

# Food-web interaction strength distributions are conserved by greater variation between than within predator–prey pairs

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*Abstract.* Species interactions in food webs are usually recognized as dynamic, varying across species, space, and time because of biotic and abiotic drivers. Yet food webs also show emergent properties that appear consistent, such as a skewed frequency distribution of interaction strengths (many weak, few strong). Reconciling these two properties requires an understanding of the variation in pairwise interaction strengths and its underlying mechanisms. We estimated stream sculpin feeding rates in three seasons at nine sites in Oregon to examine variation in trophic interaction strengths both across and within predator–prey pairs. Predator and prey densities, prey body mass, and abiotic factors were considered as putative drivers of within-pair variation over space and time. We hypothesized that consistently skewed interaction strength distributions could result if individual interaction strengths show relatively little variation, or alternatively, if interaction strengths vary but shift in ways that conserve their overall frequency distribution. Feeding rate distributions remained consistently and positively skewed across all sites and seasons. The mean coefficient of variation in feeding rates within each of 25 focal species pairs across surveys was less than half the mean coefficient of variation seen across species pairs within a survey. The rank order of feeding rates also remained conserved across streams, seasons and individual surveys. On average, feeding rates on each prey taxon nonetheless varied by a hundredfold, with some feeding rates showing more variation in space and others in time. In general, feeding rates increased with prey density and decreased with high stream flows and low water temperatures, although for nearly half of all species pairs, factors other than prey density explained the most variation. Our findings show that although individual interaction strengths exhibit considerable variation in space and time, they can nonetheless remain relatively consistent, and thus predictable, compared to the even larger variation that occurs across species pairs. These results highlight how the ecological scale of inference can strongly shape conclusions about interaction strength consistency and help reconcile how the skewed nature of interaction strength distributions can persist in highly dynamic food webs.

*Key words:* predator–prey; trophic interaction; food-web stability; feeding rate; functional response; community dynamics; stream; fish; macroinvertebrate.

## INTRODUCTION

Most attributes of food webs—including species composition and abundances, network topology, and interaction strengths—vary in space and time (Menge et al. 1994, Polis et al. 1996). Deterministic drivers of food-web variation include both biotic factors, such as species introductions or extirpations, population cycles, and organism life-history traits (Boutin et al. 1995, Vander Zanden et al. 1999, de Roos et al. 2003); and abiotic factors such as temperature, nutrients, hydrology, light, and

substrate (Menge 2000, Power et al. 2008, Byers et al. 2017). For example, migrations of anadromous fish can drive predictable seasonal changes in web topology and energy flow (Naiman et al. 2002), tropical storms can rapidly alter interaction strengths on islands (Spiller and Schoener 2007), and climate change is leading to wholesale food-web alterations on global scales (Woodward et al. 2010). Although increasingly recognized, spatial and temporal food-web variations present challenges to predicting and managing community dynamics, particularly in species-rich communities, where the relevant intrinsic and extrinsic drivers are poorly resolved (Tylianakis et al. 2008).

Although a large body of research shows that food webs are inherently variable, some empirical food-web

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patterns appear to be relatively consistent in space and time (Mora et al. 2018). Among these is the skewed frequency distribution of interaction strengths (few strong and many weak) that has been documented in nearly all studies with field-based quantitative interaction strength measures (Paine 1992, Fagan and Hurd 1994, de Ruiter et al. 1995, Raffaelli and Hall 1996, Wootton 1997, Woodward et al. 2005, Schleuning et al. 2011, Cross et al. 2013, Bellmore et al. 2015). This pattern appears insensitive to ecosystem type, network complexity, the measure of interaction strength used, and even the type of interaction under study (Wootton and Emmerson 2005, Vázquez et al. 2012). The persistence of the skewed distribution of interaction strengths suggests that (1) despite being variable, the strength of each pairwise species interaction shows consistency relative to the variation seen across co-occurring interactions, or (2) the relative position of each pairwise interaction along the distribution is dynamic, but with a distribution-conserving fraction of interactions shifting from strong to weak and vice versa. The latter might occur, for example, if predators are limited by a maximum total feeding rate across all of their prey. These two scenarios are not necessarily mutually exclusive, but may represent ends of a continuum of mechanisms that could underlie observed interaction strength distributions. Most quantitative measures of species interaction strength lack the spatial or temporal replication to test these ideas for multiple co-occurring interactions in nature.

Estimates of predator feeding rates are useful for addressing the extent to which species interaction strengths and their frequency distributions are dynamic or consistent over space and time. Moreover, there is a rich literature that seeks to describe mechanistically the factors driving variation in feeding rates (Jeschke et al. 2002). For example, functional response models generally predict that feeding rates should increase (often nonlinearly) with prey density (Holling 1959), such that fluctuations in prey should be a primary factor determining variation. Predator density, predator and prey traits (e.g., body size), and environmental conditions are also linked to variation in feeding rates (Skalski and Gilliam 2001, Rall et al. 2012, Kalinoski and DeLong 2016), with changes in each having the potential to alter interaction strengths and their frequency distribution in space and time.

In the present study, we addressed two related questions using replicated in situ feeding-rate estimates of a focal generalist predator, the reticulate sculpin (*Cottus perplexus*). First, we ask how dynamic prey-specific sculpin feeding rates are in space and time. We use the variation seen in sculpin feeding rates across their diverse prey community as a relative measure to compare against the variation seen within species pairs over space and time. Variation within species pairs across space and time that is consistently less than variation across species pairs at a given point in space and time would suggest that pairwise species

interaction strengths show consistency, which could underlie the consistency of community-wide interaction-strength frequency distributions. A conserved rank order of prey-specific feeding rates would also support this idea. Second, we ask what factors are driving within-species-pair variation in feeding rates over space and time? To address this question we quantify variation in space and time for each interaction individually and determine the extent to which changes in prey density, conspecific predator density, prey body mass, or abiotic factors can explain this variation. We quantified variation in sculpin feeding rates at spatial and temporal scales that are relevant to the local dynamics of short-lived organisms (e.g., aquatic macroinvertebrates), while incorporating relatively independent stream communities (separated by a few hundred to a few thousand meters) and environmental variation on seasonal time scales (surveys spanning ~1 yr). In this way, we were interested in the drivers of consistency (or inconsistency) of species interactions in similar stream communities at local scales, rather than broad-scale biogeographic patterns, which are often assumed to be influenced more strongly by abiotic variables than biotic interactions (Wiens 2011).

Our findings show that despite considerable within-pair variation in feeding rates, “strong” interactions tend to remain “strong,” and “weak” interactions tend to remain “weak.” As a result, interaction-strength distributions show consistency in space and time. We also find that although prey density is a primary factor driving within-pair variation in feeding rates for many prey taxa, factors including prey body mass, water temperature, and stream discharge frequently exhibit even greater effects for other taxa.

## METHODS

### *Study sites*

We estimated feeding rates of reticulate sculpin (*Cottus perplexus*) on its macroinvertebrate prey at nine stream sites within Oregon State University’s McDonald-Dunn Research Forest northwest of Corvallis, Oregon. The nine sites were each ~45 m in length and were nested within three streams (Berry, Oak, and Soap Creeks, see Preston et al. 2018). The three study streams were >4 km apart from one another, and the sites within each stream were on average 336 m apart (min = 87 m, max = 950 m). The ecology of streams in the McDonald-Dunn Research Forest has been well studied, including extensive work on the diverse (>325 species) macroinvertebrate community (Anderson and Lehmkuhl 1968, Kerst and Anderson 1975, Grafius and Anderson 1979), community interactions (Davis and Warren 1965, Hawkins and Furnish 1987), and ecosystem functioning (Warren et al. 1964). In addition to reticulate sculpin, other resident aquatic vertebrates at

our sites include cutthroat trout (*Oncorhynchus clarkii*), Pacific giant salamanders (*Dicamptodon tenebrosus*), and brook lamprey (*Lampetra richardsoni*).

