

LETTER

Landscape diversity promotes stable food-web architectures in large rivers

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Abstract

Uncovering relationships between landscape diversity and species interactions is crucial for predicting how ongoing land-use change and homogenization will impact the stability and persistence of communities. However, such connections have rarely been quantified in nature. We coupled high-resolution river sonar imaging with annualized energetic food webs to quantify relationships among habitat diversity, energy flux, and trophic interaction strengths in large-river food-web modules that support the endangered Pallid Sturgeon. Our results demonstrate a clear relationship between habitat diversity and species interaction strengths, with more diverse foraging landscapes containing higher production of prey and a greater proportion of weak and potentially stabilizing interactions. Additionally, rare patches of large and relatively stable river sediments intensified these effects and further reduced interaction strengths by increasing prey diversity. Our findings highlight the importance of landscape characteristics in promoting stabilizing food-web architectures and provide direct relevance for future management of imperilled species in a simplified and rapidly changing world.

KEYWORDS

energy flows, food web, habitat diversity, interaction strength, large river, riverscape, pallid sturgeon, secondary production, stability, sturgeon

INTRODUCTION

Human transformation of the Earth's surface is rapidly homogenizing landscapes and influencing the stability of communities and ecosystem services (Hautier et al., 2018; Olden et al., 2004; Wang et al., 2021). A reduction in physical habitat diversity can have particularly strong effects on communities by altering species distributions (Stein et al., 2014), movement (Damschen et al., 2008), and life histories (Schindler et al., 2010). In addition, changes to the spatial arrangement and composition of habitat have the potential to rewire or disrupt

the architecture of species interaction networks (Bartley et al., 2019; Grabowski et al., 2008) that define patterns of energy flux, interaction strengths, and community stability (De Ruiter et al., 1995; McCann, 2007). Thus, uncovering relationships between habitat diversity and species interactions is particularly important for understanding how changes to the landscape influence stability and persistence of biodiversity (McCann, 2012).

Theory suggests that populations in heterogeneous landscapes are more stable over time because of non-random patterns in the way species feed and interact (Rooney et al., 2008). For instance, food webs in

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physically diverse landscapes tend to exhibit a diverse resource base, high levels of omnivory, and a large proportion of weak feeding interactions (Rooney et al., 2008), all of which may dampen population oscillations and reduce overall extinction risk (McCann, 2000; Emmerson & Yearsley, 2004; Figure 1). Such characteristics are thought to emerge in diverse landscapes through a variety of mechanisms, including variation in niche space, a higher presence of prey refugia, and switching among distinct prey populations by mobile predators (Rooney et al., 2008). Although these theoretical advances have received some experimental support (Alexander et al., 2015), few studies have addressed such concepts in realistic field settings (e.g., Bellmore et al., 2015).

Large rivers are among the most biophysically complex ecosystems on Earth (Hauer et al., 2016; Ward et al., 2002), and their ongoing modification has resulted in widespread declines and extinctions of predatory megafauna (Albert et al., 2021; He et al., 2019). One such critically endangered predator, the Pallid Sturgeon (*Scaphirhynchus albus*), is a large-bodied and highly mobile fish that has suffered from a legacy of hydrologic alteration (i.e., the placement of reservoirs and dams; Guy et al., 2015) and near loss of natural recruitment in portions of its natural range (Jordan et al., 2016). Despite a history of population augmentation via hatcheries,

the long-term persistence of Pallid Sturgeon will likely depend on aspects of food-web architecture that reflect the coupling of diverse habitats that sustain energetic demands for growth, survival, and reproduction, and that may buffer against perturbations (De Ruiter et al., 2005; Naiman et al., 2012; Naman et al., 2022). Yet, quantifying connections between large-river habitat and patterns of energy flux to mobile predators remains difficult, owing to the challenges of adequately characterizing underwater habitat at large spatial scales and the extreme time and effort necessary for estimating trophic interactions *in situ*.

Here, we combined high-resolution river sonar imaging with extensive biological sampling to construct detailed food-web modules (i.e., 'sink webs', sensu Cohen, 1978; McCann, 2012) that describe weighted trophic pathways leading to the endangered Pallid Sturgeon and the sympatric Shovelnose Sturgeon (*Scaphirhynchus platyrhynchus*; "*Scaphirhynchus* spp." hereafter when together). We developed a novel approach for pairing continuous habitat mapping with food-web quantification which allowed us to simulate thousands of modules across the riverscape and examine how spatial variation in foraging may shape distributions of trophic interaction strengths and potential stability of our focal taxa. We hypothesized that consumer foraging windows with high habitat diversity would positively influence food-web stability by enhancing both prey resource diversity and production, dispersing strong top-down predation across multiple habitats, and reducing median food-web interaction strengths (Figure 1). Our study advances food-web ecology by connecting properties of the physical habitat template to metrics of food-web stability, and provides direct relevance for the management of Pallid Sturgeon.

