of the Clearwater River (BCC), St. Joe River (MCC), and Elk Creek Reservoir (ECC). The hydrologic (or topological) distances between each reach and all other reaches within a catchment (downstream point to downstream point) were also measured in ArcGIS, then averaged to determine the ecological diameter for each reach (Altermatt 2013; Carrara and others 2014): that is, $\ell_i = \left(\sum_{j,j\neq i} d_{ij}\right) \Big/ (n-1)$, where ℓ_i is the ecological diameter for reach i; d_{ij} is the hydrologic distance between reach i and reach j ($j \neq i$); and n is the total number of reaches in the catchment. [Note, the ecological diameter is the inverse of the network property of ''closeness centrality'' as defined in Newman (2010).]

Buffer canopy openness was determined by creating 50-m buffers around the reaches using ArcGIS, then for each buffer polygon, calculating land cover percentage within the USGS National Land Cover Database 2006 (''open'' percentages were the sum of scrub/shrub and herbaceous wetland and described the proportion of riparian habitat as opposed to forested habitat in the vicinity of each reach). And finally, because of the detrimental ecological impacts of roads (see Angermeier and others 2004; Wheeler and others 2005), we included road length and density as anthropogenic catchment structural factors. Road length and density were calculated for each catchment similarly to stream length and density using the USGS Transportation Data 2008 TIGER/Line Shapefile.

Mechanistic Factors

To explore potential mechanistic drivers of FCL, we examined seven factors providing coarse measures of either resource availability or disturbance regime. For resource availability, we used periphyton biomass and detrital biomass as indicators of autochthonous and allochthonous basal resources, respectively. For disturbance regime (assessed as habitat stability), we examined five indicators: large wood (LW) density, the ratio of two-year peak flow to mean annual discharge (Q_2:Q_{ma}), and bankfull discharge (Q_{bf}) (as indicators of hydrologic regime); maximum daily change in temperature (Max ΔT; an indicator of temperature variability);

and a stream Rapid Geomorphic Assessment score (RGA; an indicator of channel stability) (see for example, McHugh and others 2010; Hette-Tronquart and others 2013).

At each reach, we collected detritus samples from three locations along the length of each reach from deposits of coarse benthic organic material (CBOM) and periphyton (that is, epilithic algae) from 10 cobbles along the longitudinal length of each reach using a nylon brush. We estimated the surface area of each cobble using the ''aluminium foil method'' as outlined by Steinman and Lamberti (1996). We filtered detritus and periphyton in the laboratory, and combined the subsamples from each reach to create composite samples. We removed fine organic particulate matter (FBOM, particles <1 mm) from the detritus, leaving primarily terrestrial leaves. Subsequently, we dried detritus and periphyton samples in a 60°C oven for 48 h and weighed the samples (mg). We then calculated periphyton mass (mg mm^{-2}) using the aluminum foil area estimates. Periphyton from a subset of the samples from each reach was also ashed at 550°C for 2 h, and then reweighed in order to obtain ash-free dry mass (AFDM).

Hydrologic disturbance regime was assessed using two calculated metrics (that is, Q_2:Q_{ma} and Q_{bf}) and one in situ measure (that is, LW density). Q_2 and Q_{ma} were obtained from the USGS (2012) StreamStats program, which uses catchment features such as drainage area, mean elevation, and mean annual precipitation to estimate stream flow statistics based on regional regression curves. Q_{bf} was calculated based on survey data using Manning's equation as $A \times R^{2/3} \times S^{1/2}/n$, where A is the cross-sectional area, R is the hydraulic radius, S is the channel slope, and n is Manning's roughness coefficient. To generate LW density estimates, we surveyed all pieces of LW >0.10 m diameter and >1.0 m length (Montgomery and others 1995). The metrics Q_2:Q_{ma} and Q_{bf} can be considered descriptors of flood frequency and magnitude, respectively; whereas LW density can integrate both (see for example, Gurnell and others 2002; Benda and others 2003, 2004), although seemed to relate more to flood magnitude within the systems of this study.

For stream temperature variability, we deployed three Thermochron iButton temperature sensor–loggers (models DS1921-Z and DS19231-H, Dallas Semiconductor, Dallas, TX, USA; ±1.0°C) at upstream, mid, and downstream points longitudinally along each reach from July 2006 to September 2007. Temperatures were logged at 1–4 h intervals. Because of miscellaneous deployment and collection issues, we used a subset consisting of six reaches in BCC and four reaches in MCC with 230 overlapping days of temperature data. From these data, we estimated water temperature variability for each of 10 reaches using the maximum daily change in temperature [Max ΔT; that is, the average ($n = 230$) of the maximum minus minimum temperature per day].

Channel stability was assessed by Rapid Geomorphic Assessment (RGA; VTDEC 2003) following protocols used in companion studies in the region (for example, Sullivan 2012). We assigned a score from 0 (worst condition) to 20 (optimal condition) for each of four geomorphic adjustment processes: channel degradation (incision), channel aggradation, over-widened channel, and change in planform (VTDEC 2003). We then summed the scores of the four categories to form the composite RGA score that can range from 0 to 80.

Biotic Sampling

To minimize temporal variation, biotic sampling was largely constrained to the summer months. Summer sampling is consistent with other stream food-web studies (for example, McHugh and others 2010) and of particular importance to our design, which included terrestrial riparian consumers that are either inactive (for example, spiders) or not present (migratory birds) during other seasons. On the average, we visited each site 15–20 times from 2006 to 2011. We collected common aquatic invertebrate larvae at six longitudinally distributed locations per reach, which were kept in unfiltered stream water for 6–8 h to evacuate their guts before preserving. Streamside riparian invertebrates (spiders of the families Tetragnathidae and Araneidae), riparian ants (Formicidae), and lepidopterans were collected by surveying immediate shoreline and riparian areas (~2 m laterally into riparian zone, ~ 3 m vertical height). Sufficient numbers of each taxon were collected for isotopic analysis (typically 6–8 for smaller-bodied organisms, 2–3 for larger-bodied).