#### Estimating feeding rates

We estimated in situ feeding rates by combining gut-contents data from field surveys with information on the time period over which prey items remain identifiable in a sculpin's stomach (hereafter the "prey identification time"). Prey-specific sculpin feeding rates were estimated for each survey as

$$\hat{f}_i = \frac{n_i}{p} \frac{1}{d_i}, \quad (1)$$

where  $\hat{f}_i$  is the average sculpin's feeding rate (prey consumed  $\cdot$  predator<sup>-1</sup>  $\cdot$  time<sup>-1</sup>),  $n_i$  is the number of prey items of species  $i$  found in a sample of  $p$  predator stomachs, and  $d_i$  is prey  $i$ 's estimated identification time (see also Novak and Wootton 2008, Novak et al. 2017, Wolf et al. 2017, and Preston et al. 2018). By using prey-specific identification-time functions that are parameterized with covariates from laboratory trials (see below), this approach explicitly accounts for differences in the amount of time that prey items persist in stomach contents. When unaccounted for, differences in prey identification times will bias inferences about trophic interactions made from diet data (Hyslop 1980, Fairweather and Underwood 1983, Novak 2010, Preston et al. 2017). Our approach allows the direct estimation of feeding rates under natural conditions without relying on experiments or allometric scaling relationships based on body size or other variables (Novak and Wootton 2008, Novak et al. 2017).

#### Field surveys

To collect sculpin diet information ( $n_i$  and  $p$  in Eq. 1), we surveyed each of the nine stream sites in summer (June/July 2015), fall (September 2015), and spring (April 2016) (27 total site-by-season replicates). Sculpin were surveyed systematically throughout the area of the reach by a crew of four researchers using a backpack electroshocker (Smith-Root LR20B), a block net (1.0  $\times$  1.0 m), and two dip nets (0.30  $\times$  0.25 m). Block nets at each end prevented movement of fish in and out of the reach during surveys. We anesthetized, weighed, measured, and nonlethally lavaged each sculpin with a 60-cc syringe and blunt 18-gauge needle to obtain gut contents. Sculpin were then held in aerated stream water and released after recovery from anesthesia. We preserved stomach contents in 70% ethanol and in the laboratory identified and measured prey for total body length. To estimate dry mass, we used a conversion factor based on wet mass for sculpin (Lantry and O'Gorman 2007) and length-to-mass regressions for

invertebrates (Appendix S1: Table S1). At each site, we also estimated prey densities by collecting macroinvertebrates with 10 Surber samples (0.093 m<sup>2</sup> in area) evenly spaced along each reach. Surber samples were preserved in 70% ethanol and invertebrates were measured for body length and identified using Merritt et al. (2008). We quantified abiotic variables at each site, including stream discharge, canopy openness, substrate size, water temperature, and stream width (Appendix S1). Last, we estimated sculpin densities by correcting our electroshock sculpin counts using catch efficiency estimates from habitat-specific (pool or riffle) mark-recapture surveys conducted at each stream (Appendix S1: Materials).

#### Prey identification times

Our estimates of prey identification times ( $d_i$  in Eq. 1) were based on functions from laboratory trials during which individual sculpin were fed invertebrate prey and then lavaged over time to determine the rate at which prey became unidentifiable as a function of covariates. Our approach for estimating prey identification times is provided in detail in Preston et al. (2017) and is summarized in Preston et al. (2018). Here we provide an overview.

We estimated the prey-specific identification times for common prey types observed in sculpin diets, including mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies (Trichoptera), flies (Diptera), beetles (Coleoptera), worms (Annelida), and snails (*Juga plicifera*; Appendix S1: Table S2). Our approach therefore incorporated differences in prey traits across taxonomic groups that affect rates of digestion by sculpin. In the laboratory trials, we varied water temperature (10–20°C), prey size for each taxon (Appendix S1: Table S2), and sculpin size (32–86 mm) in a continuous and randomized manner, and then fit Weibull survival curves to the observed prey status (identifiable or not) as a function of the covariates (Klein and Moeschberger 2005). The time periods over which sculpin were lavaged after feeding ranged from 10 min to 100 h, depending on the prey type. The estimated laboratory coefficients from the Weibull survival functions were used with observed covariate information from our field surveys (i.e., predator and prey sizes and water temperatures) to estimate prey identification times for each prey item recovered from a sculpin's stomach. For each prey item, the identification time was estimated as the mean of the probability density function that corresponded to the Weibull survival function under the observed covariate values (Preston et al. 2017). We then used the average prey-specific identification times within each survey to calculate the prey-specific sculpin feeding rates using Eq. 1. For prey types other than the aforementioned seven taxa, we used survival function coefficients from morphologically similar prey types (Appendix S1: Table S3).

### Analyses

We first assessed changes in the overall distribution of all feeding rates in each survey by examining the distribution parameters including the mean, standard deviation, skewness, and kurtosis. We then quantified the within-pair variation in feeding rates seen across space and time and compared it to the variation in feeding rates seen across species pairs at a given site and time. Within-pair variation was quantified as the coefficient of variation for each species pair using the mean and standard deviation of the prey-specific feeding rates across surveys. Not all prey taxa were observed in sculpin diets from all surveys; hence these calculations included up to 9 sites  $\times$  3 seasons = 27 feeding rate estimates for each species pair (Appendix S1: Table S3). Across-pair variation was quantified for each survey as the coefficient of variation calculated using the mean and standard deviation of the survey's prey-specific feeding rates. To quantify variation within and across species pairs we focused on the 25 prey taxa (i.e., pairwise interactions with sculpin) for which we had at least 2 feeding-rate estimates per season and at least 10 estimates total across all site-season combinations (mean = 20.7 estimates; Appendix S1: Table S3). Together, these taxa represented 88% of the individual prey items that we recovered (see Results).

Next, we evaluated the consistency in the rank order of prey-specific feeding rates using Spearman's correlation coefficients. We did this by ordering the 25 focal feeding rates by their overall means across all surveys and assessing deviations from this ordering in each of the individual surveys ( $n = 27$  surveys). We also assessed deviations in the rank order across seasons (three seasons) and streams (three streams) using their respective mean values.

We examined the relative roles of space and time in contributing to the variation seen within each species pair ( $n = 25$ ) using a generalized linear mixed model (GLMM) with log-transformed feeding rates as the response (Zuur et al. 2009). Our model included the fixed effects of reach identity (i.e., "space") and of season (i.e., "time"), and random intercept terms for stream (three reaches per stream) and prey taxonomic identity (up to 27 feeding rates per prey taxon). Diagnostic plots and comparisons to a model without random intercept terms indicated that inclusion of the random effects was justified (Appendix S1). To assess the contributions of "space" and "time" fixed effects, we compared the full model to (1) a model with season only, (2) a model with reach identity only, and (3) an intercept-only null model. We compared model performance using small sample size adjusted Akaike information criterion scores ( $AIC_c$ ; Burnham and Anderson 2002) and evaluated model fit using marginal and conditional  $R$ -squared values (Nakagawa and Schielzeth 2013); marginal  $R$ -squared represents variance explained by fixed effects and conditional  $R$ -squared represents variance explained by fixed and

random effects. To examine feeding-rate variation in space and time further, we also calculated coefficients of variation for feeding rates on each of the 25 focal taxa across the 9 sites (using mean feeding rates per site) and across the three seasons (using mean feeding rates per season).

