

# Geophysical templates modulate the structure of stream food webs dominated by omnivory

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**Abstract.** Food webs show the architecture of trophic relationships, revealing the biodiversity and species interactions in an ecosystem. Understanding which factors modulate the structure of food webs offers us the ability to predict how they will change when influential factors are altered. To date, most of the research about food webs has focused on species interactions whereas the influences of surrounding environments have been overlooked. Here, using network analysis, we identified how the structure of aquatic food webs varied across a range of geophysical conditions within a whole stream system. Within a headwater basin in the Cascade Mountain Range, Oregon, USA, macroinvertebrate and vertebrate composition was investigated at 18 sites. Predator–prey interactions were compiled based on existing literature and dietary analysis. Several structural network metrics were calculated for each food web. We show that the structure of food webs was predictable based on geophysical features at both local (i.e., slope) and broader (i.e., basin size) spatial extents. Increased omnivory, greater connectance, shorter path lengths, and ultimately greater complexity and resilience existed downstream compared to upstream in the stream network. Surprisingly, the variation in food web structure was not associated with geographic proximity. Structural metric values and abundance of omnivory suggest high levels of stability for these food webs. There is a predictable variation in the structure of food webs across the network that is influenced by both longitudinal position within streams and patchy discontinuities in habitat. Hence, findings illustrate that the slightly differing perspectives from the River Continuum Concept, Discontinuity Patch Dynamics, and Process Domains can be integrated and unified using food web networks. Our analyses extend ecologists' understanding of the stability of food webs and are a vital step toward predicting how webs and communities may respond to both natural disturbances and current global environmental change.

**Key words:** community complexity; connectance; food web theory; headwater streams; network analysis; omnivory; stability; watershed.

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## INTRODUCTION

Studying the organization and interactions of species in a community through the lens of a food web reveals how biodiversity and function are maintained in an ecosystem (Paine 1980, Pimm

et al. 1991, Martinez 1992). Metanalyses from various environments have suggested that food webs are generally highly complex, that omnivores occur infrequently, and that the ratios of predator to prey species are relatively constant (Cohen 1977, May 1983). Early research has demonstrated

that interactions between species play the main role in structuring food webs (Pimm and Lawton 1978). However, links between abiotic factors and community functioning are often overlooked (Polis et al. 1997). As landscapes often vary in predictable ways (McGarigal and Cushman 2005), it is unclear whether the structure of food webs can also be predictable when incorporating information about geophysical features.

Network analysis is a relatively new approach that can be used to quantitatively evaluate structural aspects of food webs and make comparisons across systems (Delmas et al. 2019). Topological food webs analyzed as networks are different than commonly used energy flow or functional food webs (Paine 1980) and provide realistic complexity of linkages among species. Topological food webs can represent the organization of communities and their consumer interactions as networks created by nodes (taxa in the community) and links (feeding interactions; Sabo et al. 2009). Commonly used metrics, such as connectance, omnivory, and average path length (APL), describe structural aspects of topological food webs (Delmas et al. 2019). Connectance, defined here as the number of links divided by the squared value of the number of nodes in a community, is associated with the amount of complexity and inter-connectedness within a food web (Delmas et al. 2019). While measures of connectance typically range between 0.03 and 0.32 in natural ecosystems (Dunne et al. 2002a), higher values within this range may be associated with increased food web stability, defined as resilience following disturbances (Dunne et al. 2002b, Gilbert 2009). In other studies, the proportion of omnivores, organisms that feed from more than one trophic level (Fagan 1997), has been positively associated with community stability (Thompson et al. 2012) while APL, the average number of links necessary for an effect to propagate the web (Williams et al. 2002), has a negative association with stability (Pimm and Lawton 1977, Long et al. 2011). Collectively, these network metrics can be used to explore links between structural properties of topological food webs and naturally varying abiotic factors, including the surrounding landscape at local and broader spatial scales, hereafter referred to as geophysical templates.

Because stream networks are dendritic, highly connected systems with relatively predictable

variation in flow and other geophysical features, they are ideal settings in which to study patterns of variability in food web structure. Foundational work on stream ecosystems has acknowledged links between community composition and surrounding landscapes. The River Continuum Concept (RCC; Vannote et al. 1980, Minshall et al. 1983) has been pivotal in suggesting how functional trophic relationships shift predictably from headwaters to downstream with associated gradients of riparian vegetation and channel geomorphology. Other researchers have identified the importance of habitat patchiness and heterogeneity (Townsend 1989, Poff and Ward 1990, Fausch et al. 2002). Though much of this theoretical work has been supported by empirical evidence (Closs and Lake 1994, Cross et al. 2013, Schindler et al. 2015), overarching structural patterns in aquatic food webs remain unknown (Power and Dietrich 2002). For example, it is unclear in what ways aquatic food webs may change within a branching stream network, and what those changes mean for community stability.

Some geophysical attributes at both local and broader spatial scales have been found to affect community processes and species interactions in aquatic systems (Power 1992, Parker and Huryn 2013). In addition to the RCC, the concept of Process Domains has been suggested to explain differences in stream community responses to disturbance (Montgomery 1999). This concept proposes that watershed and landscape-level processes interact with channel reach geomorphology to result in varying habitat qualities and thus variation in aquatic communities. Based upon these concepts, it is possible that geophysical features combined with consistent hydrological regimes (Poff et al. 1997) may modulate the structure and composition of aquatic food webs along a stream network in predictable ways. However, though the theory exists, there is little evidence showing how geophysical features impact food web structure.