In the lab, we sorted invertebrates to order (in some cases, to family) and the most dominant taxa were identified to family using Merritt and Cummins (1996) and Triplehorn and Johnson (2005) as guides. We grouped aquatic invertebrates by the dominant orders (Ephemeroptera, Plecoptera, Trichoptera, and Diptera) for stable isotope analysis. For riparian invertebrates, groupings were the same as those targeted for collection [spiders (Tetragnathidae and Araneidae), ants (Formicidae),

and Lepidoptera]. Aquatic and riparian invertebrates were freeze-dried for 48–72 h (using a Labconco lyophilizer), ground into a fine powder using a mortar and pestle, and packed in tin capsules. We combined tissue from multiple individuals into a single composite sample for stable isotope analysis to minimize within-site variance (Lancaster and Waldron 2001). Composite samples for each study reach comprised individuals grouped by taxonomic group.

We sampled fish with a backpack electrofisher (Smith-Root® LR12, Vancouver, WA, USA) and dip nets. At each reach, we collected a minimum of eight individual adult trout (>150 mm) and six adult sculpin, representing the dominant species present at the study reaches. Fish selected for stable isotope analysis represented six species common to our northern Idaho mountain systems: brook trout (*Salvelinus fontinalis*), Westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), rainbow trout (*O. mykiss*), Westslope cutthroat/rainbow hybrid (*O. mykiss* × *O. clarkii lewisi*), slimy sculpin (*Cottus cognatus*), shorthead sculpin (*C. confusus*), and mottled sculpin (*C. bairdi*). We included adult fish of similar size in a replicate to avoid potentially confounding effects of age-specific diets on stable isotope signatures. We removed plugs of skinless dorsal muscle from each individual (Pinnegar and Polunin 1999) and then freeze-dried, pulverized (to ensure sample homogeneity), and packed them in tin capsules.

We surveyed aquatic and riparian birds multiple times in both the morning and evening hours following a modified version of the protocol outlined in Sullivan and Vierling (2009). Based on data from these preliminary surveys, we captured species observed to consistently feed in or by the stream [Supplementary material: Table S1; note that high reliance of the avian species on aquatic primary productivity was also supported by dietary isotope analysis (described below): for example, mean reliance on aquatic productivity was 50% (σ = 7%, range 42–71%) among the sampled birds and 45% (σ = 9%, range 11–73%) among the sampled fishes]. Because of the high mobility of birds, we scouted each reach for signs of breeding activity (nesting or nest building, feeding nestlings, and territorial behavior) and constrained all bird samplings to the breeding seasons of the focal species for each study year. We used 6- and 12-m passerine mist nets placed either in the riparian zone or across the stream to capture adults and recently fledged birds. We banded each bird on first capture with US Fish and Wildlife Service (USFWS) aluminum bands, drew blood from the jugular vein (for stable isotope analysis), and stored blood in centrifuge tubes and 70% ethanol following Sullivan and Vierling (2012). Except for *Hirundo rustica* (only present for one of the study years), we collected bird blood samples from each site for at least 2 years. We used bird blood to yield information related to the short-term diet: in the case of ^{15}N, reflecting diet within 9–15 days (Hobson and Clark 1992; Bearhop and others 2002). We dried all blood samples in a 60°C oven, and subsequently freeze-dried and pulverized (using a ceramic mortar and pestle) all samples to ensure sample homogeneity. We packed samples by individual in tin capsules.

Stable Isotope Analysis

All tissue and blood samples were analyzed for ^{13}C and ^{15}N using continuous flow isotope ratio mass spectrometry (EA-IRMS) at the Washington State University Stable Isotope Core (Pullman, WA, USA). The isotopic composition of samples was expressed using conventional δ notation: δ^{13}C or δ^{15}N (‰) = $[(R_{sample}/R_{standard}) - 1] \times 1000$, where R is ^{13}C/^{12}C or ^{15}N/^{14}N for the sample or standard, with Vienna Pee Dee Belemite as the standard for C and atmospheric N_2 as the standard for N. Typical analytical precision was 0.19‰ for δ^{13}C determination and 0.08‰ for δ^{15}N determination.

Trophic Position and Structure

Food-chain length was defined as the maximum trophic position (for example, Vander Zanden and others 1999; Post and others 2000; Sabo and others 2009). The trophic position (TP) for each consumer group sampled within each reach was estimated using a single-source food-web model (Post 2002a; Anderson and Cabana 2007): $TP = \lambda + (\delta_c - \delta_{base})/\Delta$, where λ is the TP of the baseline food source (for example, 2 for a primary consumer); δ_c is the δ^{15}N signature of the consumer for which the TP is being estimated; δ_{base} is the δ^{15}N signature of the baseline food source; and Δ is the enrichment in ^{15}N per trophic level [that is, 3.4‰ based on Post (2002a) and following similar aquatic-based food-web studies (for example, McHugh and others 2010); although it should be noted that more recent studies have either questioned the use of a single, fixed enrichment factor (Caut and others 2009; Hussey and others 2014) or suggested that 3.4‰ overestimates the per trophic level ^{15}N enrichment for many consumers (Vanderklift and Ponsard 2003)]. An example food web from one of the study reaches is presented in Figure 2.

We had initially collected periphyton and detrital samples to use as baseline food sources in a two-