Our next goal was to assess the capacity of prey density, predator density, prey body mass, and abiotic factors to explain the variation in prey-specific feeding rates we observed over space and time. These analyses focused on 20 of the 25 previously considered prey taxa, as 5 taxa (Dixidae, Ceratopogonidae, Copepoda, Ostracoda, Polycentropodidae) were sometimes not detected in Surber samples, precluding estimates of their density. The analyses entailed using general linear models for each focal taxon, including a full model (all four hypothesized drivers included), models with each of the four predictors alone, and an intercept-only null model (six total models per prey taxon). Although many other biologically reasonable models (i.e., variable combinations) are plausible, our primary goal was to determine the univariate explanatory power of the four variables rather than develop a predictive mechanistic model. Exploratory models also included a random intercept term for reach identity nested within stream, but these decreased relative model performance (based on  $AIC_c$  scores) and were thus not included in the final analysis (Appendix S1). Abiotic factors were incorporated as the first principal component from a principal-component analysis (PCA) of stream discharge, canopy openness, substrate size, water temperature, and stream width, using mean values per survey. Prey masses were from the Surber data and not the sculpin diet data. When a prey taxon was not detected in the Surber samples of a given survey, the corresponding feeding rate was omitted from the analysis. Feeding rates and all predictor variables other than the PC scores were log-transformed to improve conformance to model assumptions. For each prey taxon, we used  $AIC_c$  and  $R^2$  values to compare the six models. Lastly, we examined the overall univariate explanatory power of each of the four predictor variables across all taxa combined by summing the  $AIC_c$  scores of each variable's prey-specific models. Plots showing covariate correlations and model residuals are shown in Appendix S1: Fig. S1, S2.

## RESULTS

### Feeding-rate variation

The frequency distributions of feeding rates were positively skewed in all seasons and at all sites, exhibiting a consistent pattern of a few strong and many weak interactions (Fig. 1; Appendix S1: Fig. S3). Estimates of distribution skewness ranged from 1.4 to 5.4 (mean = 3.7) across surveys. These and the other distribution moments we measured did not differ consistently across streams or reaches, but did show seasonal differences in

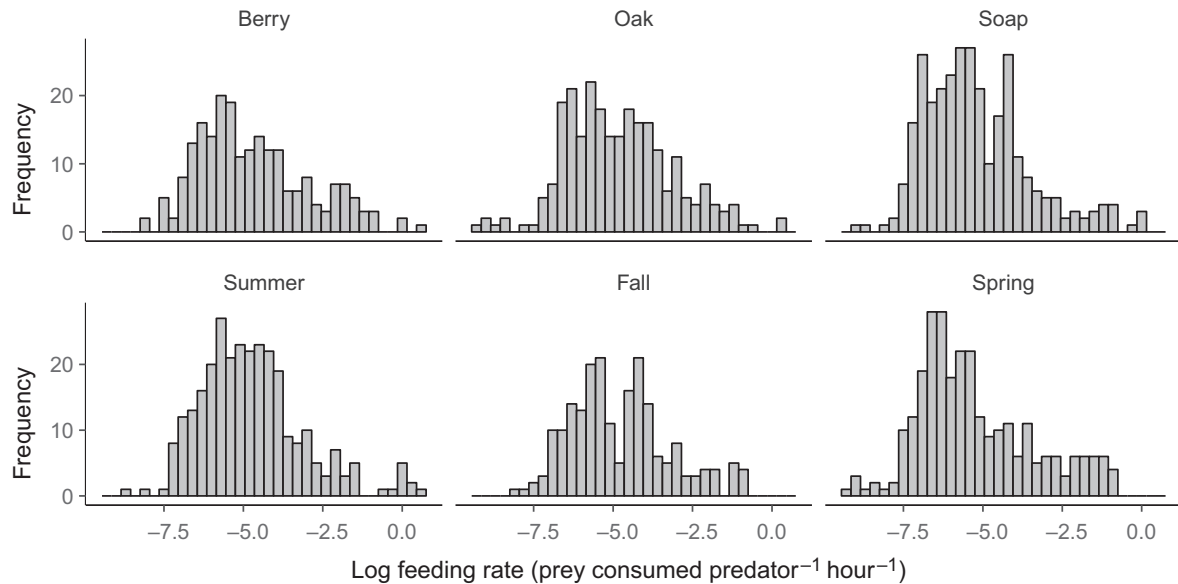


FIG. 1. Log-transformed sculpin feeding-rate distributions across three streams (top) and three seasons (bottom). Each distribution includes feeding rates from nine replicate surveys and all observed prey.

that all were generally highest in the summer (Appendix S1: Table S4).

In total, we collected 15,471 identifiable prey items from 2,068 sampled sculpin. The 25 focal prey taxa accounted for 13,564 prey items (88% of the total). The majority of these focal prey items belonged to the orders Ephemeroptera (45%), Diptera (37%), Trichoptera (9%), and Plecoptera (5%). Mean prey-specific feeding rates across the focal taxa varied by over three orders of magnitude, with the highest mean feeding rates being on Baetidae mayflies and Chironomidae midges, and the lowest being on *Juga* snails (Fig. 2).

Overall, the variation in feeding rates across species pairs within a survey was greater than the variation across surveys within a species pair (Fig. 2, inset). The mean coefficient of variation was 2.31 across species pairs (min = 1.27, max = 3.53, median = 2.38;  $n = 27$  surveys), versus 1.05 for variation within species pairs (min = 0.71, max = 1.63, median = 1.01;  $n = 25$  prey taxa). The within-pair difference from the lowest to highest feeding rates across all surveys in space and time averaged a 102-fold increase, ranging from 14-fold (Psychodidae flies) to 1,093-fold (Annelid worms).

The rank order of prey-specific feeding rates remained relatively consistent across seasons, streams, and individual surveys (Fig. 2; Appendix S1: Fig. S4). The ordering of mean feeding rates across the three seasons ( $\rho = 0.92$  in summer; 0.84 in fall; 0.80 in spring) and the three streams ( $\rho = 0.86$  at Berry Creek; 0.91 at Oak Creek; 0.86 at Soap Creek) did not differ greatly from the ordering of the overall means (Appendix S1: Fig. S4). Across surveys, the mean Spearman's correlation coefficient was 0.71 (range = 0.45–0.93), with deviations from the

order of the mean feeding rates driven primarily by variation in the lowest feeding rates.

#### *Effects of space and time on within-pair variation*

Many prey-specific feeding rates showed strong seasonal variation. Summer corresponded to the highest feeding rates for 17 of the 25 prey taxa, followed by spring (7 taxa), and fall (1 taxon; Fig. 3). Among the largest seasonal changes in mean feeding rates were those observed on mayflies, including Baetidae (a 4-fold decrease in mean feeding rates from summer to fall; Fig. 3h) and Heptageniidae (a 10-fold increase in mean feeding rates from fall to spring; Fig. 3i). General linear models fit to all 25 prey-specific feeding rates combined supported the idea that feeding-rate variation was more strongly associated with season than reach identity (Appendix S1: Table S5). The top-performing model included season alone. Nevertheless, even in the top-performing model, the fixed effect of season explained relatively little variation in feeding rates (marginal  $R^2 = 0.04$ ) compared to the random effect of prey taxon (conditional  $R^2 = 0.63$ ).