Here, we used ecological network theory to characterize the structure of topological food webs across a first- to fifth-order stream network and discuss how our findings fit into foundational ideas in stream ecology including the RCC and Process Domain Concept. Our main questions include the following: (1) How do food web structures vary between upstream and

downstream sites? (2) Can surrounding geophysical variables within the watershed explain some of this variation? And (3) how prevalent is omnivory, and is this metric strongly correlated with other structural aspects of food webs? We predict that (1) variations between upstream and downstream webs will be detected, particularly in metrics related to stability; (2) there will be associations between landscape variables and certain structural food web metrics; and (3) omnivores will be abundant in these highly dynamic stream communities. Our findings will expand ecologists' understanding of the stability and predictability of food webs and the influences of variations in geophysical template.

## METHODS

### Study sites, datasets, and sampling

We constructed food webs from 18 sites across a first- to fifth-order stream network within the

H.J. Andrews Experimental Forest (HJA) in the central western Cascade Range, Oregon, using data collected between 2001 and 2018 (Fig. 1). We had eight of our study sites in small basins (<110 ha), eight in medium basins (300–800 ha), and two in large basins (1500–6500 ha; Table 1). Forest cover is predominantly Douglas-fir (*Pseudotsuga menziesii*) with western red cedar (*Thuja plicata*), big leaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*) in the riparian areas. Stream substrates ranged from boulder to cobble, with occasional gravel and downed wood.

To compile the most complete information about food webs, we included information for aquatic invertebrates and vertebrates from both past studies ( $N = 10$ ; Appendix S1: Table S1) and our recent field surveys ( $N = 8$ ; Appendix S1: Table S1). To standardize information across different surveys, we used only presence/absence data from summer months (June–September). All sites were surveyed via both Surber sampling

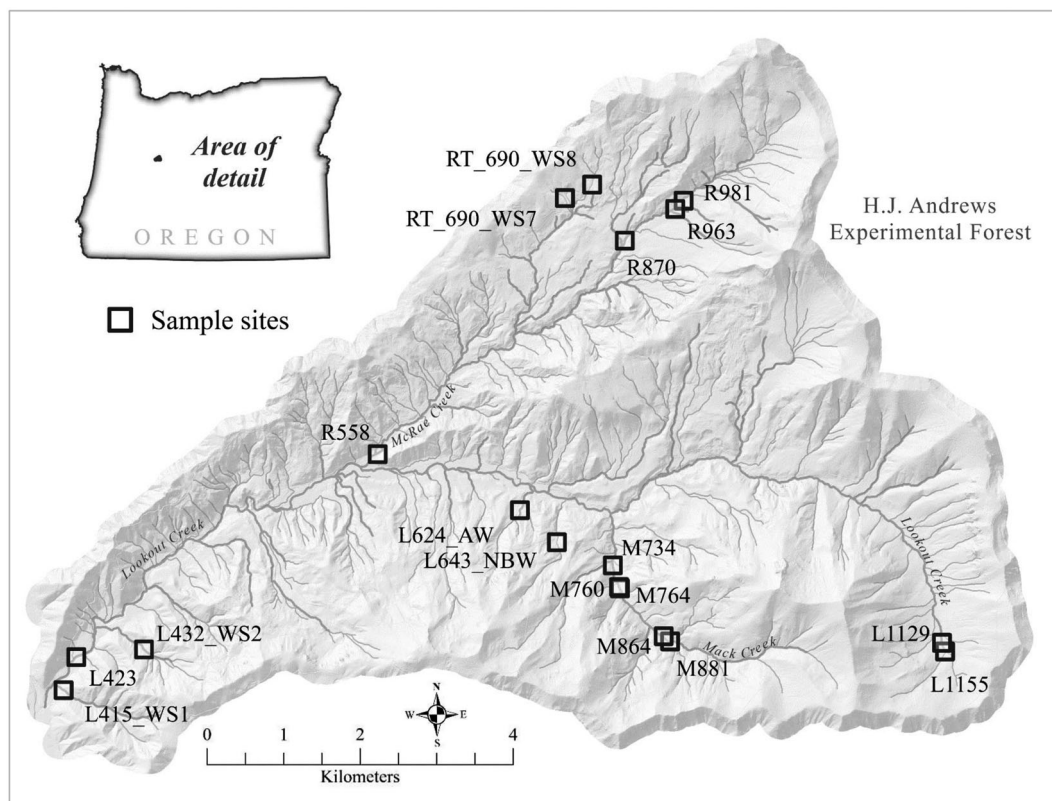


Fig. 1. Map of study sites including 18 stream food webs in Lookout Creek basin, H.J. Andrews Experimental Forest, Oregon, USA.

Table 1. Geophysical variables from each study site used to test relationships between food web metrics and surrounding landscape. Note that stream length (km) includes all tributaries above each study site.