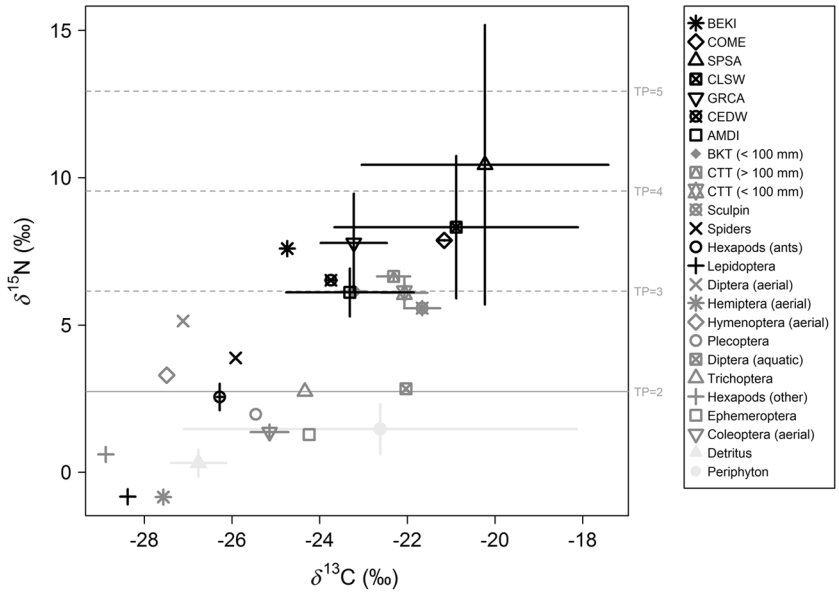

Figure 2. Isotopic (δ^{15}N vs. δ^{13}C) distribution of aquatic (*moderately shaded*) and riparian (*heavily shaded*) consumers and basal food sources (*lightly shaded*) for one of the study reaches (Mica Confluence). To estimate food-chain length (FCL), we used Trichoptera as our baseline, assigning it a trophic position (TP) of 2 and assuming a 3.4‰ enrichment in δ^{15}N per trophic step (Post 2002a). In this example, the top consumer (SPSA) was 7.7‰ above the baseline, yielding an estimated FCL of 4.3. Note also, that while a bird (SPSA) was the top consumer at this study reach, in general, top avian consumers shared a trophic niche with the large salmonid fishes [for example, AMDI and BKT (BKT point is behind AMDI)] within the sampled catchments. [*BEKI* Belted kingfisher (*C. alcyon*); *COME* common merganser (*M. merganser*); *SPSA* spotted sandpiper (*Actitis macularius*); *CLSW* Cliff swallow (*Petrochelidon pyrrhonota*); *GRCA* gray catbird (*Dumetella carolinensis*); *CEDW* Cedar waxwing (*Bombycilla cedrorum*); *AMDI* American dipper (*C. mexicanus*); *BKT* brook trout (*S. fontinalis*); *CTT* Westslope cutthroat trout (*O. clarkii lewisi*)] (*Error bars* indicate standard deviation about the mean for replicate samples).

source food-web model (Post 2002a); however, the detrital samples in particular were highly variable (for example, range of δ^{15}N across all reaches was 6.8‰) and often spanned the δ^{15}N signature range of most primary and secondary consumer groups (for example, Ephemeroptera, Trichoptera, and Plecoptera). Following recommendations of Post (2002a) and Anderson and Cabana (2007), we used invertebrates belonging to the order Trichoptera as a single baseline food source, which are generally primary consumers (for example, Anderson and Cabana 2007). Trichoptera specimens were present at all 19 reaches, had low δ^{15}N signatures, and provided a relatively stable and temporally integrated baseline in contrast to the two basal food resources, terrestrial detritus and periphyton. Trichopteran specimens belonged primarily to the families Glossosomatidae, Hydropsychidae, and Limnephilidae, which are typically scrapers, collectors, and shredders, respectively (Wiggins 2004). Note that use of the single trichopteran baseline—as opposed to using the dual periphyton (that is, aquatic) and detritus (that is, terrestrial) baselines—should not have substantially biased our estimates of FCL; as might be expected if, for example, trichopterans derived their C primarily from aquatic basal sources, whereas other consumer groups derived their C primarily from terrestrial basal sources (typically enriched in ^{15}N relative to aquatic basal sources). The mean aquatic C contribution (C_{aq}) for Trichoptera was 48%, which was in fact similar to the mean C_{aq} for each of the various consumer groups (range was 38–62%; C_{aq} determined using a dual-isotope, two-component mixing model with detritus and periphyton as the two end-members). Furthermore, we did not see a correlation between FCL and C_{aq} of the top predator (r = 0.27). Additionally, and perhaps most importantly, the trichopteran-based FCL estimates were more on par with means and ranges of FCL reported in other studies than the two-source-based FCL estimates, providing further evidence that our approach was appropriate.

Statistical Analysis

Food-chain length was first tested for spatial autocorrelation using Moran's (1950) I using two different spatial weights: (1) inverse straight-line distance [Vincenty (1975) ellipsoid] and (2) inverse

hydrologic distance [symmetric: that is, assuming upstream and downstream connectivity; for reviews of possible distance measures in streams see Peterson and others (2006) and Altermatt (2013)]. Spatial autocorrelation was a concern given our study design of sampling multiple stream reaches within a catchment; FCL, however, was not spatially autocorrelated (inverse straight-line distance: FCL, $I = -0.021$, $P = 0.80$; inverse hydrologic distance: FCL, $I = -0.017$, $P = 0.83$).

We then evaluated the 12 descriptors of catchment size and structure as potential explanatory factors for FCL using an information-theoretic model selection approach based on Akaike's information criterion (AIC) (Burnham and Anderson 2002, 2004). Competing models were selected across all three catchments combined based on the significance ($P \leq 0.05$) of the explanatory factors by linear regression. For each competing model, we calculated Akaike's information criterion with correction for small sample size (AIC_c), the relative AIC_c (that is, Δ_i), and Akaike weight or normalized model likelihood (that is, w_i) (Burnham and Anderson 2002, 2004). We evaluated models containing up to five explanatory factors. For comparison, the null model (that is, intercept only) was also included in the set of competing models. Explanatory factors were transformed as needed to meet assumptions of normality and homogeneity of variance.

Because many of the explanatory factors were highly correlated (that is, $|r| > 0.7$, none of which were included in the same model), we additionally evaluated the importance of each factor to FCL by hierarchical partitioning (Chevan and Sutherland 1991), which may be more robust to collinearity than the AIC-based model selection approach (Mac Nally 2000; Murray and Conner 2009; but see also Smith and others 2009). Following the recommendation of Murray and Conner (2009), prior to hierarchical partitioning of the factors, we first removed any factors from the list having Pearson correlations with the response variable near zero (that is, $|r| \leq 0.1$). Note that, because the software package we used to determine hierarchical partitioning was sensitive to parameter order if more than nine explanatory factors (Olea and others 2010; we had 11 parameters after removing those with near zero correlations), we randomized the parameter order ($n = 1000$) and used the mean hierarchical partitionings from the randomizations.

Model selection was followed by regression analysis of FCL and key size and structural attributes with purported mechanistic factors related to resource availability and disturbance regime (see for example, Sabo and others 2010). Following McHugh and others (2010) and Warfe and others (2013), we combined the metrics of resource availability and disturbance regime into single multivariate factors using Principal Component Analysis (PCA). For resource availability, we used the second principal component (PC) axis (from the PCA of the two metrics related to resource availability), which represented 50% of the variance and a gradient of increasing periphyton and detrital biomass (PC1 was not used in the regression because it represented opposing gradients of resource availability: that is, increasing periphyton biomass and decreasing detrital biomass). For disturbance regime, we used the first PC axis (from the PCA of the five metrics related to disturbance regime), which contained 47% of the variance and represented a gradient of increasing disturbance (primarily, lower LW density and higher Max ΔT and Q_{bf}).