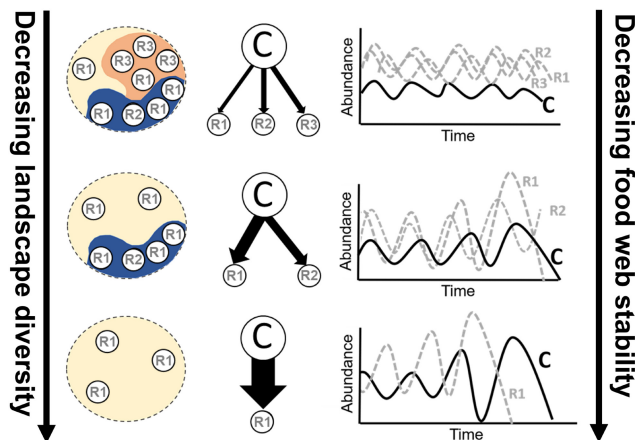


FIGURE 1 Hypothesized relationships among landscape and resource diversity (left), trophic interaction strengths in food-web modules (middle; size of arrows indicate relative interaction strength), and the stability and persistence of populations (right). R1-R3 represent different prey resources, whereas C represents a hypothetical predatory consumer. Diverse land- or riverscapes (top) are predicted to contain a high diversity of resources (left), leading to dispersed predation by consumers (middle), and dampened population fluctuations of both consumers and prey resources over time (right). As diverse environments become simplified, indicated by losses in the orange and blue areas, we predict that fewer unique (R2 only occurs in blue habitats, R3 only occurs in orange habitats) and redundant (R1 occurs in all three habitats) prey resources will be available for predator consumption. These lost resource opportunities are predicted to lead to stronger top-down predation and larger median interaction strengths. Such patterns can theoretically lead to larger fluctuations in population abundance and extinctions over time.

MATERIALS AND METHODS

Study area

We studied a 38-km segment of the Missouri River between the confluence of the Yellowstone River and the headwaters of Lake Sakakawea in Montana and North Dakota, USA (Figure 2; Figure S1). This segment contains a diversity of river habitats that support the life-history requirements of the highly mobile Pallid Sturgeon, and offers an ideal setting to explore connections between habitat diversity and food-web dynamics in a key area for Pallid Sturgeon recovery (Webb et al., 2005).

Riverscape habitat characteristics

Spatially explicit understanding of habitat diversity provides the foundation for linking riverscape patterns to food-web characteristics supporting the Pallid

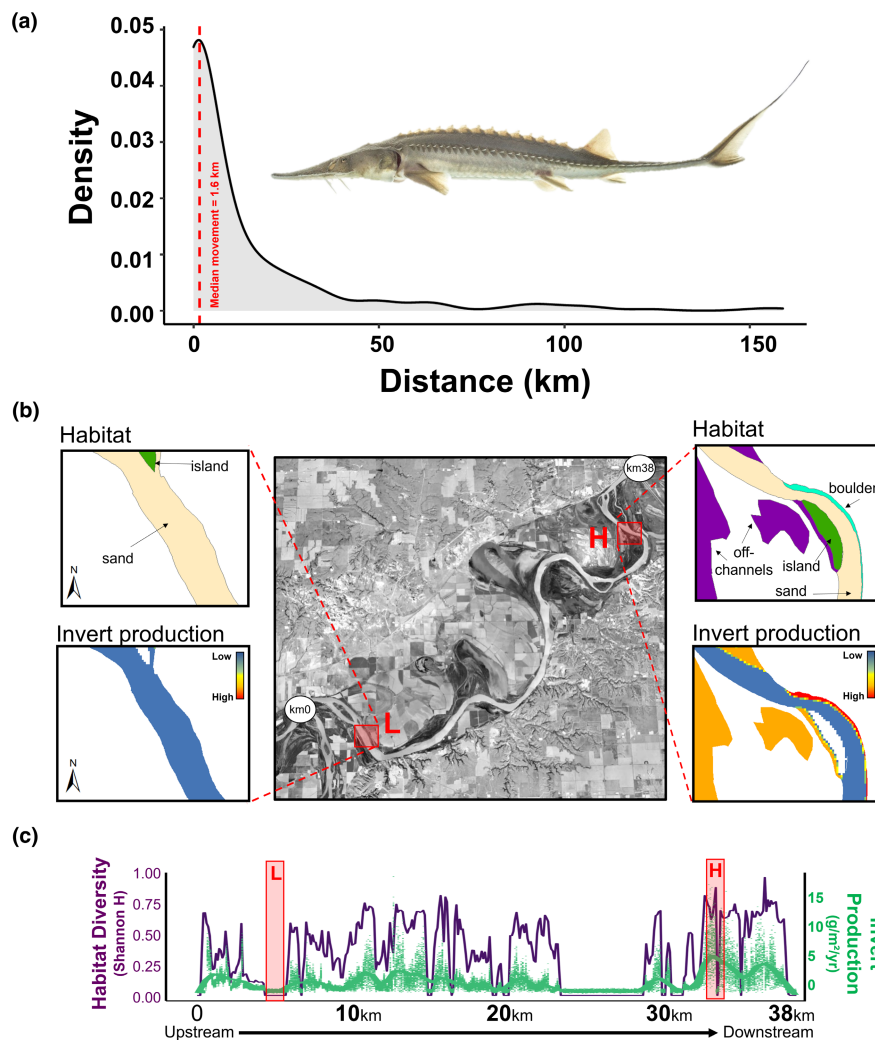


FIGURE 2 (a) Sturgeon mark and recapture data were used to estimate the most relevant spatial scale of foraging windows used for food-web analyses (red dashed line, median: 1.6 km). (b) Using this 1.6-km window size, we simulated food-web modules across the Missouri River to estimate the relationship between habitat diversity and trophic interaction strengths. Shown are two example 1.6-km windows of low habitat diversity (red box L and left figures) represented by sand and low invertebrate production, and high habitat diversity (red box H and right figures) represented by multiple different habitat patches and higher invertebrate production. (c) Both habitat diversity (Shannon H' , bottom graph purple line) and invertebrate secondary production (g AFDM/m²/year; bottom graph green line and dots) varied considerably throughout the river segment, which provided an ideal setting to explore the relationship between habitat diversity and food-web interaction strengths (red boxes L and H correspond to 1.6-km windows illustrated above).