Site ID	Elevation (m)	Stream length (km)	Basin area (km <sup>2</sup> )	Stream network channel density†	Average canopy cover (%)‡	Sinuosity§	Stream slope¶
L1141	1141	1.68	0.92	1.1	75.9	1.12	15.0
L1129	1129	1.81	1.09	0.9	75.9	1.01	12.1
L423	423	232.14	62.06	1.9	78.9	1.01	2.2
R981	981	9.1	3.74	1.3	75.0	1.01	21.2
R958	958	9.21	3.80	1.3	75.1	1.01	17.7
R870	870	12.61	4.90	1.3	73.8	1.02	12.1
R558	558	13.48	5.28	1.3	74.3	1.07	10.2
M881	881	14.38	5.37	1.4	74.5	1.03	7.5
M864	864	12.3	2.93	2.2	76.6	1.09	11.8
M770	770	13.06	3.13	2.1	77.5	1.04	16.1
M764	764	33.02	7.56	2.2	78.1	1.10	27.0
M734	734	68.3	15.30	2.3	81.7	1.00	3.4
RT_690_WS7	690	0.82	0.21	2.0	79.2	1.00	16.3
RT_690_WS8	690	1.39	0.27	2.7	79.4	1.01	14.6
L643_NBW	643	1.56	0.46	1.7	78.1	1.01	27.5
L624_AW	624	1.27	0.50	1.3	78.1	1.04	17.8
L415_WS1	415	3.17	0.96	1.7	77.9	1.02	23.7
L432_WS2	432	3.18	0.64	2.6	83.8	1.02	11.5

Note: A full description of sites can be found in Appendix S1: Table S1.

† Stream length divided by basin area.

‡ Average canopy cover per basin area.

§ Sinuosity of stream reach 50 m above food web site.

¶ Slope of stream reach 50 m above food web site.

for aquatic macroinvertebrates and backpack electrofishing for vertebrates. Macroinvertebrates were immediately preserved in 95% ethanol and later identified in a laboratory to the highest possible taxonomic resolution. Vertebrates were identified in the field to species. This region experienced a drought in 2015 (Kaylor et al. 2019), but complete aquatic datasets for that year were not used in this study.

#### Food web construction

The list of taxa used in our analysis included presence/absence of all macroinvertebrates and vertebrates at each site. Trophic interactions among taxa were determined by a literature review of previously conducted studies that included diet analyses (laboratory and field observations) and stable isotope analysis (Appendix S1: Table S2), except for the predatory dragonfly nymph *Octogomphus* spp. (club-tailed dragonfly). To determine the trophic interactions for the club-tailed dragonfly, we conducted stomach content analysis from 80 individuals collected from Oak Creek and Rock Creek in Benton County, Oregon (L. Zatkos, I. Arismendi, W.

Gerth, unpublished data). As recommended by Cuffney et al. (2007), we used the distribute-parents-among-children method of data standardization and distributed coarsely resolved (order level) taxa amongst the more finely resolved taxa of that category. This eliminates redundant nodes from the web that would potentially skew metrics and helps to standardize data collected from different studies.

We used datasets of taxa presence/absence and the compiled a list of trophic interactions obtained from literature review to construct topological food webs at each site, using the package Cheddar (Hudson et al. 2012) in R (version 3.5.2). Cheddar allows users to visualize and analyze ecological food webs by plotting interaction properties and calculating structural metrics (Table 2; see Appendix S1: Table S3 for all metrics used in our analysis). We searched the literature to complete datasets that included minimum resource and minimum consumer methods for all taxa (Appendix S1: Table S2). We followed methods provided by Gray et al. (2015) to identify the minimum taxonomic resolution at which a taxon has been observed to be either a

Table 2. Main structural food web metrics used in this study.

Structural food web metric	Definition
Connectance ( $L/S^2$ ) <sup>†</sup>	Proportion of links that occur in a community compared to the maximum number of theoretical links; calculated in Cheddar as $L/S^2$
Average path length <sup>‡</sup>	Average number of links necessary for energy, information, or an effect to propagate the network; calculated as the mean of all path lengths in a web
Fraction of omnivory <sup>§</sup>	Proportion of taxa that feeds from $\geq 2$ trophic levels, taxa that have non-integer trophic level

*Note:* A full description of the 16 food web metrics used in this study can be found in Appendix S1: Table S3.

<sup>†</sup> Delmas et al. (2019).

<sup>‡</sup> Williams et al. (2002).

<sup>§</sup> Thompson et al. (2007).

resource (prey) or consumer (predator). We combined our datasets with those found in the function WebBuilder (Gray et al. 2015) and used Cheddar to calculate 16 structural network metrics for each food web/study site (Table 2; Appendix S1: Table S3). Cheddar identified which taxa were omnivores, predators, and prey based on the provided dietary interactions list from our literature review and existing built-in datasets in WebBuilder.

### Geophysical features and data analyses

We used ArcGIS (ESRI; version 10.5.1) and datasets available on the HJA Open Data Hub (<https://data-osugisci.opendata.arcgis.com/>) to calculate eight geophysical variables that characterize the surrounding landscape at each site (Table 1). We then used both univariate and multivariate approaches to answer our questions pertaining to how structural metrics differed between webs and how entire structures were influenced by landscape attributes. For the univariate approach, we performed simple Pearson correlation analyses to test individual associations between metrics of food web structure and basin size to assess how structures varied along the stream network by drainage areas. In addition, we compared the all 16 structural metrics of food webs between small and medium/large basins using a Student's t-test and, when normality or equal variance assumptions were not met, we used a Mann-Whitney U-test. For the

multivariate approach, we created resemblance matrices using normalized Euclidean distances to examine similarities in food web structure (all 16 metrics), surrounding landscape (eight metrics), and geographic proximity (both stream and geographic distances) among study sites. These analyses allowed us to test both how web structures may vary from small to large stream sites and how geophysical gradients affect web shape.