All trophic calculations and statistical analyses were performed in R 2.15.1 (R Development Core Team 2012). The test for spatial autocorrelation additionally required use of the R packages GEOSPHERE (Hijmans and others 2014) and APE (Paradis and others 2014); hierarchical partitioning was performed using the R package HIER.PART (Walsh and Mac Nally 2013); and PCA required the R package VEGAN (Oksanen and others 2013).

Results

Catchment size as measured by drainage area averaged 45 km^2 ($\sigma = 51$ km^2) and ranged from 1.3 to 161.4 km^2 across the 19 reaches, with the smallest drainage area within a subcatchment of MCC and the largest in BCC (Table 1, Supplementary material: Table S2). Drainage area was correlated strongly with the other descriptor of stream or catchment magnitude ($r = 0.9$): that is, cross-sectional area (a local measure of ecosystem size), which averaged 6.6 m^2 ($\sigma = 9.4$ m^2, range 0.5–38.4 m^2). Drainage area also correlated strongly with descriptors of structure: for example, stream order, $r = 0.9$; elevation, $r = -0.8$; stream length, $r = 1.0$; confluence distance, $r = -0.8$; number of junctions, $r = 0.9$; road length, $r = 1.0$. Stream order averaged 3 ($\sigma = 1$, range 1–4); and stream length averaged 56.2 km ($\sigma = 62.8$ km, range 2.0–202.9 km; Table 1, Supplementary material: Table S2). Measures of connectivity between reaches within a catchment included distance to confluence, which averaged 12.3 km ($\sigma = 7.7$ km) and ranged from 0.2 km (in BCC) to 23.6 km (in MCC), and ecological diameter, which

Table 1. Summary of Catchment Characteristics Across All 19 Reaches and for the Reaches Within Each of the Three Catchments

	All	BCC	ECC	MCC
Size				
Drainage area (km^2)	45.0 (50.7)	67.6 (65.1)	37.6 (36.7)	27.6 (39.8)
Cross-sectional area (m^2)	6.6 (9.4)	12.3 (13.8)	3.4 (2.0)	3.2 (3.9)
Structure				
Stream order	3 (1)	3 (1)	3 (1)	3 (1)
Elevation (m)	3030 (620)	2600 (550)	3090 (260)	3410 (640)
Buffer canopy openness (%)	33.3 (37.3)	41.7 (33.9)	35.5 (41.1)	23.2 (41.1)
Stream length (km)	56.2 (62.8)	84.4 (78.5)	44.9 (43.2)	36.0 (54.1)
Tributary junctions	28 (31)	38 (35)	21 (20)	23 (35)
Drainage density (km km^{-2})	1.3 (0.2)	1.4 (0.2)	1.2 (0.3)	1.3 (0.3)
Confluence distance (km)	12.3 (7.7)	10.7 (7.7)	8.5 (5.0)	16.6 (8.0)
Ecological diameter (km)	8260 (3450)	9410 (2110)	5980 (2420)	8730 (4610)
Road length (km)	77.6 (111.2)	152.2 (154.0)	42.6 (42.4)	28.2 (42.5)
Road density (km km^{-2})	1.4 (0.7)	2.1 (0.6)	1.0 (0.3)	1.0 (0.3)

Values provided are mean (standard deviation in parentheses) across or within catchments.
BCC = Beaver Creek Catchment; ECC = Elk Creek Catchment; MCC = Mica Creek Catchment.

Table 2. Summary of FCL and Characteristics of Resource Availability and Disturbance Across All 19 Reaches and for the Reaches Within Each of the Three Catchments

	All	BCC	ECC	MCC
FCL	3.4 (0.5)	3.2 (0.4)	3.7 (0.6)	3.4 (0.5)
Resource availability				
Periphyton biomass (μg mm^{-2})	1.26 (1.04)	1.30 (1.17)	1.16 (1.03)	1.28 (1.08)
Detrital biomass (g)	1.75 (1.29)	1.21 (0.59)	3.90 (1.13)	1.20 (NA)
Disturbance				
LW density (no m^{-2})	0.046 (0.051)	0.040 (0.047)	NA	0.053 (0.057)
Q_2:Q_{ma}	7.9 (1.5)	7.7 (2.2)	7.5 (0.5)	8.5 (1.0)
Q_{bf} (m^3 s^{-1})	36.0 (66.5)	76.5 (100.0)	11.8 (2.9)	12.7 (14.5)
Max ΔT (°C)	5.2 (2.6)	4.5 (2.2)	NA	6.2 (3.1)
RGA	62.3 (6.3)	65.4 (5.1)	56.8 (6.2)	63.1 (5.5)

Values provided are mean (standard deviation in parentheses) across or within catchments.
BCC = Beaver Creek Catchment; ECC = Elk Creek Catchment; MCC = Mica Creek Catchment.

Table 3. Comparison of Competing Models ($\Delta_i \leq 4$) for Food-Chain Length from All Three Catchments

	R^2	P	AIC_c	Δ_i	w_i
Tributary junctions + road density	**0.49**	**<0.01**	**−28.7**	**0**	**0.35**
Tributary junctions	***0.35***	***0.01***	***−27.2***	***1.5***	***0.16***
Confluence distance	0.33	0.01	−26.5	2.2	0.12
Drainage area*	0.32	0.01	−26.4	2.3	0.11
Road length + road density	0.42	0.01	−26.2	2.5	0.10
Stream length	0.30	0.02	−25.7	3.0	0.08
Stream order	0.29	0.02	−25.4	3.2	0.07

See text for how the pools of competing models were selected. The reported parameters are the coefficient of determination (R^2), significance (P), AIC corrected for small sample size (AIC_c), relative AIC_c (Δ_i), and Akaike weight (w_i). The best models (that is, $\Delta_i = 0$) are in bold; and models having strong support (that is, $\Delta_i \leq 2$) are in bold italic. Factors related to ecosystem size are asterisked; non-asterisked factors represent ecosystem structure.

averaged 8260 km (σ = 3450 km) and ranged from 4180 km (in ECC) to 18,920 km (in MCC; Table 1, Supplementary material: Table S2). Measures of structural complexity included the number of tributary junctions, which averaged 28 (σ = 31) and ranged from 0 to 95, and drainage density,