The coefficients of variation for feeding rates in space versus time reflected the different effects of season on each prey taxon. The CVs were higher across sites than across seasons for seven of eight fly and worm taxa (Appendix S1: Fig. S5). In contrast, for mayflies, stoneflies, and caddisflies, the CVs were higher across seasons than across sites for 8 of 11 taxa (Appendix S1: Fig. S5). In general, the taxa with high variation across seasons showed consistent differences in mean seasonal feeding rates (Fig. 3), whereas taxa showing higher variation in

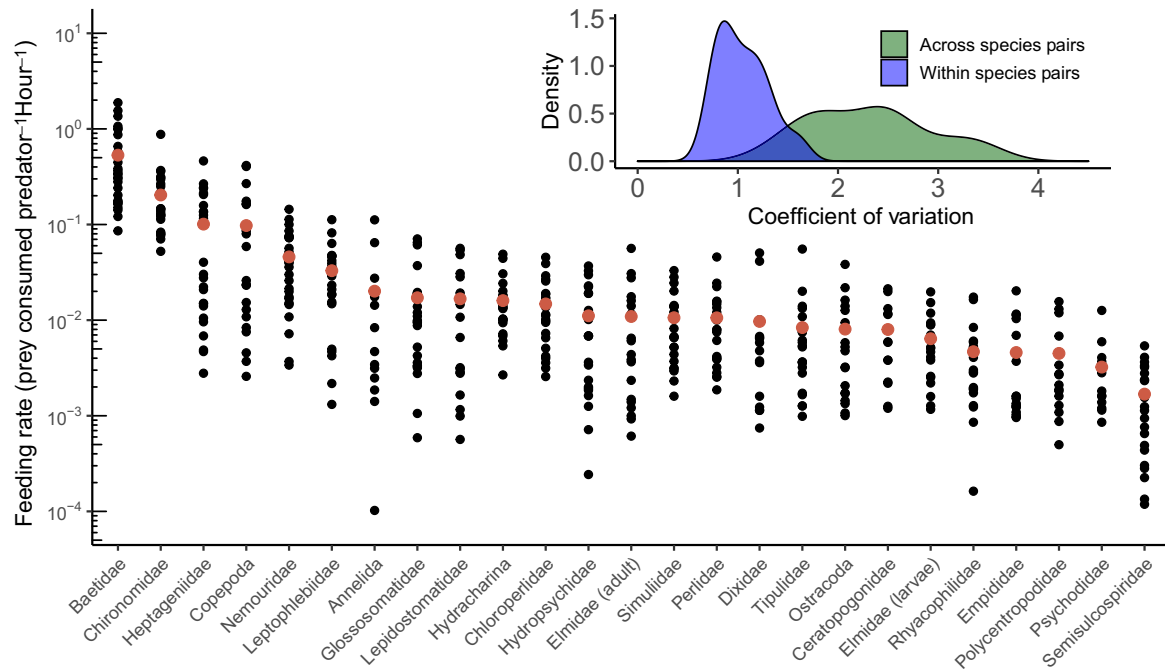


FIG. 2. Feeding rates of reticulate sculpin on 25 taxa of invertebrate prey. In the main panel, the red points indicate the mean feeding rates across all surveys within a prey taxon and the black points represent individual surveys. Note the log scale on the y-axis and that the prey-specific feeding rates are ordered by their means. The inset panel shows the replicate coefficients of variation for sculpin feeding rates within a species pair across surveys in space and time ( $n = 25$  taxa shown in blue) and across species pairs within a survey at a specific site ( $n = 27$  surveys shown in green). The mean coefficient of variation (CV) within species pairs is 1.1 and the mean CV across species pairs is 2.3. In the larger panel, within-pair variation corresponds to variation in the vertical direction for each prey taxon, and across-pair variation corresponds to variation in the horizontal direction across prey taxa in a survey.

space were not necessarily associated with consistent differences in mean reach- or stream-level feeding rates.

#### *Drivers of within-pair variation*

The four hypothesized explanatory variables for within-pair variation in feeding rates (i.e., prey density, prey body mass, predator density, and abiotic factors) varied more across seasons than across sites for most prey taxa. The densities for nine of the taxa considered in these prey-specific analyses ( $n = 20$ ) were highest in summer, while another nine were highest in fall and two were highest in spring (Appendix S1: Fig. S6). Nine of the taxa had the largest mean body size in spring (Appendix S1: Fig. S7). Of the abiotic variables measured, water temperature and stream discharge showed the largest variation, with low flows (mean =  $0.01 \text{ m}^3/\text{s}$ ) and warm temperature (mean =  $15^\circ\text{C}$ ) in summer, followed by lower temperatures (mean =  $10^\circ\text{C}$ ) and higher flows (mean =  $0.09 \text{ m}^3/\text{s}$ ) in spring (Appendix S1: Fig. S8). The first principal component from the PCA analysis, which was associated with 41% of the variation in the abiotic data, was positively associated with lower water temperatures and higher discharge (Appendix S1: Fig. S9). Sculpin densities were highest in summer (mean =  $2.8 \text{ m}^{-2}$ ) and decreased slightly in fall and

spring (mean =  $2.1 \text{ m}^{-2}$  for both) (Appendix S1: Fig. S10).

Variation in prey density and abiotic factors showed relatively consistent directional associations with within-pair variation in feeding rates. Feeding rates increased with prey density for 18 of the 20 prey taxa (Appendix S1: Fig. S11, Table S6); the two exceptions being Empididae flies and Hydracharina mites, which showed negative relationships. The first principal component of our PCA analysis of abiotic variables was negatively associated with feeding rates for 14 of the 20 taxa (Appendix S1: Fig. S12, Table S6), indicating that feeding rates decreased at lower temperatures and higher flows.

The directional nature of the relationships between feeding rates and variation in prey mass and sculpin density differed widely across the 20 taxa. Prey body mass was positively associated with feeding rates for 13 taxa and negatively associated for 7 taxa, without a clear taxonomic divide in either the sign or magnitudes of correlations (Appendix S1: Fig. S13, Table S6). Sculpin densities were positively associated with feeding rates for half of the taxa and negatively associated with feeding rates for the other half (Appendix S1: Fig. S14, Table S6).

The ability of prey density, prey body mass, predator density, and abiotic factors to explain variation in