Sturgeon. To accomplish this, we used side-scan sonar and aerial photography to map riverbed substrate (e.g., sand, cobble-gravel) and off-channel habitats throughout the study area with a high spatial scope (i.e., quantitative ratio of extent to resolution; Schneider, 2001). Side-scan sonar is a remote sensing system that produces two-dimensional imagery of the riverbed by transmitting and receiving high-frequency sound waves from a boat that are reflected off underwater objects (Kaeser & Litts, 2010). After collecting imagery in the field, we geoprocessed and rectified the raw sonar images to create spatially accurate and seamless sonar image mosaics. Unique habitat features (e.g., sand, boulder and cobble-gravel) were delineated and outlined using polygons based on an a priori classification scheme in ArcGIS® (Scholl et al., 2021). Our habitat classification scheme

relied on observations, tactile information, and preliminary sonar mapping with the goal of characterizing spatial patterns of habitats with direct ecological relevance to the foraging of sturgeon.

Habitat proportions at a given river location were extracted to estimate Shannon habitat diversity (Shannon, 1948) using the equation:

$$H' = - \sum_{i=1}^s p_i \ln p_i, \quad (1)$$

where habitat diversity (H') is a function of the proportion of habitat i (p_i) and the natural logarithm of this proportion ($\ln p_i$), summed across all habitat types (s). Habitat-weighted sediment size was estimated by multiplying habitat-specific median sediment size (Wentworth, 1922)

by habitat proportions and summing across all habitats. Woody debris was not effectively quantified using side-scan sonar and was assumed to compose 2% of the total available habitat (cf. Gippel et al., 1996: 2%, Benke et al., 1984: 5%). Using extensive ground-truthing, we estimated an overall habitat classification accuracy of 78% for all other habitats (Scholl et al., 2021).

Invertebrate structure and production

Benthic invertebrates were sampled throughout the study segment on five occasions in 2014 and 2015 to estimate abundance on major substrate types and off-channel areas ($n=30$ samples per date; Benke & Huryn, 2017). On each occasion, we used a stratified sampling design based on areal proportions of major benthic habitats and care was taken to allocate sampling throughout the entire length of the site. Although random sampling was desirable, some of our sample locations were selected based on feasibility of sampling from a boat or river-bank. A variety of sampling modes were used to collect invertebrates from different habitat types on each date; sand habitat: a Ponar dredge sampler (0.052 m^2 , $n=10$) attached to a sounding reel on a boat; cobble-gravel: a Hess sampler (0.086 m^2 , $n=5$); woody debris: $250\text{ }\mu\text{m}$ mesh bags ($n=5$); depositional off-channels: a stovepipe core (0.031 m^2 , $n=5$); and large colluvial talus: buckets while a D-frame dip net was held downstream to collect any dislodged macroinvertebrates ($n=5$). All samples were poured onto a $250\text{-}\mu\text{m}$ sieve and preserved in 8% buffered formalin for subsequent processing and analysis. One length and three circumference measurements were taken to estimate the surface area (m^2) of each piece of large woody debris sampled using the formula for a cylinder. Digital pictures of all large rocks were taken in the field and surface areas were measured using Image J® image-analysis software.

In the laboratory, invertebrate samples were rinsed through stacked metal sieves to separate coarse ($>1\text{ mm}$) and fine ($<1\text{ mm}$ $>250\text{ }\mu\text{m}$) organic matter size classes. Invertebrates in the two size classes were removed from organic materials under a dissecting microscope at 10–15X magnification. Fine samples with large numbers of invertebrates (>200) were subsampled using a Folsom plankton wheel. Invertebrates were identified to the lowest possible taxonomic level, in most cases genus, using Merritt et al. (2008) and Smith (2001). Invertebrates were counted to estimate abundance and measured to the nearest millimetre (body length) to estimate biomass (g dry mass) using published length-mass regressions (Benke et al., 1999). Multiple correction factors based on broad taxonomic categories (e.g., shelled molluscs vs. insect larvae) were applied to dry mass estimates to estimate ash-free dry mass (AFDM; Benke et al., 1999). For prohibitively large samples, the first 30 individuals of each taxon were measured, and individuals counted

but not measured were assumed to have the same size distribution (as in Cross et al., 2013).

Invertebrate secondary production (ash free dry mass; g AFDM/ m^2 /year), hereafter “secondary production”, was estimated for each population by habitat type using the size-frequency method, instantaneous growth rate method, or by multiplying bootstrapped annual biomass estimates by published production/biomass ratios (Benke & Huryn, 2017; Table S1). For the size–frequency method, we corrected our estimates of production using cohort production intervals (CPIs) based on size–frequency data. For each method described above, we used bootstrapping to estimate medians and 2.5% and 97.5% quantiles of annual invertebrate abundance, biomass, and production (Benke & Huryn, 2017). We sampled with replacement (1000 times) size-specific abundance data from replicate samples taken from each habitat to generate vectors of mean size-specific abundance and biomass (see Cross et al., 2013 for details). We additionally used the bootstrapped vectors of mean habitat-specific annual biomass (g AFDM/ m^2) to estimate assemblage diversity metrics (described in more detail below).