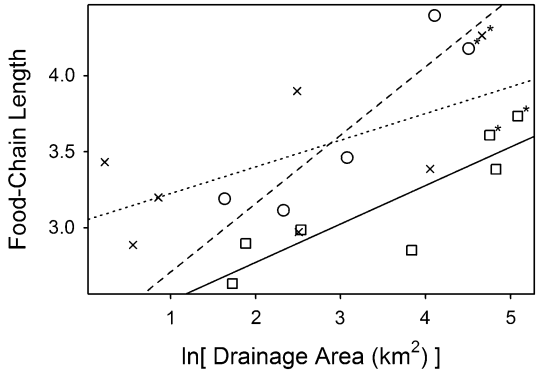

Figure 3. Food-chain length versus drainage area (log-transformed). Data points are coded by catchment: *squares* = BCC; *circles* = ECC; and *crosses* = MCC (study reaches whose apical consumers were birds are asterisked; fish represented apical consumers at the remaining study reaches). Regression lines are also indicated: *solid* = BCC; *dashed* = ECC; and *dotted* = MCC. Regression statistics are as follows (in order from strongest to weakest): ECC, FCL = 2.3 + 0.45*ln[DA] with R^2 = 0.85 (P = 0.03); BCC, FCL = 2.3 + 0.25*ln[DA] with R^2 = 0.77 (P = 0.01); and MCC, FCL = 3.1 + 0.18*ln[DA] with R^2 = 0.38 (P = 0.14). *FCL* food-chain length; *DA* drainage area.

which averaged 1.3 km km^{-2} (σ = 0.2 km km^{-2}) and ranged from 0.8 to 1.9 km km^{-2} (Table 1, Supplementary material: Table S2). Additional physical characteristics assessed were road length ($\bar{x}$ = 77.6 km, σ = 111.2 km, range 1.8–375.6 km) and road density ($\bar{x}$ = 1.4 km km^{-2}, σ = 0.7 km km^{-2}, range 0.5–2.9 km km^{-2}), elevation ($\bar{x}$ = 3030 m, σ = 620 m, range 1690–4000 m), and buffer canopy openness ($\bar{x}$ = 33%, σ = 37%, range 0–100%; Table 1, Supplementary material: Table S2).

FCL averaged 3.4 (3.2, 3.7, and 3.4 for BCC, ECC, and MCC, respectively), with a standard deviation of 0.5 and range of 2.6–4.4 across the three study catchments (Table 2, Supplementary material: Table S3). The mean and range were comparable to those observed for other stream systems (for example, Vander Zanden and Fetzer 2007; McHugh and others 2010; Sabo and others 2010). Resource availability and disturbance regime also varied considerably across reaches (Table 2, Supplementary material: Table S3).

Food-Chain Length versus Catchment Size and Structure

Similar to several previous studies (for example, Thompson and Townsend 2005; McHugh and others 2010; Sabo and others 2010), we observed a positive, albeit weak, relationship between FCL and drainage area (that is, ecosystem size: R^2 = 0.32, P = 0.01; Table 3). These relationships were generally stronger on a per catchment basis (for example, BCC and ECC; Figure 3). Whereas ecosystem size was a significant determinant of FCL, structural characteristics were equally or more important: for example, number of tributary junctions, road density, stream length, and road length (Table 3). The two models having the strongest support (that is, $\Delta_i \leq 2$) were FCL as a function of number of tributary junctions and road density and FCL as a function of number of tributary junctions only.

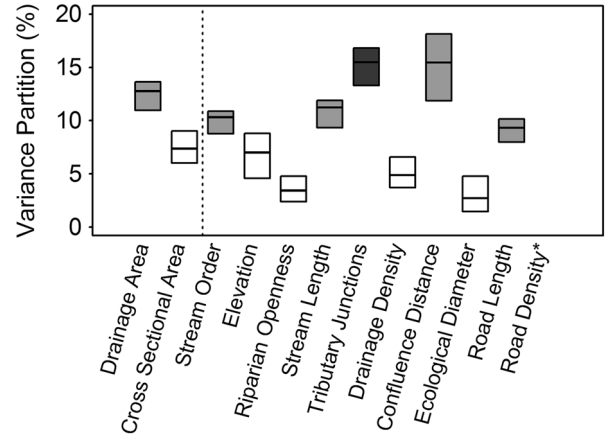

Figure 4. Summary of results from hierarchical partitioning of the 12 explanatory variables for food-chain length (FCL). The vertical bars indicate the 95% confidence intervals and the contained horizontal bars indicate the means from the variance partitions of n = 1000 randomized parameter orders (see "Methods" section). Explanatory variables with lightly shaded bars were included in the competing models identified by AIC ($\Delta_i \leq 4$) and darkly shaded bars were included in the AIC-identified models having strong support ($\Delta_i \leq 2$). The vertical *dotted line* partitions the explanatory variables according to whether they are indicators for size or structure [* Following Murray and Conner (2009), explanatory variables having correlations with the response variable near zero ($|r| \leq 0.1$) were not included in the list of parameters for hierarchical partitioning: hence, road density was excluded for FCL (but note that road density was included in the models with strong support by AIC)].

The results from hierarchical partitioning in terms of identifying the most important explanatory variables for FCL were generally consistent with those identified in the AIC competing models ($\Delta_i \leq 4$) and models with strong support ($\Delta_i \leq 2$; Figure 4; Table 3). With the exception of road density, hierarchical partitioning identified the same top explanatory variables as the AIC-based model selection approach (tributary junctions, confluence distance, drainage area, stream length,

