RESEARCH ARTICLE

Habitat availability determines food chain length and interaction strength in food webs of a large lowland river

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Abstract

Many large rivers used for navigation have lost their hydromorphological heterogeneity, which has led to the widespread loss of native biodiversity and the concurrent establishment of non-native communities. While the effects on biodiversity are well-described, we know little about how the loss of natural habitats and the restructuring of communities cumulate into effects on riverine food webs. We constructed binary and ingestion webs for benthic macroinvertebrates and their resources in the Elbe River (Germany) and compared if food chain length, food web complexity, robustness, ingestion rates, and consumer-resource interaction strength differ among three shoreline engineering practices. Food webs at profoundly altered shorelines were significantly less complex and had significantly shorter food chains than the food web at the semi-natural shoreline. However, food web robustness to a simulated loss of species was comparable at all shorelines. Total ingestion rates were up to eight times lower at highly altered shorelines due to significantly lower ingestion rates by native species. Predator–prey interaction strength was comparable among shorelines due to higher shares of non-native predators, indicating that non-native predators can be functionally equivalent to native predators. We attributed the observed food web differences to the absence of complex habitats at profoundly altered shorelines and the accompanied absence of specialized consumers. Our study provides empirical evidence that hydromorphological modifications reduce the efficiency of food webs to control organic matter dynamics and may ultimately affect the provisioning of riverine ecosystem services.

KEYWORDS
Elbe River, hydromorphological degradation, interaction strength, non-native species, organic matter flows, secondary production

1 | INTRODUCTION

Spatial heterogeneity is a significant property of large river-floodplain systems characterized by a mosaic consisting of the lotic main and side channels and lentic backwaters. Both are dynamically connected during high river discharges, making a temporal variation of discharge another significant component of large river-floodplain systems (Peipoch, Brauns, Hauer, Weitere, & Valett, 2015; Ward, Tockner, & Schiemer, 1999). Fluvial ecologists have long recognized that spatio-temporal heterogeneity is a strong driver of diversity and determines the composition of biological communities (Carrara, Rinaldo, Giometto, & Altermatt, 2014; Guégan, Lek, & Oberdorff, 1998). This

is related to the positive relationship between heterogeneity and the availability of ecological niches (Peipoch et al., 2015) and contributes to the fact that spatially complex river-floodplain systems are hot-spots of lotic biodiversity (Ward et al., 1999). However, large rivers with catchment areas >50,000 km^2 (European Commission, 2021) support biodiversity and a multitude of trophic interactions in food webs of lotic and lentic riverine habitats. There are currently not enough studies to extract generalities regarding the structure and functioning of food webs in large rivers, but the available empirical studies indicate that riverine food webs exhibit high complexity (Cross et al., 2013; Mor et al., 2018), long food chains with up to five trophic levels (Hoeinghaus, Winemiller, & Agostinho, 2008; Kautza & Sullivan, 2016) and large fluxes of organic matter (Rosi-Marshall & Wallace, 2002). Moreover, landscape complexity, defined as is the diversity of river and floodplain habitats, may influence the strength of consumer-resource interactions, with complex river-floodplain systems having larger proportions of weak trophic interactions (Bellmore, Baxter, & Connolly, 2015). Most large rivers worldwide have been modified by engineering structures such as wing dikes, levees, and rip rap to enable navigation, power production, and flood protection (Best, 2019). Engineering structures disconnect rivers from side channels and backwaters, and the decoupling of river-floodplain systems prevents the exchange of biological communities, organic matter, and nutrients between both ecosystems (Ward et al., 1999). Moreover, engineering structures narrow the main channel, confine the river flow, and thus cause incision of the main channel (Sukhodolov, Uijttewaal, & Engelhardt, 2002) while altering sediment dynamics, especially in sandy rivers (Surian & Rinaldi, 2003). Finally, fallen trees and other large woody debris are removed continuously from navigable rivers, and the loss of this crucial component of riverine heterogeneity (Gurnell, Tockner, Edwards, & Petts, 2005) exacerbates the effects of navigation on riverine hydromorphology. Reduced connectivity, loss of aquatic-terrestrial coupling, and incision have severe consequences for the diversity of in-stream and floodplain habitats. The loss of hydromorphological complexity is associated with lower diversity of ecological niches within simplified ecosystems (Peipoch et al., 2015). These human modifications can potentially alter the complexity and resource allocation in food webs, but predicting potential consequences is challenging as hydromorphological alterations simultaneously affect different levels of biological organization. Food web theory related to food chain length makes several competing predictions regarding how food webs may respond to such hydromorphological alterations. For example, resource quantity can be lower at modified shores (Elosegi & Sabater, 2013), and food webs may follow reductions of resource quantity with lower food chain length (Post, 2007; Schoener, 1989). However, higher spatial and temporal dynamics at natural shores can lower food chain length, as predicted by the dynamic stability hypothesis (Pimm & Lawton, 1977). Two studies lent empirical support to this hypothesis and showed that food chains at hydrologically altered sites were longer than at reference sites (Mor et al., 2018; Ruhi et al., 2016).