Invertebrates were not sampled from hard-clay, riprap, or cobble-gravel habitats due to their rarity in the environment ($<2\%$ of area for these habitats combined). Assemblages in hard-clay and riprap habitats were assumed to be similar to assemblages in sand and talus, respectively, and invertebrate samples collected from a nearby riffle in the Yellowstone River were used to approximate cobble-gravel invertebrate assemblages.

Sturgeon production, diets, and movement

Scaphirhynchus spp. abundance and size structure were estimated from mark-recapture efforts in the Missouri River in September 2014. Briefly, we targeted a 5-km area of high abundance aggregation and low movement, and used trammel nets to capture fish. All sturgeon were marked and released back into the population, and the site was sampled for recaptures on five occasions. Population abundance was estimated from mark-recapture data using closed-population models in Program MARK (White & Burnham, 1999), and empirically measured lengths and weights were used to estimate size structure. Size-at-age curves were used to convert estimates of size (g) to age-specific abundances and estimate annual growth rates for each age class (Braaten et al., 2012; Koch & Steffensen, 2009). Growth rates were combined with estimates of mean annual biomass for each age class to quantify secondary production for the population using the instantaneous growth rate method (Tables S2 and S3).

Diets of *Scaphirhynchus* spp. were collected throughout 2013–2014 using trammel netting and gastric lavage ($n=16$ shovelnose; $n=27$ Pallid; Dutton, 2018). In the laboratory, invertebrates in diets were identified, counted,

and weighed using similar protocols as benthic invertebrates described above.

The spatial extent of foraging by Pallid Sturgeon was estimated within the study segment using tagging and recapture events that occurred between 2003 and 2013 ($n=257$; Montana Fish Wildlife and Parks, *unpublished*). To avoid inclusion of large spawning migrations, we excluded fish that were caught and recaptured during the late spring-early summer spawning season. Foraging distance was estimated by calculating the river distance between tagging and recapture events. We could not obtain similar information for the movement of Shovelnose Sturgeon and thus assumed equivalent foraging movement patterns for our food-web analysis.

Simulating interaction strengths across the riverscape

It would not be logistically feasible to sample and construct unique quantitative food webs at many (e.g., 100) river locations that vary in habitat characteristics. We therefore developed a novel approach to simulate food-web modules in a wide variety of different habitat contexts (i.e., homogenous sand to diverse habitat mosaics) by combining habitat maps, habitat-specific invertebrate production estimates, and *Scaphirhynchus* spp. movement, diets, and production. We first selected 100 random locations in the study segment with a longitudinal (i.e., upstream-downstream) window size of 1.6 km, the median foraging distance of *Scaphirhynchus* spp. (see [Results](#)). For each 1.6-km window, we summarized habitat proportions, habitat-weighted sediment size, and habitat diversity. Next, to generate taxon-specific estimates of habitat-weighted invertebrate production, we multiplied 1000 bootstrapped estimates of habitat-specific production by the habitat proportions measured at each location, and summed the values across all river habitats. We similarly quantified habitat-weighted invertebrate assemblage biodiversity (Shannon H' and Simpsons evenness; weighted by mean annual biomass) and richness (total number of species) at all 100 locations (using the R package “vegan” Oksanen et al., 2020). Our food-web modules represent different ‘foraging landscapes’ for sturgeon at our study site, and are based on one set of bootstrapped values of prey production (per habitat type) derived from our single study river. We therefore acknowledge that metrics (e.g., interaction strengths) derived from food-web modules must be considered as pseudoreplicates in our statistical analyses (see below).

Annual estimates of prey consumption or energetic demand (g AFDM/m²/year) using the trophic basis of production method require information about *Scaphirhynchus* spp. production, diet composition, and literature-derived energetic efficiencies (Benke & Huryn, 2017), the collection of which are described above. Consumption fluxes were estimated by first

calculating the relative fraction of annual sturgeon production attributed to each prey type (F_i) as:

$$F_i = G_i * AE_i * NPE \quad (2)$$

where G_i is the proportion of prey type i in the diet, AE_i is the assimilation efficiency of prey type i (0.75 for invertebrate prey items, 0.95 fish tissue in this study), and NPE is the net production efficiency (0.25 used for juvenile sturgeon [<600 mm fork length], 0.125 for adult sturgeon in this study, Bellmore et al., 2013). Next, we calculated the actual amount of sturgeon j 's production attributed to each food type (PF_{ij} ; their ‘trophic basis of production’) as:

$$PF_{ij} = \frac{F_i}{\sum_{i=1}^n F_i} * P_j \quad (3)$$

where P_j is the annual production of sturgeon j . Finally, we calculated the annual consumption of each food type i by species j (FC_{ij}) as:

$$FC_{ij} = \frac{PF_{ij}}{AE_i * NPE} \quad (4)$$

Annual consumption estimates were combined with bootstrapped invertebrate production (g AFDM/m²/year) to simulate 1000 food-web modules at each location. We quantified taxon-specific interaction strengths by dividing annual consumption of each prey item by the mean annual habitat-weighted production of that prey item in each 1.6-km window (i.e., coloured dots in [Figure 3](#); Woodward et al., 2005). Interaction strengths equal to 1 indicate that annual consumption of a given prey taxon is equal to its total annual production, and thus represent a maximum trophic interaction strength. Although values greater than 1 may occur transiently, they are theoretically impossible over longer time frames unless prey availability was underestimated in our sampling or fish consumptive demand was overestimated; these relatively infrequent values (between 10 and 27% total interactions) were assumed equal to 1. Production of prey fish found in diets was not estimated in the environment and thus could not be incorporated into our estimates of interaction strength. We used generalized additive models (GAM; using the R package “mgcv” Wood & Wood, 2015) to quantify the importance of habitat diversity and sediment size (both smoothed terms) in driving patterns of interaction strengths.