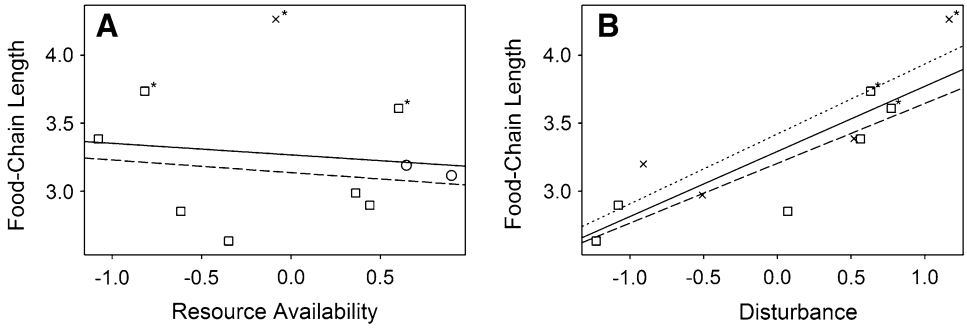

Figure 5. Food-chain length versus multivariate factors of **A** resource availability and **B** disturbance regime (assessed as habitat stability). Data points are coded by catchment: *squares* = BCC; *circles* = ECC; and *crosses* = MCC (study reaches whose apical consumers were birds are asterisked; fish represented apical consumers at the remaining study reaches). Regression lines are also indicated: *solid* = across catchments; *long-dashed* = BCC; and *dotted* = MCC (note that, data were unavailable from some locations and regressions could not be evaluated for ECC and MCC in **A** and for ECC in **B**). In **A**, the multivariate factor represented a gradient of increasing periphyton and detrital biomass and was based on principal component (PC) 2 from the PCA of resource availability. The relationship was not significant either across catchments ($R^2 = 0.01$, $P = 0.74$) or for BCC ($R^2 = 0.02$, $P = 0.75$). In **B**, the multivariate factor represented a gradient of increasing disturbance (primarily, lower LW density and higher Max ΔT and Q_{bf}) and was based on PC1 from the PCA of disturbance regime. The relationship was significant across catchments ($R^2 = 0.71$, $P < 0.01$) and for BCC ($R^2 = 0.76$, $P = 0.02$), but not for MCC ($R^2 = 0.74$, $P = 0.14$).

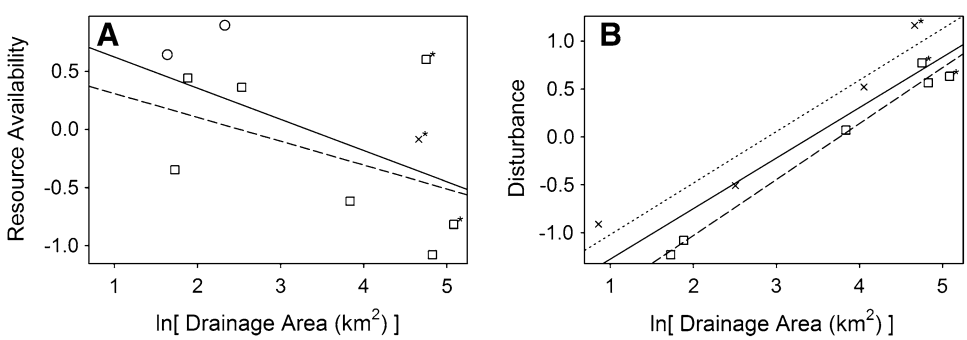

Figure 6. Do resource availability and disturbance regime scale with ecosystem size? In **A**, the multivariate factor represented a gradient of increasing periphyton and detrital biomass and was based on PC2 from the PCA of resource availability. The relationship was not significant either across catchments ($R^2 = 0.31$, $P = 0.09$) or for BCC ($R^2 = 0.20$, $P = 0.32$). In **B**, the multivariate factor represented a gradient of increasing disturbance (primarily, lower LW density, and higher Max ΔT and Q_{bf}) and was based on PC1 from the PCA of disturbance regime. The relationship was significant across catchments ($R^2 = 0.88$, $P < 0.01$), as well as for BCC ($R^2 = 0.98$, $P < 0.01$) and MCC ($R^2 = 0.93$, $P = 0.03$). [Data points are coded by catchment: *squares* = BCC; *circles* = ECC; and *crosses* = MCC (study reaches whose apical consumers were birds are asterisked; fish represented apical consumers at the remaining study reaches). Regression lines are also indicated: *solid* = across catchments; *long-dashed* = BCC; and *dotted* = MCC. Note that, data were unavailable from some locations and regressions could not be evaluated for ECC and MCC in **A** and for ECC in **B**].

stream order, and road length, which collectively explained 75% of the total variance in FCL and were included in the AIC competing models). Notably, the most influential explanatory variable identified through both methods was the number of upstream tributary junctions, although through hierarchical partitioning it was as influential as distance to confluence (each explaining 15% of the total variance; Figure 4; Table 3).

Mechanisms Driving FCL

Regressions of FCL against the multivariate factor representing resource availability revealed no significant relationships either across the catchments or per catchment (Figure 5A). For disturbance regime (assessed as habitat stability), FCL exhibited positive relationships with the multivariate factor representing a gradient of increasing disturbance

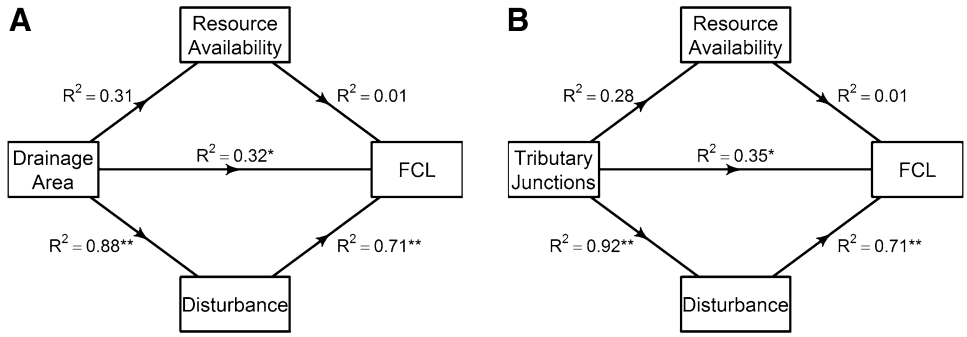

Figure 7. Diagrams illustrating the hypothesized direct and indirect (that is, via resource availability and disturbance regime) pathways linking **A** drainage area (that is, ecosystem size) and **B** number of tributary junctions (that is, ecosystem structure) with FCL. The path coefficients are the coefficients of determination (R^2) from pairwise regression analyses (*$P < 0.05$; **$P < 0.01$). Note that the small sample size of this study precluded more formal testing of the hypothesized relationships through structural equation modeling (see for example, Sabo and others 2010).

(for example, $R^2 = 0.71$, $P < 0.01$, across catchments; Figure 5B).