We used a non-metric multi-dimensional scaling technique (nMDS; 9999 random starts) to visualize potential similarities of food webs including all structural metrics that were measured. The nMDS allows for the comparisons of all metrics and was chosen to show clustering of webs based on metric values. A cluster analysis (single link method; Simprof including 999,999 random permutations) was conducted to explain and visualize the relevancy of geographic proximity in the similarities of web structures. This will further validate and help examine similarities between web structures and how physical location within the watershed influences web variation. We performed Mantel tests to examine associations between distance matrices of food web structure (i.e., similarities in structure), geophysical variables, and geographic proximity. To validate relationships between landscape and web structures, we used a Pearson correlation analysis to evaluate the association between the resulting nMDS 2D coordinates and gradients of surrounding geophysical variables. Lastly, we grouped sites based on basin area (small, medium, and large) and evaluated similarities (ANOSIM) among food web structures that included all possible permutations. For these analyses, we used the software Primer7 (Clarke and Gorley 2015).

## RESULTS

Food webs ranged in size from 49 to 84 taxa, had linkage densities ranging from 7.8 to 14.7, and connectance values of 0.13–0.20 (Appendix S1: Table S4). The proportion of omnivorous taxa in each web ranged from 0.34 to 0.57 with an average path lengths (APL) of 1.69 (Appendix S1: Table S4). Regardless of this variation, there was a strong clustering of food webs by basin size (Fig. 2) with sites located in small basins being most dissimilar than those

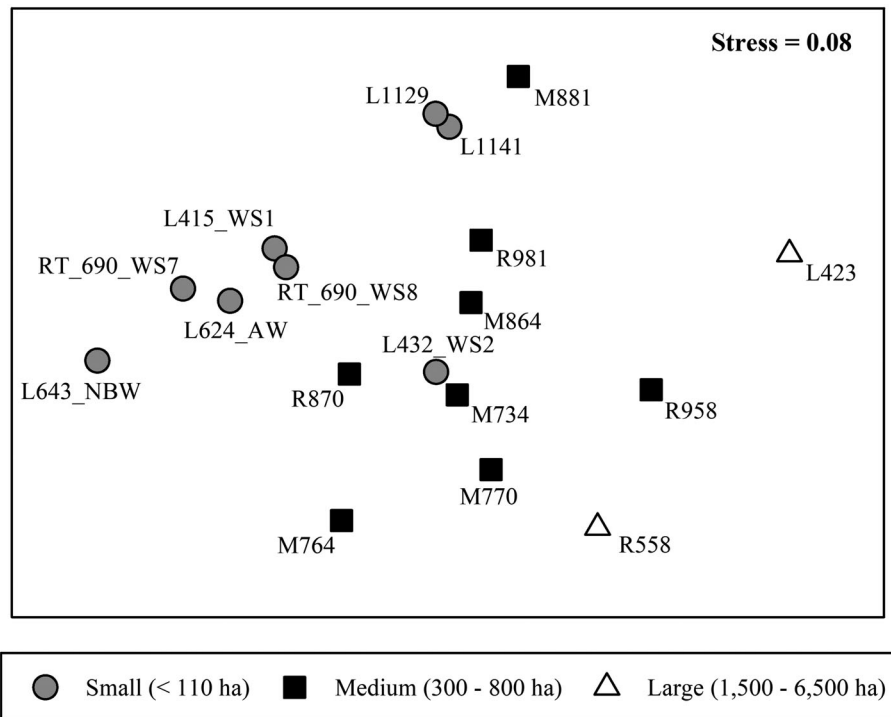


Fig. 2. Non-metric multi-dimensional scaling ordination (nMDS) plot of stream food webs by basin size (ha). Symbols represent the structure of food webs at each study site whereas the distance between symbols indicates their degree of similarity (higher proximity of symbols indicates a higher similarity, whereas food webs that are more dissimilar are placed further apart).

Table 3. ANOSIM contrasting food web structures among basin size groups including small, medium, and large basin areas.

Groups	R statistic	pseudo-P	Level of significance
Small vs. large	0.828	<b>0.022</b>	*
Small vs. medium	0.291	<b>0.010</b>	*
Medium vs. large	0.250	0.178	ns

Notes: Overall sample R statistic = 0.37, significance level of sample statistic = 0.001. Statistically significant values in bold at alpha = 0.05. Abbreviation is ns = not significant. \*pseudo-P < 0.05.

located in medium and large basins (Table 3). Additional variation was observed between food web structures of different basin size groups, including statistically significant differences in omnivory, APL, and connectance (Fig. 3; Appendix S1: Table S5). Although metric values varied among sites (Appendix S1: Tables S4, S6), connectance and omnivory generally were lower (Fig. 3a,b) whereas APL was higher (Fig. 3c) in

food webs from sites located in small basins compared to medium/large basin sizes (Appendix S1: Table S6).