Untangling connections among habitat, invertebrate prey, and food-web interaction strengths

To more explicitly examine how invertebrate prey assemblages mediate connections between river habitat

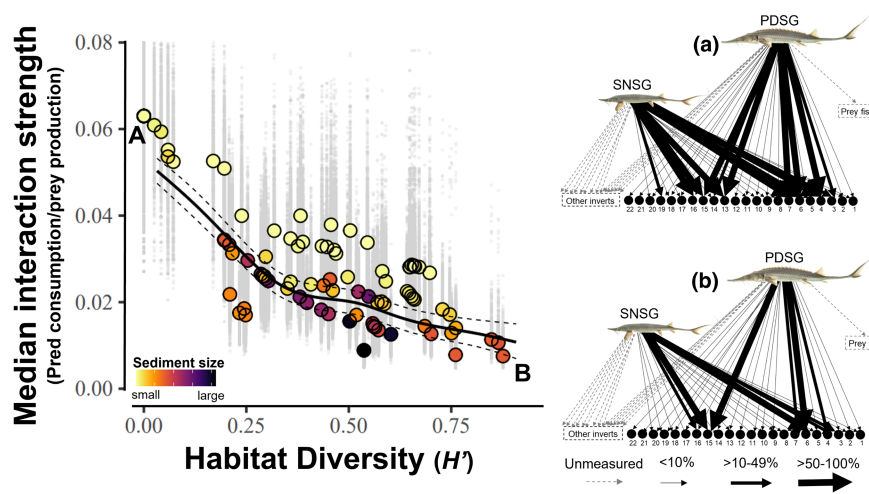


FIGURE 3 Median interaction strength (predator consumption [g AFDM/m²/year]/prey production [g AFDM/m²/year]) of *Scaphirhynchus* spp. food-web modules declined with increasing habitat diversity (estimated as the Shannon index [H']; left). Small grey dots represent simulated food-web modules ($n=1000$ per 1.6-km window location; 100,000 total bootstraps). Coloured circles represent median interaction strength at each location. Circle colour indicates habitat-weighted sediment size varying from small diameter (light yellow; <1 mm) to large sediments (dark purple; 16 mm). Predictions and 95% confidence intervals from a GAM using habitat diversity and sediment size as smoothed terms are represented by the bold and dashed black lines. Representative interaction strength modules (right) at river locations with low (a) and high (b) habitat diversity. Arrow thickness indicates the relative magnitude of interaction strengths. Dashed lines indicate unmeasured interaction strengths which occurred when a prey item was present in the diet, but its production in the environment was not estimated. PDSG, Pallid Sturgeon; SNSG, Shovelnose Sturgeon. Numbers at the bottom of the food web represent invertebrate prey taxa (see Tables S5 and S6 for taxon names).

and trophic interaction strengths (see hypotheses and Figure 1), we used structural equation modelling (SEM, Grace, 2006, Shipley, 2016). In particular, we were interested in the causal relationships that link habitat characteristics (i.e., habitat diversity and sediment size), invertebrate communities (i.e., biodiversity and secondary production), and median interaction strengths of food-web modules. We hypothesized that median interaction strength would be reduced by both invertebrate assemblage biodiversity and secondary production, suggesting that elevated prey diversity and productivity can stabilize food-web modules. We also hypothesized that invertebrate diversity and productivity would be positively related to habitat diversity and sediment size because these characteristics likely provide diverse and physically stable benthic substrata. We fit SEM models with singular dimensions of biodiversity that captured different aspects of the prey assemblage (i.e., species richness, Shannon-Wiener entropy [H'], and Simpson's evenness [D]), as well as a model with biodiversity treated as a latent variable including all three metrics using the lavaan package (ver. 0.6–15, Rosseel, 2012). Standardized regression coefficients were estimated to account for the different magnitude of measurements and to quantify the relative importance of each driver on food-web interaction strengths. We present the results of the latent variable model below and provide more information about the singular models in Data S1. All statistical analyses were conducted in R (R Core Team 2022).

RESULTS

Foraging distance, riverscape habitat characteristics, and patterns of prey production

Pallid Sturgeon movements were highly skewed towards small distances (mean = 7.6 km, median = 1.6 km), with a few individuals moving large distances (e.g., >50 km; Figure 2a). We therefore applied a 1.6-km foraging window when constructing detailed food-web modules (see below). We observed abrupt shifts in habitat diversity and composition throughout the riverscape, reflecting the presence of off-channels, colluvial talus, cobble-gravel, and riprap habitats embedded in the sand-dominated river (Figures 2b,c; Figure S1). Patterns of invertebrate assemblage production were strongly related to changes in habitat (Figures 2b,c; Figure S2), with low production on sand habitat and much higher and more variable production in off-channels and hard and stable substrates, such as cobble-gravel and talus (Table 1; Tables S1 and S4). Similarly, invertebrate diversity was lowest on sand, intermediate in off-channels, and considerably higher on larger substrates (Table 1; Figure S2).

Sturgeon diets and trophic basis of production

Shovelnose Sturgeon fed on a diverse assemblage of invertebrates ($n=29$ taxa); however, non-Tanytopodinae

TABLE 1 Habitat-specific mean annual invertebrate production (g AFDM/m²/year [95% confidence intervals]), total annual species richness, and mean annual invertebrate diversity (Shannon H') estimates (\pm standard deviation).