Because ecosystem size may influence FCL by integrating other mechanistic factors such as resource availability and disturbance regime (for example, Sabo and others 2010; Takimoto and Post 2013), we also examined whether these factors scaled with ecosystem size. Disturbance regime increased with drainage area both across and within catchments (for example, across catchments, $R^2 = 0.88$, $P < 0.01$; Figure 6B). Resource availability, however, was independent of ecosystem size (Figure 6A).

Equally strong or stronger relationships were observed between mechanistic factors and number of tributary junctions—which we hypothesized might also integrate resource availability and disturbance regime. Across catchments, for example, number of tributary junctions was positively related to disturbance regime ($R^2 = 0.92$, $P < 0.01$; Supplementary material: Figure S1B); the relationship with resource availability, however, was not significant (Supplementary material: Figure S1A). Figure 7 summarizes the hypothesized relationships among drainage area, number of tributary junctions, resource availability, disturbance regime, and FCL.

Discussion

Our results contribute important evidence to ongoing enquiry into drivers of FCL in fluvial ecosystems. In particular, we introduce data that ecosystem structure may be as important as ecosystem size in regulating FCL. We found that the number of tributary junctions and distance from the confluence with the receiving system emerged as important controls. Our post hoc analysis of potential mechanistic drivers of FCL supports the importance of disturbance regime as a significant although variable driver. Disturbance regime also was correlated with drainage area and number of tributary junctions, underscoring the interrelationship with both ecosystem size (Sabo and others 2009; McHugh and others 2010; Sabo and others 2010; Takimoto and others 2012) and structure. Findings from this research lead us to hypothesize that catchment structural characteristics integrate both ecosystem size as well as more mechanistic drivers of FCL, and thus may represent an important environmental determinant of food webs and set the stage for future research that more explicitly addresses the causal relationships between ecosystem structure and FCL.

Although ecosystem size (in terms of drainage area) emerged as an important variable for FCL ($\Delta_i = 2.3$), the weight of evidence was stronger for ecosystem structural properties. Collectively for all three catchments, drainage area was only a weak positive predictor $R^2 = 0.32$, which falls within the range of other published stream studies reporting coefficients of determination from 0.00 (Warfe and others 2013) to 0.48 (Sabo and others 2010). Multiple models received greater support than drainage area, including number of tributary junctions + road density ($R^2 = 0.49$, $P < 0.01$; $\Delta_i = 0.0$), number of tributary junctions ($R^2 = 0.35$, $P < 0.01$; $\Delta_i = 1.5$), and distance from confluence ($R^2 = 0.33$, $P = 0.01$; $\Delta_i = 2.2$) (Table 3). Number of tributary junctions and distance from confluence, in particular, were also identified as key variables through hierarchical partitioning (Figure 4).

Notably, cross-sectional area—a common metric of local ecosystem size (McHugh and others 2010;

Sabo and others 2010)—was not among the competing models for FCL in this study. However, correlations between many of the ecosystem structural properties and ecosystem size were evident. Number of tributary junctions, for example, was strongly correlated with drainage area ($r = 0.9$) and when normalized by drainage area (that is, confluence density), its relationship with FCL became insignificant. Nevertheless, an equally strong argument could be made that structural effects can be cumulative and thus scale with ecosystem size. The Network Dynamics Hypothesis (NDH) proposed by Benda and others (2004), for example, argues that greater drainage or confluence density will result in greater morphological heterogeneity and ultimately biological diversity. Stream confluences have been observed to be zones of heightened habitat heterogeneity, biological productivity, and diversity of fish and macroinvertebrates (Kiffney and others 2006; Collier and Lill 2008), and it is expected that such effects will be cumulative (Benda and others 2004). The strong relationship between number of tributary junctions and FCL in the current work provides further support for the NDH.

We observed a 2.6–4.4 range in FCL, which is on par with the approximately two trophic level range reported in purely aquatic stream studies (and which used a similar 3.4‰ per trophic level ^{15}N enrichment factor: for example, 2.6–4.2; McHugh and others 2010). Inclusion of the riparian food-web compartment did not appreciably increase FCL, suggesting some trophic redundancy among the aquatic and riparian food-web components of this study. For example, top avian consumers in our study system (for example, *Ceryle alcyon*, *Cinclus mexicanus*, and *Mergus merganser*) consume fish and aquatic invertebrates (Supplementary material: Table S1) and thus may often share a trophic niche with large salmonid fishes (for example, *O. mykiss* or *S. fontinalis*), which were present at all reaches (compare *C. mexicanus* and *S. fontinalis* in Figure 2). However, note that at the largest, downstream-most reaches larger-bodied piscivorous birds occupied higher trophic positions than the salmonid fishes (for example, compare *M. merganser* and *S. fontinalis* in Figure 2; *M. merganser* was also top consumer at the most downstream reach in BCC). Piscivorous birds also appeared to occupy a higher trophic position than piscivorous fishes for several streams in northern Australia (although the authors noted that sampling of the avian species was opportunistic; Warfe and others 2013).

Food-chain lengthening likely occurred primarily through either insertion of intermediate taxa or changes in omnivory (Post and Takimoto 2007) given that within a catchment, top consumers tended to belong to a single species (for example, *O. mykiss* for BCC, and *S. fontinalis* for MCC and ECC). Food-chain lengthening via addition of new top-level taxa (Post and Takimoto 2007) occurred at the largest, most downstream reaches where the top consumers were avian species (for example, *C. alcyon* and *M. merganser*; see also Figure 2). Given the linked stream–riparian food webs in our study, changes in habitat geometry that affect both in-stream processes as well as aquatic–terrestrial exchanges of organic matter might influence FCL (Power and Dietrich 2002). The most apparent shift in habitat occurs via downstream increases in volume or area, where wider and more-open network channels support more aquatic predators than tributary streams largely due to greater habitat volume (see for example, Loegering and Anthony 1999).