Both local-level (i.e., stream slope) and watershed-level (i.e., basin size) geophysical features showed a strong association with the structure of food webs, captured by evaluating all 16 metrics of all webs (Fig. 4; Table 4). There were statistically significant associations between both stream slope and basin size with connectance, APL, and omnivory (Fig. 5; Appendix S1: Table S6). Stream slope had a negative association with connectance (Pearson correlation coefficient  $r = -0.768$ ,  $P < 0.001$ ; Fig. 5a) and omnivory ( $r = -0.593$ ,  $P = 0.009$ ; Fig. 5b), and a positive association with APL ( $r = 0.703$ ,  $P = 0.001$ ; Fig. 5c). Basin area had a positive association with connectance ( $r = 0.51$ ,  $P = 0.03$ ; Fig. 5d) and omnivory ( $r = 0.495$ ,  $P = 0.04$ ; Fig. 5e), and a negative association with APL ( $r = -0.519$ ,  $P = 0.03$ ; Fig. 5f). The remaining four geophysical features measured did not have a strong association with food

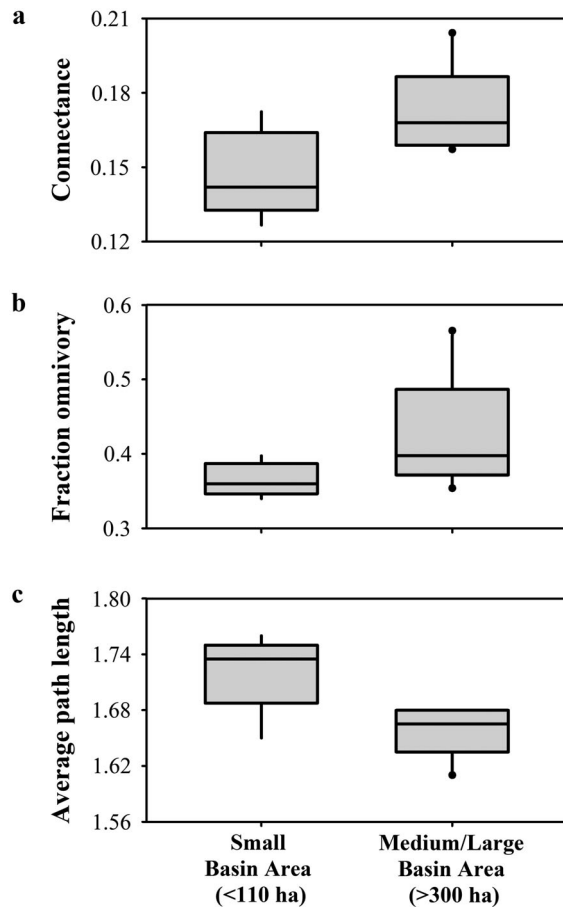


Fig. 3. Box-plots of selected food web structural metrics showing statistically significant differences between basin size groups. Appendix S1: Table S5 shows results of a similar analysis including all food web metrics.

web metrics. We note that these structural web metrics are not colinear. Individual correlations between all food web metrics and geophysical variables can be found in Appendix S1: Table S6.

We found no evidence that geographic proximity plays a role explaining differences in food web structures. Results of the Mantel test showed that neither Euclidean ( $r = 0.018$ , pseudo- $P = 0.41$ ) nor stream distance ( $r = -0.07$ , pseudo- $P = 0.74$ ) among sites explained variation in structural composition of food webs. Similarly, idiosyncratic grouping of webs in the cluster analysis revealed that proximity did not explain structural dissimilarities of food webs (Appendix S1: Fig. S1). Lastly, the proportion of omnivorous taxa in the food webs showed a strong association with other

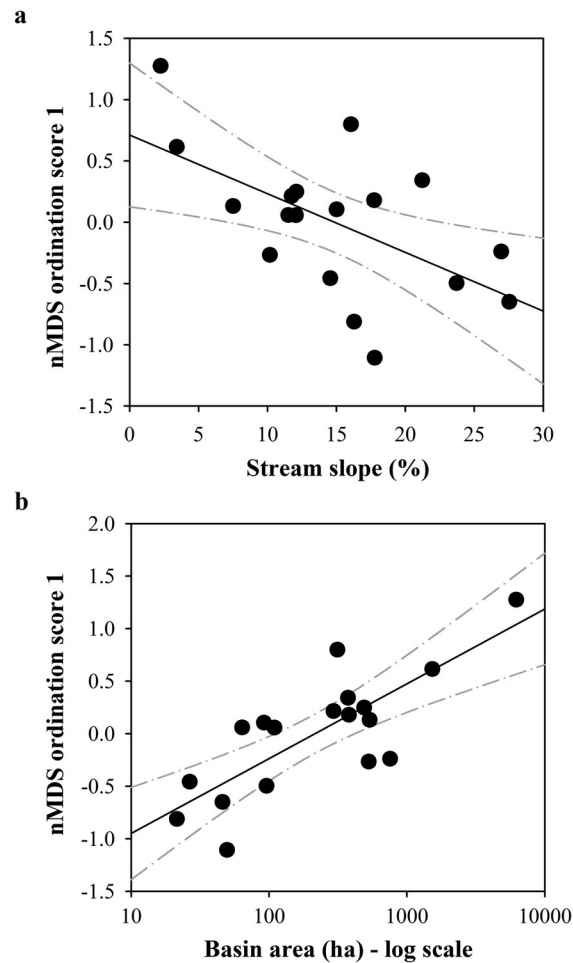


Fig. 4. Relationship between the structure of food webs (nMDS  $x$  coordinate) and selected geophysical variables. Dashed lines represent a 95% confidence interval. A similar analysis including all geophysical variables is shown in Table 4.

structural metrics (Fig. 6; Appendix S1: Table S7), including a positive association with connectance ( $r = 0.763$ ,  $P < 0.001$ ; Fig. 6a) and a negative association with APL ( $r = -0.664$ ,  $P = 0.001$ ; Fig. 6b). Individual correlations between omnivorous taxa and other food web metrics can be found in the Appendix S1: Table S7.