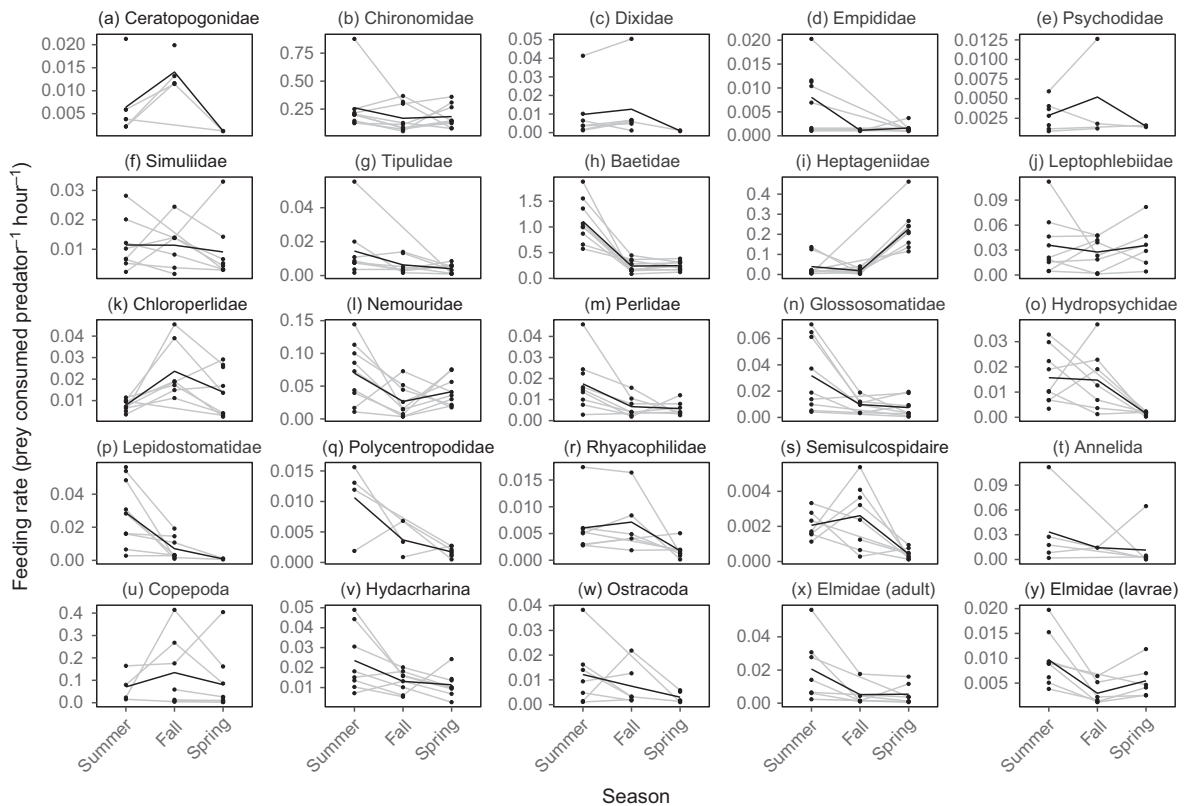


Fig. 3. Spatial and temporal variation in reticulate sculpin feeding rates on 25 invertebrate prey taxa. The black lines show the seasonal mean feeding rates, and the gray lines connect the same sites over time. Note the differences in the  $y$ -axis scale across panels.

feeding rates differed widely across the 20 prey taxa (Appendix S1: Table S7). For three taxa, the top-performing model was the full model with all four covariates and for two taxa, the intercept-only model outperformed all other models (Table 1). Of the other 15 taxa, the top model included only prey density for 7 taxa, abiotic factors for 5 taxa, and prey mass for 3 taxa (Table 1). The variation explained by the top models averaged 37% ( $R^2$  range: 0.14 to 0.81) after excluding the two taxa for which the intercept-only model performed best (Appendix S1: Table S7). Summing the  $AIC_c$  scores across the 20 taxa resulted in the model including only abiotic factors having the best relative performance, followed by models including only prey density, prey mass, the intercept-only model, the full model, and only predator density (Table 1).

## DISCUSSION

Ecologists are increasingly grappling with the dynamic nature of species interactions and the consequences of food-web variation for the structure and functioning of communities (Poisot et al. 2015, Lopez et al. 2017, Tylianakis and Morris 2017). Alongside this growing appreciation for variation, there remains the longstanding

realization that many properties of communities are conserved (McCann et al. 1998). This includes the skewed distribution of interaction strengths (many weak, few strong), which has often been linked to the stability of species-rich communities (McCann et al. 1998, Borrvall et al. 2000, Wootton and Emmerson 2005, Gellner and McCann 2016). This leads to an interesting inconsistency: if interactions in food webs are highly dynamic, why is the skewed distribution of interaction strengths apparently conserved? Our results help to reconcile the seemingly contradictory nature of these two properties by showing how the scale of inference shapes conclusions about whether species interactions are dynamic or consistent. From the perspective of community-wide variation, the pairwise interactions in our study system were relatively consistent in space and time; “strong” interactions remained “strong” and “weak” interactions remained “weak.” Although within-pair variation averaged a 100-fold difference from the lowest to highest observed feeding rate, it was much smaller than the variation seen across pairs, leading to a consistent rank order and overall frequency distribution of interaction strengths. Our results therefore emphasize how food webs with dynamic interactions can yield properties that are nonetheless conserved in space and time.

TABLE 1. Comparisons of the model performance of six sets of models that were used to predict prey-specific feeding rates for each prey taxon individually.

Model	Summed AIC <sub>c</sub>	Δ AIC <sub>c</sub>	Top model for prey taxa
Abiotic-PC1	1,185	0	Empididae, Annelida, Glossosomatidae, Hydropsychidae, Rhyacophilidae
Prey density	1,191	6	Elmidae adults, Chironomidae, Tipulidae, Leptophlebiidae, Nemouridae, Perlidae, Lepidostomatidae
Prey mass	1,232	47	Hydracharina, Elmidae larvae, Simuliidae
Intercept only	1,252	67	Psychodidae, Chloroperlidae
Full model	1,275	90	Baetidae, Hetpageniidae, Semisculcospiridae
Predator density	1,284	99	None

*Notes:* The models include each predictor alone (prey density, prey mass, predator density, or abiotic variables summarized with a principle-components analysis), a full model with all four predictors, or an intercept-only null model (six models per prey taxon). The summed AIC<sub>c</sub> scores are the totals from the prey-specific models ( $n = 20$  taxa per model) and the change in AIC<sub>c</sub> is relative to the top-performing model. The prey taxa listed indicate the prey for which each model was the top performing (lowest AIC<sub>c</sub>). Model statistics and partial residual plots are provided in Appendix S1.

The consistency of the pairwise interactions relative to community-wide variation has several implications. It suggests the existence of fundamental characteristics that drive interaction strengths within versus between interacting species pairs. That is, although within-pair variation was explained by distinct prey-specific factors (especially abiotic variables and prey density), the variation seen across species pairs indicates a more fundamental role of prey identity (Preston et al. 2018). Species identity is associated with a wide range of relevant traits to foraging predators that are consistent across prey taxa over the spatiotemporal scale of our surveys. The persistence of common structural characteristics in food webs, such as motif frequencies and “backbone” interactions (Mora et al. 2018), may also be explained in part by the relative consistency of species interaction strengths at the community scale. Thus, although our findings should be interpreted within the spatial, temporal, and ecological (i.e., focal prey community) scale of our surveys, they collectively show that from a community-wide perspective, interaction strengths may be more predictable than commonly assumed.

The skewed distributions of interaction strengths observed in our study and others have parallels to species abundance distributions, which generally show a skewed distribution with many rare species and a few common species (MacArthur 1960, Whittaker 1965). As with interaction strength distributions, the mechanisms generating the skewed species abundance distribution have been a topic of debate, and have included various statistical and biological processes (McGill et al. 2007). Similar to interaction strengths, there is evidence that “rare” species tend to remain “rare” and “common” species remain “common” (McGill et al. 2005). Given the effects of prey density on the magnitude of prey-specific predator feeding rates, the shape of species abundance distributions is potentially a contributing factor in shaping interaction strength distributions. Conversely, biotic interactions are hypothesized drivers of species abundance distributions, making it possible that both

distributions feed back to influence one another. The presence of skewed (e.g., log-normal) distributions of other biological properties, including community body sizes (Blackburn and Gaston 1994, Limpert et al. 2001), suggests the possibility of unifying mechanisms underlying diverse community properties, which presents a promising area for future work (McGill et al. 2007).

The relative consistency of the pairwise interactions and resulting interaction strength distributions seen in our study is striking, given that we focused on a generalist predator in species-rich streams that typically show large variation in biotic and abiotic factors (Fisher et al. 1982, Power et al. 2008, Death 2010). Pairwise interaction strengths in streams are expected to be dynamic because interaction-strength-altering abiotic drivers themselves vary greatly over time (Power et al. 1988, Peckarsky et al. 1990, Wootton et al. 1996, Tonkin et al. 2017). Spatial heterogeneity in stream habitat can also shape community structure over small spatial scales (Palmer and Poff 1997), and the life histories of many stream organisms result in fluctuating population abundances and size structures across seasons (Huryn and Wallace 2000). The observed variation in prey-specific feeding rates in our study is usefully interpreted in the context of these factors.