Habitat	Production (g AFDM/m ² /year)		Richness (total # taxa)	Diversity (H')	
Cobble-gravel	10.79 ^b	(8.73–13.07)	34	1.43 ^c	(± 0.29)
Off-channels	7.60 ^b	(4.52–10.88)	28	0.69 ^{ab}	(± 0.40)
Sand	0.41 ^a	(0.32–0.51)	27	0.45 ^a	(± 0.42)
Talus	9.15 ^b	(5.69–13.11)	40	1.02 ^b	(± 0.46)
Wood	8.62 ^b	(5.09–12.41)	35	1.02 ^b	(± 0.46)

Note: Superscript letters indicate statistical differences among habitat types based on overlapping 95% confidence intervals for production and the pairwise results from a mixed model accounting for repeated monthly sampling for diversity.

Chironomidae, Hydropsychidae, Ceratopogonidae, and Isonychiidae fuelled the bulk (>80%) of their annual production (Table S5; Figure S3). In contrast, Pallid Sturgeon fed on invertebrates, but larger individuals (>400mm) also relied on prey fish to support their production (Table S6). Hydropsychidae, Isonychidae, non-Tanypodinae, Ephoron, Traverella, and Ametropus comprised ~93% of the invertebrate diet items and fuelled 35% of total annual Pallid Sturgeon production (Table S6; Figure S3). Many prey items of both sturgeon taxa were produced solely on small patches of cobble-gravel, talus, wood, and off-channels, highlighting the importance of these patchy habitats in providing energy for *Scaphirhynchus* spp. production.

Food-web interaction strengths

River habitat within foraging windows had a strong effect on the distribution of interaction strengths leading to sturgeon (deviance explained by GAM=97.7%). Habitat diversity was strongly and negatively related to species interaction strengths, with the highest median interaction strengths in food-web modules with the lowest habitat diversity ($F=254.0$, $EDF=5.7$, $p<0.001$, Figure 3; Figure S2). As an example, in homogenous river reaches with the most simplified prey base, we observed 11 trophic interactions in which consumption exceeded 95% of what was produced in the environment (Figure 3a). As habitat diversity increased, median interaction strengths weakened, driven largely by reductions in the strongest interactions described above, which declined by an average of 40% from 0.996 to 0.399 (Figure 3b).

Habitat identity also had a significant influence on interaction strengths of food-web modules across the riverscape. In particular, we found that foraging windows including habitats with larger sediment sizes had consistently lower (i.e., potentially stabilizing) median interaction strengths than those with smaller sediment sizes ($F=52.1$, $EDF=6.1$, $p<0.001$, Figure 3; Figure S2). The influence of both habitat diversity and sediment size on median interaction strengths was consistent across an order of magnitude in spatial extent (Figure S4).

Linking physical habitat, prey assemblage characteristics, and interaction strengths

Connections between river habitat and food-web interaction strengths were mediated by both the diversity and production of invertebrate prey times. Increases in invertebrate prey biodiversity and secondary production were both associated with weaker median food-web interaction strengths (Figure 4; Data S1, Tables S7–S12, Figures S5 and S6). Thus, for a given amount of prey production, increasing the diversity of prey items was associated with weaker interaction strengths (-0.555 , $[-0.62-0.489]$, 95% CI; box in Figure 4a), and for a given level of prey biodiversity, increasing production had similar effects (-0.711 , $[-0.788-0.633]$, 95% CI; box in Figure 4b). Invertebrate assemblage diversity and production were positively related to different aspects of the physical habitat template, with sediment size positively related to prey diversity (SEM standardized coefficient: 0.782 [0.701–0.863], 95% CI) and habitat diversity positively related to secondary production (0.981 [0.963–0.999], 95% CI). Finally, we found an unexpected, but relatively weak, negative relationship between biodiversity and secondary production (-0.088 $[-0.171-0.040]$, 95% CI), driven by a high proportion of off-channel areas in many foraging windows which had high prey secondary production but low diversity (Table 1).

DISCUSSION

Human activities are degrading and simplifying landscapes globally (Sage, 2020), and the ways in which trophic networks respond to these changes will influence the persistence of biological communities that maintain ecosystems (McCann, 2007). Although theoretical advances have demonstrated the importance of diverse landscape features for weakening interaction strengths and enhancing food-web stability (Rooney et al., 2008; Ryser et al., 2021), our study provides important evidence of these dynamics in nature. We found a significant relationship between habitat simplification and strong, potentially destabilizing, interaction strengths that was intensified in the absence of large and stable sediments.