## DISCUSSION

Using a food web approach and network analysis, we demonstrate that food web structures are predictable along two geophysical attributes. Stream slope and basin size are best predictors of

Table 4. Spearman correlation analysis results between nMDS ordination  $x$  and  $y$  scores representing food web structures and each geophysical variable tested in this study.

Geophysical variable	Rho for nMDS ( $x$ coordinate)	$P$	Level of significance	Rho for nMDS ( $y$ coordinate)	$P$	Level of significance
Elevation (m)	0.393	0.107	ns	0.730	0.087	ns
log-Basin area (km <sup>2</sup> )	-0.036	0.889	ns	0.638	<b>0.004</b>	**
Stream network channel density	-0.292	0.239	ns	0.071	0.781	ns
Average canopy cover (%)	-0.157	0.533	ns	-0.039	0.877	ns
Sinuosity	0.016	0.950	ns	-0.035	-0.889	ns
Stream slope (%)	0.289	0.245	ns	-0.578	<b>0.012</b>	*

Note: Statistically significant values in bold at alpha = 0.05. Abbreviation is ns = not significant.

\*\*  $P < 0.01$ ; \*  $P < 0.05$ .

food web structures suggesting that both local- and broad-scale geophysical attributes simultaneously play a role influencing aquatic food webs. Elevation, stream network channel density, average canopy cover, and sinuosity were not found to be significantly correlated with any of our investigated food web structures. While elevation and average canopy cover have been found to influence food webs in large-scale studies (Robinson and Minshall 1986, Dodds et al. 2019), the relative similarities of these values between our study sites may make correlations with web metrics undetectable within a single watershed. In addition, as our study watershed consists of mountainous first- through fifth-order streams, values of channel sinuosity were similarly low at all 18 sites. This may explain why this geophysical feature was not significantly correlated with food web structures. It is known that high levels of sinuosity can increase retention of coarse particulate organic matter and thus influence food webs (Lamberti and Gregory 2007), so research conducted in larger watersheds with meandering stream channels may find different results.

Our approach has the potential to provide a framework to unify different ideas in stream ecology. First, our results support the River Continuum Concept (Vannote et al. 1980) that gradual changes in geophysical templates may predict aquatic communities at broad spatial extents. However, our findings related to stream slope as the local-scale predictor of food web structures and the lack of predictability of geographic proximity support the idea of Discontinuity Patch Dynamics (Townsend 1989) and Process Domains (Montgomery 1999) which both state that unique landscape and habitat features

influence communities at smaller spatial extents. Importantly, structural metrics directly associated to food web stability exhibit lower values in headwaters compared to downstream suggesting that stability may be related to size and diversity of habitats. In our stream network, omnivory is consistently prevalent across food webs suggesting omnivores may play an integral part in keeping food webs relatively stable across conditions that are highly seasonal. The combined influences of omnivory and geophysical gradients illustrate that both abiotic and biotic processes can modulate food web structures and thus their function.

Our findings support the idea of geophysical templates playing a significant role in structuring stream ecosystems. We show that connectance, omnivory, and APL are strongly associated with both local- and landscape-level geophysical factors including stream slope and basin area. Interestingly, these structural food web metrics have been shown to be related to community resilience following disturbances. In our stream network, food webs are likely more stable downstream, based on high connectance and omnivory, which have been proposed to be positively related to stability (Fagan 1997, Belgrano et al., 2005, Gilbert 2009) and lower APL, which has been suggested to be negatively related to stability (Pimm and Lawton 1977, Long et al. 2011).

Previous studies have focused on explaining the influence of habitat variation and geophysical gradients on omnivory, connectance, and APL as individual descriptors of food web structure. For example, connectance and its association with habitat size and primary production have been the focus of several studies (Warren 1989, Thompson and Townsend 2005a, Neutel et al.