However, the importance of the number of tributary junctions and the distance from confluence in our study suggests that regional availability of new top predators in streams is a result of not only ecosystem size, but also connectivity to both the tributary and receiving systems. For example, while the study reaches where avian consumers were observed and sampled tended to have the largest subcatchments ($\bar{x} = 87$ km^2, $\sigma = 44$ km^2 vs. $\bar{x} = 7$ km^2, $\sigma = 5$ km^2 at reaches without avian consumers), these study reaches also had the greatest number of upstream tributary junctions ($\bar{x} = 54$, $\sigma = 27$ vs. $\bar{x} = 5$, $\sigma = 5$) and were nearest the major downstream confluence ($\bar{x} = 7.8$ km, $\sigma = 6.7$ km vs. $\bar{x} = 16.3$ km, $\sigma = 6.3$ km). Similarly, other aquatic-based studies have demonstrated the importance of stream network position to richness and composition of consumer assemblages (for example, Osborne and Wiley 1992; Smith and Kraft 2005). This is somewhat in contrast to our observation that connectivity in terms of dispersal effects—as represented by ecological diameter—was not a significant factor for FCL. Collectively, thus, it appears that the context of connectivity is most relevant for FCL (for example, connectivity to mainstem confluence more important than connectivity to a tributary); and it is not only species dispersal that is important for FCL, but also the dispersal of which species (for example, top predators).

Sabo and others (2010) suggest that other potential controls on FCL (for example, resource availability and disturbance regime) may scale with drainage area, thereby mechanistically linking ecosystem size to FCL. For instance, from small to

mid-order streams (as in this study), the River Continuum Concept (RCC; Vannote and others 1980) predicts a decrease in allochthonous food sources and increases in autochthonous food sources and temperature variation with increasing stream size. Although the multivariate factor representing resource availability did not scale with size (or structure) in this study, the absence of this relationship could be because we measured the standing crop of periphyton (as opposed to actual productivity), which can be limited by grazer activity depending on food-web structure (Mazumder 1994; Power and Dietrich 2002). Other studies have provided some support for a relationship between ecosystem size and resource availability. Both Warfe and others (2013) and Lamberti and Steinman (1997), for example, observed a positive relationship between ecosystem size and resource availability: Warfe and others (2013) in terms of total dissolved nutrients and Lamberti and Steinman (1997) in terms of gross primary productivity. A more robust assessment of resource availability (that is, rates of primary productivity, measures of stream metabolism, etc.) may help explain the relationships between ecosystem size or structure and FCL in future efforts.

In contrast, the relationships observed between ecosystem size and disturbance and between disturbance and FCL (as assessed through the multivariate factor indicating disturbance), were significant (for example, Fig. 7A). Although conceptually supportive of the mechanistic linkage proposed by Sabo and others (2010), these relationships were in fact opposite those observed in their study (that is, disturbance increased with size in this study)—emphasizing that disturbance may be a significant, albeit variable, driver of FCL.

Our multivariate disturbance factor represented primarily a gradient of increasing temperature variation and flood magnitude (with flood magnitude represented by decreasing LW density). The positive relationship between disturbance and ecosystem size was consistent with the RCC (Vannote and others 1980) with regard to temperature variation and was also consistent with the expectation that larger streams would be characterized by more powerful flows (for example, Benda and others 2003). The scaling relationship was even stronger between disturbance and tributary junctions (R^2 = 0.92 vs. R^2 = 0.88; Figure 7) and with respect to temperature variation could be explained by the flattening and widening of stream channels and slowing of water velocity upstream of tributary junctions (Benda and others 2004), allowing more time for water to equilibrate with air temperatures. The relationship between disturbance and tributary junctions could also reflect magnification of hydrologic disturbances at tributary junctions (Benda and others 2004).

Less straightforward, however, is the mechanistic link between disturbance in terms of either temperature variation or flood magnitude and FCL. The dynamical stability hypothesis predicts that disturbance will shorten FCL (Pimm and Lawton 1977; Jenkins and others 1992; Sabo and others 2009; Takimoto and others 2012), which is supported by two temperature-based disturbance studies (McHugh and others 2010; Hette-Tronquart and others 2013) and one hydrologic-based disturbance study (Sabo and others 2010). In contrast, we observed an increase in FCL with greater temperature variability and flood magnitude (as represented by the multivariate disturbance factor) for the three catchments. Thus, the relationship between disturbance and FCL across aquatic-terrestrial boundaries is likely complex and requires further investigation.

It should also be noted that the disturbance, as well as resource availability, metrics we evaluated were primarily aquatic-based and the inclusion of only a few terrestrial metrics (that is, buffer canopy, road density and length, and some components of the RGA) presents a limitation of this study. Although the terrestrial consumers in this study were those that rely heavily on aquatic food resources (Supplementary material: Table S1) and are intimately tied to the aquatic environment, and were thus expected to respond both indirectly and directly to disturbances and resources within the aquatic environment; the dynamical stability hypothesis in particular emphasizes the importance of direct impacts on top consumers in determining FCL (Pimm and Lawton 1977; Pimm 1982; Jenkins and others 1992). Inclusion of additional terrestrial-based metrics in future studies might result in more definitive and/or consistent relationships within linked stream–riparian food webs.

We additionally call attention to the potential importance of anthropogenic structural features in determining FCL. Although we focused on number of tributary junctions and distance from confluence, road density appeared in the FCL model with the strongest support (negative impact). Other studies have reported detrimental impacts of roads on aquatic biota via multiple mechanisms (for example, see Angermeier and others 2004).

Summary

Whereas resource availability, disturbance regime, and ecosystem size have been explored individually

and in concert, we found strong support for catchment structure as an additional, and sometimes stronger, determinant of food-web structure. In particular, measures of catchment connectivity were most important to FCL, increasing as number of tributary junctions increased and distance from confluence decreased. Catchment connectivity, like size (for example, Sabo and others 2010), appeared to influence food-web structure at least in part through its integrative effect on disturbance regime (a positive effect in this case). An additional mechanism, although not well supported in this study, might be through effects on resource availability. Our observations complement the Network Dynamics Hypothesis (Benda and others 2004) and other studies that have highlighted how the spatial arrangement of tributaries in a river network interacts with catchment disturbances to influence spatiotemporal patterns of habitat heterogeneity, biological productivity, and diversity. Connectivity in terms of dispersal ability may also be important, albeit depending on relative location within the catchment (for example, distance to confluence). Though limited in geographic scope (that is, mountainous streams of northern Idaho, USA), our study contributes to the growing collection of fluvial food-web studies and furthermore provides an in-depth perspective of food webs within a macroecological context (for example, Thorp 2014). Further exploration of the mechanisms through which ecosystem structure influences food webs will be a fruitful area of future research and may be particularly relevant to other dendritic-like ecosystems such as caves and mountain ridges, as well as the increasing number of fragmented natural landscapes resulting from human activities (for example, Bodin and Norberg 2007).

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