When considered in a univariate fashion, abiotic factors explained the most variation in feeding rates for five prey taxa, indicating that knowledge traditionally seen as vital to predator functional responses was of little utility for these species. The importance of abiotic conditions was further underscored by the prey-specific models, including only abiotic factors having the lowest summed AIC<sub>c</sub> scores. This role of abiotic factors in driving feeding-rate variation was less apparent in our previous single-season study (Preston et al. 2018), which emphasizes the importance of spatiotemporal replication and scale dependence in considering interaction strength variation and its drivers. Prey-specific sculpin feeding rates correlated negatively with stream flow and positively with water temperatures, consistent with



expected effects of these variables on energetic demands, activity levels, and possibly foraging conditions for fishes (Elwood and Waters 1969, Kishi et al. 2005).

We found that univariate prey-density models had the second-best performance behind models with abiotic variables in explaining within-pair feeding-rate variation. For most prey (18 of 20 taxa), prey-specific feeding rates increased as prey-specific density increased, suggesting that sculpin are opportunistically consuming prey that they encounter, especially at low prey densities. The relative role of prey density across pairwise interactions was associated with the life histories of the prey taxa, such as voltinism and length of the nymphal period. These factors also contributed to differences in variation associated with space versus time. In general, the seasonal patterns in feeding rates on mayflies, stoneflies, and caddisflies were likely driven by their mostly univoltine lifecycles, where densities and size distributions change markedly over the season and often peak in spring and summer (Anderson and Wold 1972, Kerst and Anderson 1974). For instance, the large seasonal changes in feeding rates on baetid mayflies (highest in summer) and heptageniid mayflies (highest in spring) correspond with peak emergence periods, after which decreases in nymphal densities because of emergence result in lower feeding rates (Lehmkuhl 1968, 1969). Feeding rates on prey taxa that showed less seasonal variation may in turn be related to longer larval periods or multiple generations per year that result in less temporal fluctuation in prey density and size (e.g., many dipterans; Dudley and Anderson 1987).

The slopes of the within-pair relationships between feeding rates and the densities of each prey taxon are informative because they allow comparisons with predictions from predator functional response models. These slopes were less than one on the log-log scale for all but one prey taxon (for which the slope was approximately one; Appendix S1: Table S6) reflecting decelerating positive (i.e., saturating) relationships on the natural scale (Menge et al. 2018). This finding is consistent with nearly all parametric models of predator functional responses (Jeschke et al. 2002). The mechanisms underlying the saturation of prey-specific feeding rates, however, are not necessarily clear in that an accelerating (nonsaturating) slope between feeding rates and prey densities was observed when considering the relationship across all prey species combined (Preston et al. 2018 and Appendix S1: Fig. S2). In other words, feeding rates increased with within-species differences in prey density in a decelerating (saturating) form but increased with between-species differences in prey density in an accelerating (nonsaturating) fashion. Further lines of evidence indicate that the overall feeding rates of sculpin are not limited by either handling or digestion times, which are the typically invoked rate-limiting steps for saturating functional responses. For instance, the mean number of prey observed per sculpin was <30 times the maximum observed, demonstrating that most sculpin are able to

consume far more prey than is observed in their stomachs (a widespread characteristic of fishes; Armstrong and Schindler 2011). It is also noteworthy that for most taxa (13 of 20) the top-performing model did not include prey density, and that for 8 taxa prey body mass or abiotic factors explained more of the univariate variation in within-pair feeding rates. Together, these findings show that functional response models that focus only on variation in prey density within a single taxon may poorly predict feeding rates in the field, and that current functional response models (developed on the basis of variation in density within a prey species) may not be as easily scaled up to predicting total or between-prey variation in feeding rates, as often assumed.

Prey mass was most closely associated with feeding-rate variation for relatively few prey taxa (3 of 20), suggesting that efforts to infer interaction strengths based on pairwise predator-prey size relationships should be applied to food webs containing generalist predators with caution. Across the entire feeding-rates data set, there appears to be an “optimal” prey mass associated with the highest feeding rates (Preston et al. 2018 and Appendix S1: Fig. S2). In general, predators are thought to select for prey of intermediate predator-prey body-size ratios, thereby increasing energetic gains from prey while avoiding large prey that are less efficiently consumed (Brose 2010, Kalinkat et al. 2013). This could result in either monotonic positive or negative relationships between feeding rates and prey size within a given prey taxon, depending on where a prey type lies relative to the optimum. We observed both positive and negative correlations between prey mass and prey-specific feeding rates in our analysis, but the direction of the relationships was not consistent with a single optimal prey mass across all prey taxa. Some prey likely showed negative relationships between mass and feeding rates because large prey individuals (e.g., *Juga* snails) present challenges for consuming and digesting prey. Recent research also indicates that differences in the mean and the standard deviation of predator-prey size relationships across food webs are linked to changes in overall prey availability (Costa-Pereira et al. 2018).

Predator (i.e., sculpin) density was not a primary factor underlying variation in prey-specific feeding rates in our data set. The presence and relative importance of predator dependence has been a debated topic (Abrams and Ginzburg 2000, Baraquand 2014), with relatively few studies having assessed predator dependence in field settings (Novak et al. 2017). The lack of a relationship for most prey taxa is interesting given that (1) we observed a negative correlation between sculpin density and feeding rates across all combined prey taxa from summer (Preston et al. 2018), and (2) sculpin in streams are known to be territorial such that increases in density are expected to increase intraspecific interactions and decrease time spent feeding (Grossman et al. 2006). It is possible that wider variation in predator densities, beyond what was observed naturally at our sites would

be more effective at revealing whether or not predator interference occurs in this system. That said, our results indicate that over the observed range of species densities, predator dependence is unlikely to shape sculpin feeding rates strongly relative to other factors.

Several aspects of our study are of relevance in evaluating the generality of our results. We focused on a single predator species and, for most analyses, only a subset of its prey taxa. Although sculpins are generalists, as are most predators, focusing on other predators in our system could have altered some conclusions. For instance, cutthroat trout in our streams show less consistency in their prey-specific feeding rates across seasons because of highly variable terrestrial prey availability (Falke et al. 2018). Similarly, incorporating the entire prey community, including all rare prey, would likely increase both within and across-pair variation in feeding rates. Lastly, although streams in general are highly dynamic, our sites typically do not dry completely in late summer, unlike some Mediterranean climate streams, and they no longer support anadromous fishes, both of which can drive wholesale food-web alterations (Gasith and Resh 1999, Naiman et al. 2002).

An important remaining question involves understanding how changes in spatial and temporal scale influence variation in species interaction strengths. Increases in temporal scale are more likely to capture infrequent events (e.g., severe floods or droughts) and long-term directional change (e.g., climate shifts) that can expand the range of observed environmental variation, leading to nonstationarity in community structure (Williams and Jackson 2007, Wolkovich et al. 2014). Such processes are likely to increase interaction strength variation, but whether they affect across- and within-species variation to a similar magnitude is challenging to predict (Parmesan 2006). As spatial scale increases, surveys would increasingly capture larger variation in species abundances and turnover in species composition due to environmental filters and range limit boundaries. This too, should increase variation in species interactions. On the other hand, ecological communities are increasingly becoming homogenized across large spatial scales because of ongoing species introductions and habitat alteration (Olden 2006). As rare species are lost and common species are added, community composition and relative abundances often become more consistent across space and time (McKinney and Lockwood 1999), potentially driving concurrent increases in the consistency of species interaction strength distributions. There is a need for more quantitative food-web studies that explore the roles of ecological, temporal, and spatial scale (McCann et al. 1998) and for further integration of biotic interactions in explaining biogeographic and macroecological patterns (Wisz et al. 2013, Poisot et al. 2015, Gravel et al. 2019).