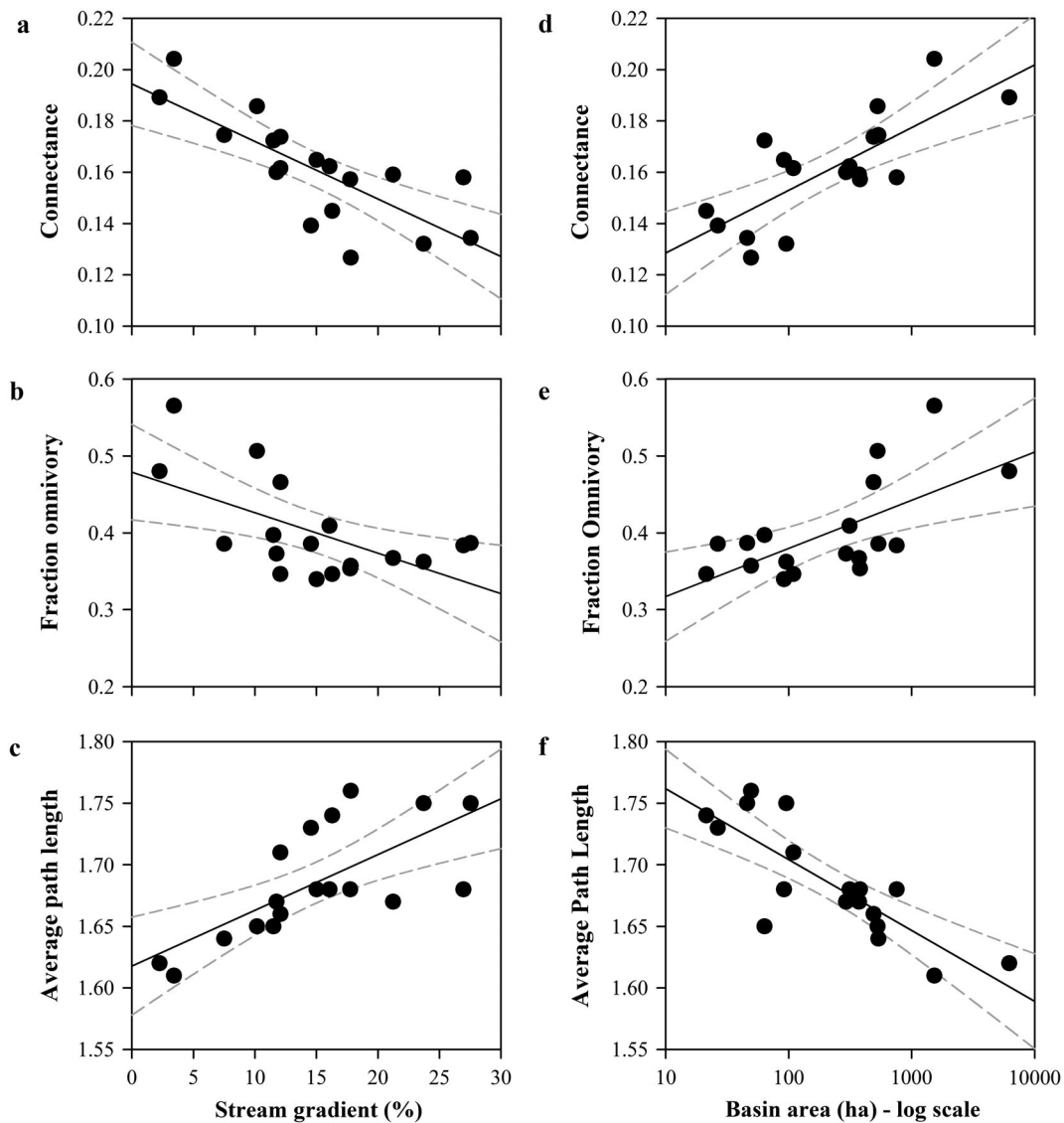


Fig. 5. Relationship between selected food web metrics and selected geophysical variables. Dashed lines represent a 95% confidence interval. Appendix S1: Table S6 shows results of a similar analysis including all possible combinations.

2007). Yet, little is known about how connectance is associated with geophysical features. Only one study shows that habitat variability (i.e., stream depth, width, and streamflow) and the scale at which food webs were investigated (i.e., reach vs. patch) may influence levels of connectance (Thompson and Townsend 2005b). A positive relationship between complex habitat and refugia, and between APL and omnivory has been described in lake food webs using a modeled

experiment fitted with empirical data (Ziegler et al. 2017). Patterns of APL in our study differ from those conducted in multiple river systems (Sabo et al. 2010), but our overall findings that abiotic stream characteristics can influence food web shape and stability are similar. Collectively, these studies show differences between up- and downstream food web structures that are explained, in part, by habitat variation. However, the influence of geophysical gradients on web

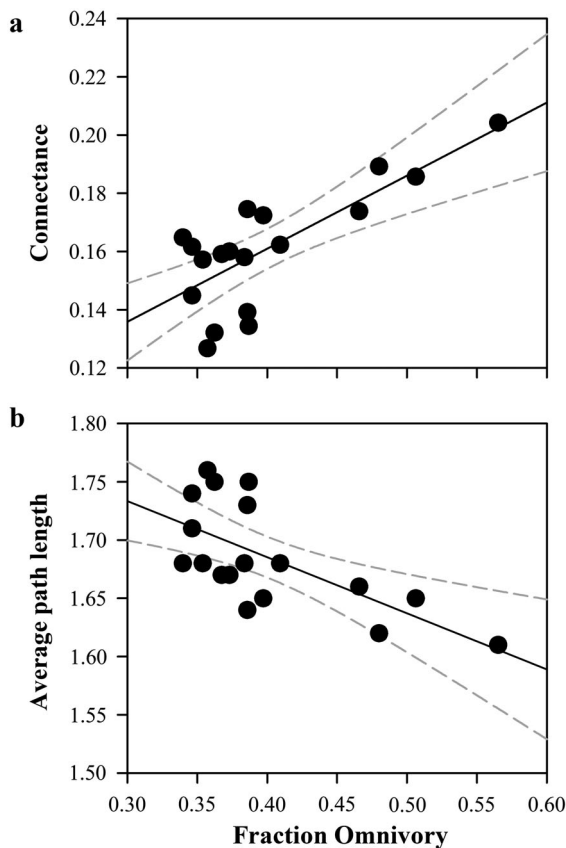


Fig. 6. Relationship among selected food web metrics. Dashed lines represent a 95% confidence interval. Appendix S1: Table S7 shows a similar analysis including all food web metrics.

structure within a habitat continuum had gone unaddressed until now.

Variations and amount of habitat in headwaters vs. downstream appear to explain the differences in food web structure across the stream network. In smaller, steeper streams (i.e., small basin size), there may be less achievable stability in these communities, perhaps constrained by a lack of refuge or deep water habitat for organisms to seek shelter during frequent disturbances (i.e., droughts and floods). This idea is supported by both ecological theory (McCann and Hastings 1997, Kratina et al. 2012) and by empirical and modeling studies (Carpenter et al. 1992, Dunne et al. 2002b). Differences between upstream and downstream food webs have been reported in other riverine systems (Power and Dietrich 2002,

Rosi-Marshall and Wallace 2002, Smits et al. 2015).