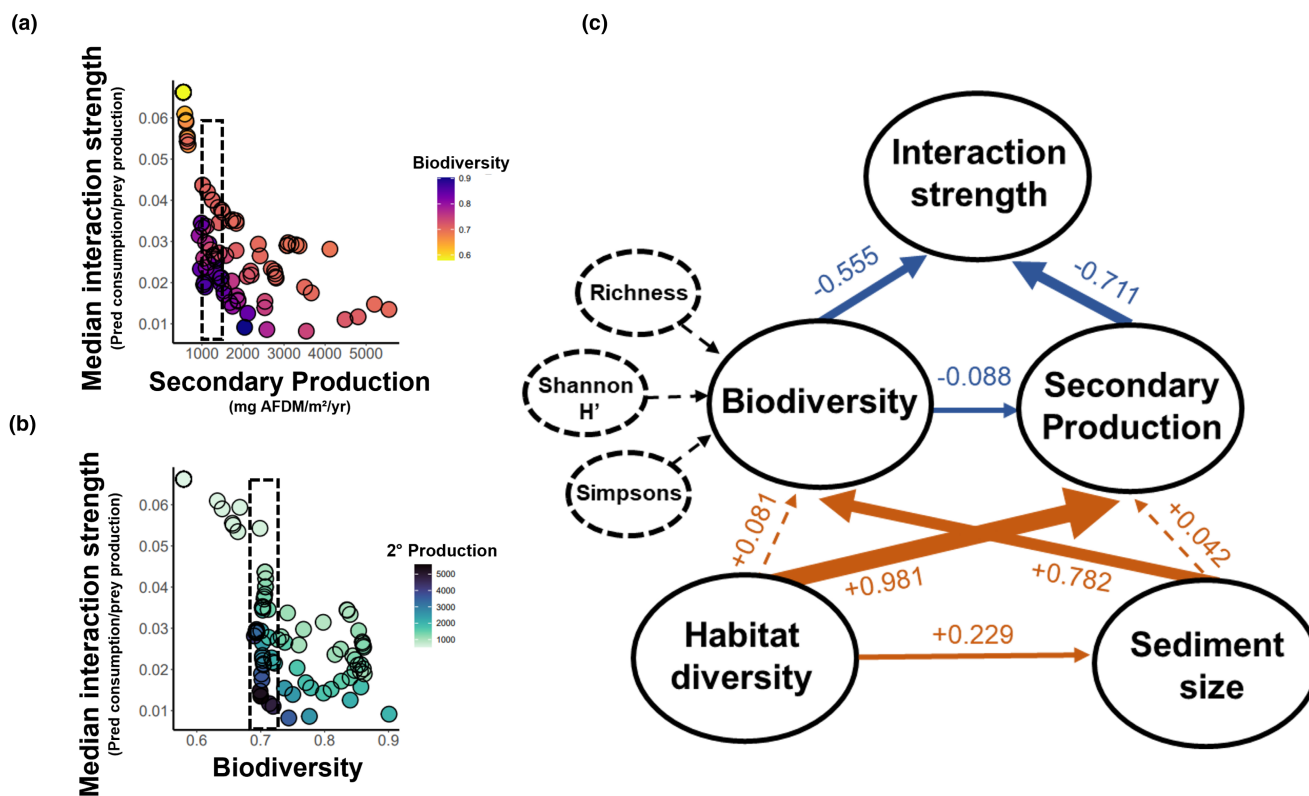


FIGURE 4 Median interaction strength (predator consumption [g AFDM/m²/year]/prey production [g AFDM/m²/year]) of *Scaphirhynchus* spp. food-web modules declined with increasing (a) annual secondary production (mg AFDM/m²/year) and (b) biodiversity (Simpsons evenness) of invertebrate assemblages. Dashed boxes illustrate example foraging landscapes where, for a given level of secondary production, increasing diversity further reduces interaction strengths and vice-versa. Structural equation modelling (c) highlighted relationships among habitat variables, prey assemblages, and food-web interaction strengths. Standardized path coefficients are shown for all modelled relationships and arrow widths are proportional to effect sizes for significant ($p < 0.05$) relationships. Dashed arrows represent non-significant effects. The SEM shown uses biodiversity as a latent variable, however independent relationships using invertebrate richness, Simpson's evenness, and Shannon (H') diversity can be found in Figure S5.

These connections between the landscape and trophic interaction strengths were mediated by changes in invertebrate prey diversity, which was strongly related to sediment size, and prey production, which was largely governed by habitat diversity. Given continued alteration to river habitat and declines in endemic megafauna, our findings should be useful for prioritizing future river rehabilitation and management efforts (DeBoer et al., 2020; Feio et al., 2023; Whitney et al., 2020).

We consistently found the strongest trophic interactions in homogenous sand-bed reaches, a common habitat of many large, low-gradient rivers. In these reaches, *Scaphirhynchus* spp. often consumed nearly all of the available prey production, and there were cases where consumption estimates exceeded the production of relatively rare prey taxa. These results suggest that sand-bed reaches in our study segment are unlikely to provide sufficient energy to support existing fish populations (including the many sympatric fishes, Dutton, 2018) due to their low prey diversity and production. They also suggest that fishes must either depend on drifting subsidies from upriver or move and forage in more diverse and productive habitats to meet their energetic demands.

Thus, if river habitat was homogenized to 100% sand and sturgeon were unable to forage across multiple habitat patches, energetic demands could outpace prey production, with the potential to destabilize food webs. Our results also support previous research on low-gradient streams, where, despite predominantly sandy substrates, many predatory fish rely on invertebrates produced on patches of large woody debris (Benke et al., 1985). However, future work is needed to understand whether these patterns are only apparent in sand bed rivers with large variation in prey production among habitats, or if they are also important in rivers dominated by larger and more productive sediment types.

As foraging windows transitioned from sand to a diverse mosaic of habitat types, we observed a consistent weakening of interaction strengths driven by two factors that relate to our initial hypotheses (Figure 1). First, the addition of habitats with larger and more stable sediment sizes provided unique and more diverse foraging opportunities for invertebrate prey. For example, Isonychiid mayflies fuelled 26% of juvenile Pallid Sturgeon production, but were only found on wood, cobble-gravel, or talus habitat types. Thus, incorporating patches of large

sediments in the foraging landscape of sturgeon likely dispersed predation across multiple unique prey that were either entirely absent or at extreme low abundance on other habitats, weakening median trophic interaction strengths. Second, more diverse habitat created many redundant foraging opportunities for taxa that, while present in sand, had much higher production per unit area on other habitats. For example, non-Tanypodinae midges, which comprised 78% of total sand production, and nearly half of Shovelnose Sturgeon consumption, had ~10x higher production in off-channel habitats. Foraging landscapes with even small proportions of off-channel habitat thus greatly increased the annual supply of midges to *Scaphirhynchus* spp. relative to their demand, reducing interaction strengths. Together, these results illustrate the importance of *both* habitat diversity and composition in dispersing consumption across diverse (i.e., only occurring in certain habitats) and redundant (i.e., occurring in multiple habitats at different abundances) prey resources, and reinforce similar findings in theoretical (Rooney et al., 2008), experimental (Alexander et al., 2015), and observational (Bellmore et al., 2015) studies.