Although the complexity and dynamics of food webs can appear intractable (Polis 1991), our results indicate that the dynamics of trophic interactions may be

predictable over space and time based on characteristics of the interacting species and their environment. Species interactions can thus be highly dynamic while generating empirical patterns that prove ubiquitous across unique food webs (Wootton and Emmerson 2005). Promising next steps include developing and testing mechanistic models that incorporate species densities, species traits beyond body size, and environmental covariates in shaping the strength and functional form of interactions in species-rich communities. Achieving this aim will benefit from future empirical work that bridges across scales of interactions in space and time, ranging from species pairs to multiple food webs.

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#### LITERATURE CITED

- Abrams, P. A., and L. R. Ginzburg. 2000. The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology and Evolution* 15:337–341.
- Anderson, N. H., and D. M. Lehmkuhl. 1968. Catastrophic drift of insects in a woodland stream. *Ecology* 49:198–206.
- Anderson, N. H., and J. L. Wold. 1972. Emergence trap collections of Trichoptera from an Oregon stream. *Canadian Entomologist* 104:189–201.
- Armstrong, J. B., and D. E. Schindler. 2011. Excess digestive capacity in predators reflects a life of feast and famine. *Nature* 476:84–88.
- Baraquand, F. 2014. Functional responses and predator–prey models: a critique of ratio dependence. *Theoretical Ecology* 7:3–20.
- Bellmore, J. R., C. V. Baxter, and P. J. Connolly. 2015. Spatial complexity reduces interaction strengths in the meta-food web of a river floodplain mosaic. *Ecology* 96:274–283.
- Blackburn, T. M., and K. J. Gaston. 1994. Animal body size distributions: patterns, mechanisms and implications. *Trends in Ecology & Evolution* 9:471–474.
- Borrvall, C., B. Ebenman, and T. J. Tomas Jonsson. 2000. Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters* 3:131–136.
- Boutin, S., C. J. Krebs, R. Boonstra, M. R. T. Dale, S. J. Hannon, K. Martin, A. R. E. Sinclair, J. N. M. Smith, R. Turkington, and M. Blower. 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. *Oikos* 74:69–80.
- Brose, U. 2010. Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Functional Ecology* 24:28–34.

- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.
- Byers, J. E., Z. C. Holmes, and J. C. Malek. 2017. Contrasting complexity of adjacent habitats influences the strength of cascading predatory effects. *Oecologia* 185:107–117.
- Costa-Pereira, R., M. S. Araújo, R. da. S. Olivier, F. L. Souza and V. H. Rudolf. 2018. Prey limitation drives variation in allometric scaling of predator–prey interactions. *American Naturalist* 192:139–149.
- Cross, W. F., C. V. Baxter, E. J. Rosi-Marshall, R. O. Hall, T. A. Kennedy, K. C. Donner, W. Kelly, A. Holly, S. E. Seegert, and K. E. Behn. 2013. Food-web dynamics in a large river discontinuum. *Ecological Monographs* 83:311–337.
- Davis, G. E., and C. E. Warren. 1965. Trophic relations of a sculpin in laboratory stream communities. *Journal of Wildlife Management* 29:846–871.
- de Roos, A. M., L. Persson, and E. McCauley. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecology Letters* 6:473–487.
- de Ruiter, P. C., A.-M. Neutel, and J. C. Moore. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* 269:1257.
- Death, R. G. 2010. Disturbance and riverine benthic communities: what has it contributed to general ecological theory? *River Research and Applications* 26:15–25.
- Dudley, T. L., and N. H. Anderson. 1987. The biology and life cycles of *Lipsothrix* spp. (Diptera: Tipulidae) inhabiting wood in Western Oregon streams. *Freshwater Biology* 17:437–451.
- Elwood, J. W., and T. F. Waters. 1969. Effects of floods on food consumption and production rates of a stream brook trout population. *Transactions of the American Fisheries Society* 98:253–262.
- Fagan, W. F., and L. E. Hurd. 1994. Hatch density variation of a generalist arthropod predator: population consequences and community impact. *Ecology* 75:2022–2032.
- Fairweather, P. G., and A. J. Underwood. 1983. The apparent diet of predators and biases due to different handling times of their prey. *Oecologia* 56:169–179.
- Falke, L. P., J. S. Henderson, M. Novak, and D. L. Preston. 2018. Temporal shifts in intraspecific and interspecific diet variation: effects of predator body size and identity across seasons in a stream community. *bioRxiv*. <https://doi.org/10.1101/476374>
- Fisher, S. G., L. J. Gray, N. B. Grimm, and D. E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* 52:93–110.
- Gasith, A., and V. H. Resh. 1999. Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics* 30:51–81.
- Gellner, G., and K. S. McCann. 2016. Consistent role of weak and strong interactions in high- and low-diversity trophic food webs. *Nature Communications* 7:11180.
- Grafius, E., and N. H. Anderson. 1979. Population dynamics, bioenergetics, and role of *Lepidostoma quercina* Ross (Trichoptera: Lepidostomatidae) in an Oregon woodland stream. *Ecology* 60:433–441.
- Gravel, D., B. Baiser, J. A. Dunne, J.-P. Kopelke, N. D. Martinez, T. Nyman, T. Poisot, D. B. Stouffer, J. M. Tylianakis, and S. A. Wood. 2019. Bringing Elton and Grinnell together: a quantitative framework to represent the biogeography of ecological interaction networks. *Ecography* 42:401–415.
- Grossman, G. D., R. E. Ratajczak, J. T. Petty, M. D. Hunter, J. T. Peterson, and G. Grenouillet. 2006. Population dynamics of mottled sculpin (Pisces) in a variable environment: information theoretic approaches. *Ecological Monographs* 76:217–234.
- Hawkins, C. P., and J. K. Furnish. 1987. Are snails important competitors in stream ecosystems? *Oikos* 49:209–220.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91:385–398.
- Huryn, A. D., and J. B. Wallace. 2000. Life history and production of stream insects. *Annual Review of Entomology* 45:83–110.
- Hyslop, E. J. 1980. Stomach contents analysis—a review of methods and their application. *Journal of Fish Biology* 17:411–429.
- Jeschke, J. M., M. Kopp, and R. Tollrian. 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs* 72:95–112.
- Kalinkat, G., F. D. Schneider, C. Digel, C. Guill, B. C. Rall, and U. Brose. 2013. Body masses, functional responses and predator–prey stability. *Ecology Letters* 16:1126–1134.
- Kalinowski, R. M., and J. P. DeLong. 2016. Beyond body mass: how prey traits improve predictions of functional response parameters. *Oecologia* 180:543–550.
- Kerst, C. D., and N. H. Anderson. 1974. Emergence patterns of Plecoptera in a stream in Oregon, USA. *Freshwater Biology* 4:205–212.
- Kerst, C. D., and N. H. Anderson. 1975. The Plecoptera community of a small stream in Oregon, USA. *Freshwater Biology* 5:189–203.
- Kishi, D., M. Murakami, S. Nakano, and K. Maekawa. 2005. Water temperature determines strength of top-down control in a stream food web. *Freshwater Biology* 50:1315–1322.
- Klein, J. P., and M. L. Moeschberger. 2005. Survival analysis: techniques for censored and truncated data. Springer Science & Business Media, New York, New York, USA.
- Lantry, B. F., and R. O’Gorman. 2007. Drying temperature effects on fish dry mass measurements. *Journal of Great Lakes Research* 33:606–616.
- Lehmkuhl, D. M. 1968. Observations on the life histories of four species of *Epeorus* in western Oregon. *Pan-Pacific Entomologist* 44:129–137.
- Lehmkuhl, D. M. 1969. Biology and downstream drift of some Oregon Ephemeroptera. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Limpert, E., W. A. Stahel, and M. Abbt. 2001. Log-normal distributions across the sciences: keys and clues. *BioScience* 51:341–352.
- Lopez, D. N., P. A. Camus, N. Valdivia, and S. A. Estay. 2017. High temporal variability in the occurrence of consumer–resource interactions in ecological networks. *Oikos* 126:1699–1707.
- MacArthur, R. 1960. On the relative abundance of species. *American Naturalist* 94:25–36.
- McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. *Nature* 395:794–798.
- McGill, B. J., R. S. Etienne, J. S. Gray, D. Alonso, M. J. Anderson, H. K. Benecha, M. Dornelas, B. J. Enquist, J. L. Green, and F. He. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters* 10:995–1015.
- McGill, B. J., E. A. Hadly, and B. A. Maurer. 2005. Community inertia of Quaternary small mammal assemblages in North America. *Proceedings of the National Academy of Sciences of the United States of America* 102:16701–16706.
- McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* 14:450–453.