The overall degree of omnivory throughout our study system is relatively high compared to other systems (Dunne et al. 2002a). Omnivory is known to enhance community stability by increasing the number of weak interactions between species, and buffering systems during and post-disturbance (Rosi-Marshall and Wallace 2002, Pillai et al. 2011). Though multiple definitions exist for what taxa are considered omnivorous (Wootton 2017), the overall conclusions reached about increased omnivory at downstream sites in this study should remain consistent regardless of what definition is used. Because these taxa are known to feed from multiple trophic levels, omnivores have non-integer trophic levels and add numerous links to food web networks, thus increasing complexity and stability. Similar associations between omnivory and APL found within this study are documented in freshwater planktonic food webs (France 2012), and similar conclusions between omnivory and connectance have also been noted (Dunne et al. 2002a). The strong associations between omnivory and a variety of metrics related to community stability in our stream network suggest that omnivory can play an important role stabilizing food webs, especially in larger basin areas.

The different composition of large aquatic predators between our small, medium, and large basin sites may also help explain the lower levels of stability in small basins. Larger drainage areas at downstream sites support populations of Signal Crayfish (*Pacifastacus leniusculus*), sculpins (*Cottus* spp.), Rainbow Trout (*Oncorhynchus mykiss*), and dace (*Rhinichthys* spp.), smaller order upstream sites lack this diversity of predators. A portion of small-order streams supports Coastal Cutthroat Trout (*O. clarkii clarkii*) and Coastal Giant Salamander (*Dicamptodon tenebrosus*), but many streams in small basins contain Coastal Giant Salamanders as the sole large aquatic vertebrate predator, possibly due to physical barriers to fish movement. This may have implications for food web structuring, as increased diversity of intermediate- and top-level predators has been shown to decrease interaction strengths within food webs, thus stabilizing communities

(Finke and Denno 2004, Jonsson et al. 2007, Woodward et al. 2008).

Food webs can be studied a variety of ways with each methodology providing different information. While focus on interaction strengths (i.e., energy flow webs) has become one of the most commonly used tools to investigate communities, these webs often purposefully omit taxa that do not interact strongly with other taxa (Paine 1980, Post 2002). So while this method is used to address questions about energy flow through a system, it does not always provide complete information about the organization of the entire food web or trophic positions of taxa. Conducting a network analysis on topological webs can also answer questions about energy flow via examination of path lengths between taxa, in addition to providing community-wide information on stability, complexity, and size (Dunne et al. 2002a). Because energy flow and topological food webs are constructed differently, they can be used to answer different questions about communities, with both methods being important to broaden our knowledge of food web functioning.

As with any food web study, the current science still has its limitations. Many aquatic taxa undergo ontogenetic shifts in diet, which are not explicitly taken into account in the webs analyzed here; however, diets of multiple life stages were included when information was available. Similarly, diet contents collected in studies investigating multiple fish life stages were included to extend the breadth of possible predator–prey interactions between fish and other taxa. While we did not conduct our own dietary analyses of the included taxa (except for *Octogomphus* spp.), observed interactions found in existing literature, though perhaps incomplete, could be considered sound and relatively robust. Summer food webs do not capture the complete seasonal variability of food webs (Warren 1989, Closs and Lake 1994, Frady et al. 2007), but provide important insight into how lotic communities function during the season of lowest flow. Further, there is an inherent variability in data collection efforts and taxonomic resolution across studies that we minimize by focusing on presence/absence data as well as by adopting the distribute-parents-among-children method (Cuffney et al. 2007). Because presence/absence rather than body mass

data were available, interaction strengths were not analyzed. To answer the call for more standardization in food web ecology, we chose a tool that is becoming more commonly used in the field and we calculated quantitative results based on commonly defined metrics.

In conclusion, we demonstrate how food web structure changes along mountainous geophysical templates, a component currently missing from the growing body of food web research in ecology. This study also illustrates the importance of a watershed-scale focus to understand the organization of stream food webs. Although we study sites within a fifth-order stream network, our food webs were sufficiently different to demonstrate the utility of our approach. Omnivory dominates these study streams and food webs are stable and highly predictable by geophysical features at both local (i.e., stream slope) and broader spatial scales (i.e., basin size). Interestingly, across this stream network, communities in headwaters exhibit relatively lower levels of connectance and omnivory and longer APLs than at downstream sites, suggesting downstream communities can achieve higher levels of food web stability. This research highlights the role that landscape positions play in modulating aquatic food web structure, stability, and function. Being able to characterize aquatic food web dynamics and identify existing structural patterns is a vital step toward understanding and predicting how webs and communities may respond to both natural disturbances and current global environmental change.

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## DATA AVAILABILITY

Data from the H.J. Andrews Experimental Forest are available at: <http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=SA022> and <https://doi.org/10.6073/pasta/0fd89ea87c5b13959209a6e2f64a501b> (Johnson and Frady 2019). <http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=AS011> and <https://doi.org/10.6073/pasta/a1271ef4e52f51a35e57b15baa4e2e84> (Johnson and Penaluna 2019). NEON data can be found at <https://data.neonscience.org/browse-data> using ID code NEON.DOM.SITE.DP1.20120.001.

## SUPPORTING INFORMATION

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