Although our findings illustrate that landscape characteristics played an important role in reducing trophic interaction strengths, the specific mechanisms underpinning these results are likely to vary with environmental context. For example, Bellmore et al. (2013, 2015) examined relationships between habitat diversity and interaction strengths in a much smaller river in which potential prey production was relatively high and similar among different habitats. In their study, reduced interaction strengths emerged from (a) repeated predator–prey linkages in multiple habitats and (b) the presence of prey refugia in particular habitats. In our study, we found much greater variation in prey production and prey diversity among different habitats, and both of these characteristics played a substantial role in reducing median interaction strengths. Interestingly, our SEM model demonstrated that production and diversity of the prey base were enhanced by very different components of the physical habitat. In particular, prey *production* was highest in foraging landscapes that contained the greatest levels of habitat diversity that included productive habitats such as cobble-gravel, colluvial talus, and fine-sediment backwaters. In contrast, prey *diversity* was highest in foraging landscapes that contained larger sediment sizes, as these habitat patches provided rare physical stability in a large matrix of shifting sand and tended to support much higher levels of prey biodiversity. Thus, in light of our results and those of Bellmore et al. (2013, 2015), it is clear we still have much to learn about how environmental context influences the mechanisms by which landscape diversity drives trophic interactions in nature. In addition, with respect to riverine ecosystems, additional research is needed to reveal spatially explicit relationships among hydrogeomorphic variation, river ‘functional

process zones’ (Thorp et al., 2006), and patterns of food-web structure and function (Scholl et al., 2023).

Our methods for simulating food-web modules require further consideration, as they have the potential to influence the interpretation of our results. Spatial patterns of food-web interaction strength can result from changes in predator consumption relative to prey availability, changes in prey availability relative to predator consumption, or both. Our estimates of interaction strength were driven by spatial variation in prey availability, as opposed to changes in predator consumption which was held constant in our simulations. Although this approach differs from previous studies (see Bellmore et al., 2015), we believe it best represents the feeding behaviour of *Scaphirhynchus* spp., which forage over long distances to utilize and integrate multiple habitat types. In addition, it is worth noting that we did not quantify interaction strengths between sturgeon and prey fish, invertebrate predators and their prey, or invertebrate primary consumers and basal resources. However, we are confident that inclusion of these interactions would not influence our results because more diverse and productive habitat would also tend to reduce the strength of interactions between prey fish, invertebrate predators, and primary consumers. Furthermore, our study employed a ‘biomass flux’ method for estimating interaction strengths (sensu Berlow et al., 2004), which differs from experimental approaches in which per-capita interaction strengths are measured via predator removal (Paine, 1980; Wootton & Emmerson, 2005), a technique not possible in large river food webs. Consequently, our study does not address food-web dynamics at relatively short time scales or indirect interactions that may occur throughout the food web following the removal of a predator. Despite these limitations, approaches such as ours that utilize the trophic basis of production method have proven useful for understanding food-web dynamics and energy fluxes in many other systems (Bellmore et al., 2013; Benke, 2018; Cross et al., 2013).

Revealing life's “devious strategies” that underpin the persistence and stability of food webs is a long-standing endeavour in ecology (Rooney & McCann, 2012) and has emerged as a key conservation priority (May, 2009; McDonald-Madden et al., 2016). Although many studies have documented connections between biodiversity and food-web stability (McCann, 2000), the influence of physical habitat in modulating these connections has only recently come into focus (Ward et al., 2023). Revealing the ways in which nature's stage (sensu Lawler et al., 2015) shapes food-web dynamics is a frontier in food-web ecology, and pioneering syntheses (Polis et al., 1997) and theoretical models (McCann, 2012; Rooney et al., 2008) have provided the groundwork for observational studies, such as ours, to validate and improve our understanding of connections between the landscape and the persistence of biodiversity. Indeed, it is the balance among theory, experiments, observation, and synthesis

that is needed for advancing the relevance of our field (Naeem et al., 2002). As the physical environment continues to be simplified in ecosystems around the world, future conservation strategies will benefit greatly from understanding how such simplification influences the dynamics and stability of food webs.

AUTHOR CONTRIBUTIONS

Eric A. Scholl: Designed the study, collected the data, performed analyses, interpreted results, and wrote the manuscript. Wyatt F. Cross: Conceived the study, procured funding, discussed results and interpretation, edited earlier draft of the manuscript. Christopher S. Guy: Conceived the study, procured funding, discussed results and interpretation, edited earlier draft of the manuscript. Adeline J. Dutton: Collected the data, edited earlier draft of the manuscript. James R. Junker: Performed analyses, discussed results and interpretation, edited earlier draft of the manuscript.

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DATA AVAILABILITY STATEMENT

All data and scripts used for data visualization and statistical analysis in this study are available on Dryad: <https://doi.org/10.5061/dryad.15dv41p30>.

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