- Menge, B. A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology and Ecology* 250:257–289.
- Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* 64:249–286.
- Menge, D. N., A. C. MacPherson, T. A. Bytnerowicz, A. W. Quebbeman, N. B. Schwartz, B. N. Taylor, and A. A. Wolf. 2018. Logarithmic scales in ecological data presentation may cause misinterpretation. *Nature Ecology & Evolution* 2:1393–1402.
- Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. An introduction to the aquatic insects of North America. Kendall Hunt, Dubuque, IA.
- Mora, B. B., D. Gravel, L. J. Gilarranz, T. Poisot, and D. B. Stouffer. 2018. Identifying a common backbone of interactions underlying food webs from different ecosystems. *Nature Communications* 9:2603.
- Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* 5:399–417.
- Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Novak, M. 2010. Estimating interaction strengths in nature: experimental support for an observational approach. *Ecology* 91:2394–2405.
- Novak, M., and J. T. Wootton. 2008. Estimating nonlinear interaction strengths: an observation-based method for species-rich food webs. *Ecology* 89:2083–2089.
- Novak, M., C. Wolf, K. E. Coblenz, and I. D. Shepard. 2017. Quantifying predator dependence in the functional response of generalist predators. *Ecology Letters* 20:761–769.
- Olden, J. D. 2006. Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography* 33:2027–2039.
- Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature* 355:73–75.
- Palmer, M. A., and N. L. Poff. 1997. The influence of environmental heterogeneity on patterns and processes in streams. *Journal of the North American Benthological Society* 16:169–173.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637–669.
- Peckarsky, B. L., S. C. Horn, and B. Statzner. 1990. Stonefly predation along a hydraulic gradient: a field test of the harsh–benign hypothesis. *Freshwater Biology* 24:181–191.
- Poisot, T., D. B. Stouffer, and D. Gravel. 2015. Beyond species: why ecological interaction networks vary through space and time. *Oikos* 124:243–251.
- Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist* 138:123–155.
- Polis, G. A., R. D. Holt, B. A. Menge, and K. O. Winemiller. 1996. Time, space, and life history: influences on food webs. Pages 435–460 *in* G. A. Polis, and K. O. Winemiller, editors. *Food webs*. Springer, New York, New York, USA.
- Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Matthews, P. B. Moyle, B. Statzner, R. Irene, and W. De Badgen. 1988. Biotic and abiotic controls in river and stream communities. *Journal of the North American Benthological Society* 7:456–479.
- Power, M. E., M. S. Parker, and W. E. Dietrich. 2008. Seasonal reassembly of a river food web: floods, droughts, and impacts of fish. *Ecological Monographs* 78:263–282.
- Preston, D. L., J. S. Henderson, L. P. Falke, and M. Novak. 2017. Using survival models to estimate invertebrate prey identification times in a generalist stream fish. *Transactions of the American Fisheries Society* 146:1303–1314.
- Preston, D. L., J. S. Henderson, L. P. Falke, L. M. Segui, T. J. Layden, and M. Novak. 2018. What drives interaction strengths in complex food webs? A test with feeding rates of a generalist stream predator. *Ecology* 99:1591–1601.
- Raffaelli, D. G., and S. J. Hall. 1996. Assessing the relative importance of trophic links in food webs. Pages 185–191 *in* G. A. Polis, and K. O. Winemiller, editors. *Food webs*. Springer, New York, New York, USA.
- Rall, B. C., U. Brose, M. Hartvig, G. Kalinkat, F. Schwarzmüller, O. Vucic-Pestic, and O. L. Petchev. 2012. Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society B* 367:2923–2934.
- Schleuning, M., N. Blüthgen, M. Flörchinger, J. Braun, H. M. Schaefer, and K. Böhning-Gaese. 2011. Specialization and interaction strength in a tropical plant–frugivore network differ among forest strata. *Ecology* 92:26–36.
- Skalski, G. T., and J. F. Gilliam. 2001. Functional responses with predator interference: viable alternatives to the Holling type II model. *Ecology* 82:3083–3092.
- Spiller, D. A., and T. W. Schoener. 2007. Alteration of island food-web dynamics following major disturbance by hurricanes. *Ecology* 88:37–41.
- Tonkin, J. D., M. T. Bogan, N. Bonada, B. Rios-Touma, and D. A. Lytle. 2017. Seasonality and predictability shape temporal species diversity. *Ecology* 98:1201–1216.
- Tylianakis, J. M., and R. J. Morris. 2017. Ecological networks across environmental gradients. *Annual Review of Ecology, Evolution, and Systematics* 48:24–45.
- Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351–1363.
- Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* 401:464–467.
- Vázquez, D. P., S. B. Lomáscolo, M. B. Maldonado, N. P. Chacoff, J. Dorado, E. L. Stevani, and N. L. Vitale. 2012. The strength of plant–pollinator interactions. *Ecology* 93:719–725.
- Warren, C. E., J. H. Wales, G. E. Davis, and P. Doudoroff. 1964. Trout production in an experimental stream enriched with sucrose. *Journal of Wildlife Management* 28:617–660.
- Whittaker, R. H. 1965. Dominance and diversity in land plant communities: numerical relations of species express the importance of competition in community function and evolution. *Science* 147:250–260.
- Wiens, J. J. 2011. The niche, biogeography and species interactions. *Philosophical Transactions of the Royal Society B* 366:2336–2350.
- Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5:475–482.
- Wisz, M. S., J. Pottier, W. D. Kissling, L. Pellissier, J. Lenoir, C. F. Damgaard, C. F. Dormann, M. C. Forchhammer, J.-A. Grytnes, and A. Guisan. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews* 88:15–30.
- Wolf, C., M. Novak, and A. I. Gitelman. 2017. Bayesian characterization of uncertainty in species interaction strengths. *Oecologia* 184:327–339.
- Wolkovich, E. M., B. I. Cook, K. K. McLauchlan, and T. J. Davies. 2014. Temporal ecology in the Anthropocene. *Ecology Letters* 17:1365–1379.

- Woodward, G., D. C. Speirs, A. G. Hildrew, and C. Hal. 2005. Quantification and resolution of a complex, size-structured food web. *Advances in Ecological Research* 36:85–135.
- Woodward, G. et al. 2010. Ecological networks in a changing climate. *Advances in Ecological Research* 42:71–138.
- Wootton, J. T. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. *Ecological Monographs* 67:45–64.
- Wootton, J. T., and M. Emmerson. 2005. Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution, and Systematics* 36:419–444.
- Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of disturbance on river food webs. *Science* 273:1558–1561.
- Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York, New York, USA.

#### SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2816/suppinfo>

#### DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sr6888t>.