However, food web effects from hydromorphological alterations may go beyond mere changes of topological properties. Cross et al. (2013) studied the effects of an experimental flood on energy flows in the food web of the Colorado River (United States). The flood reduced the production of dominant macroinvertebrates substantially, but fish production increased after the flood. This counterintuitive result was due to changes in predator–prey interaction strengths, where the production of Simuliidae and Chironomidae increased, followed by increasing predation pressure and energy flow to fish. Our previous work showed that macroinvertebrate secondary production is lower at hydromorphologically altered shores (Brabender, Weitere, Anlanger, & Brauns, 2016) and that the trophic basis of macroinvertebrate primary consumers varies with the degree of hydromorphological alteration (Brauns, Brabender, Gehre, Rinke, & Weitere, 2019).

Human-modified river reaches are often dominated by non-native species (Johnson, Olden, & Vander Zanden, 2008; van Riel et al., 2006). To which extent their establishment affects native biodiversity is still debated (MacDougall & Turkington, 2005), but non-native species often exhibit traits different from their native counterparts (Little & Altermatt, 2018; Van Kleunen, Dawson, Schlaepfer, Jeschke, & Fischer, 2010). The dominance of non-native species on highly modified shores makes predictions of the food web consequences of hydromorphological alterations even more difficult as non-native species may or may not be functional equivalents of native species.

The present research aimed to test the extent to which qualitative and quantitative properties of benthic food webs differ among riverine shorelines subjected to different hydromorphological alterations. Our research builds on a previously described gradient of habitat availability associated with three different engineering structures commonly found in large navigable rivers (Brabender et al., 2016; Brauns et al., 2019). Here, we constructed binary and ingestion webs for these structures based on benthic macroinvertebrate consumers and their resources and compared how food chain length, food web complexity, food web robustness, ingestion rates, and the strength of consumer-resource interactions differ with shoreline engineering practices. We hypothesized that the food web at the semi-natural shoreline would have higher trophic complexity, longer food chains, and higher interaction strength than the shorelines with altered hydromorphology. Due to higher trophic complexity and corresponding functional redundancy, we hypothesized that the food web at the semi-natural shoreline would be more robust against species loss than the two highly altered shorelines.

2 | METHODS

2.1 | Study site

We studied a 4 km section of the Elbe River (Germany), an eighth order lowland river with a catchment of 148,268 km^2 and a mean discharge during the study period of 417 m^3 s^{-1} (range: 160–1,080 m^3 s^{-1}). Our study covered the three most common engineering structures found on the Elbe River, that is, an off-bankline revetment (51°53′1.40″N, 12°18′33.43″E), a section of rip rap (51°53′2.65″N,

12°18′27.49″E) and a wing dike (51°52′28.50″N, 12°16′38.37″E). The off-bankline revetment is a stone bar installed 5–30 m in front of the shore parallel to the flow direction (Brabender et al., 2016). An upstream and downstream opening created a hydraulic connection to the main channel except during low water levels (Figure 1). The rip rap consisted of layered, rectangular stones covering the shore from the long-term mean water level to the lowest low water level. The wing dike (also called spur dike or groyne) consisted of stone bars installed perpendicular to the shore. Engineering structures differed in their degree of natural-ness. The off-bankline was semi-natural as the shoreline remained unaltered (Figure 1), having a significantly higher percentage of macro-phytes and silt than the rip rap and the wing dike (Brabender et al., 2016). Conversely, the rip rap and wing dike shoreline were pro-foundly altered and characterized by significantly higher proportions of boulders (Figure 1). Hydromorphological differences did not affect food resource availability as resource standing stocks were comparable among sites except for higher standings stocks of benthic organic matter (BOM) at the off-bankline revetment (Brabender et al., 2016).

2.2 | Secondary production

Macroinvertebrate samples for secondary production were collected monthly from April 2011 to March 2012, except for January and February 2012, where a flood prevented sampling. At each engineering structure, three distinct mesohabitats, that is, the transi-tion zone, dike field, and stones, were sampled. The transition zone and dike field were sampled with a Surber sampler with five replicates each. The mesohabitat stone was sampled by brushing off macroinvertebrates from three to five randomly selected boulders. Replicates from each mesohabitat were pooled into a composite sam-ple, preserved in the field, and processed in the laboratory by counting and identifying individuals to the lowest possible taxonomic level. We determined individual mass using length-mass relationships established for the Elbe River or relationships taken from the litera-ture (Brabender, 2014). We calculated mesohabitat-weighted biomass by weighting individual biomass by the wetted area of the mes-ohabitats for a given engineering structure. Secondary production (mg dry weight m^{-2} y^{-1}) was estimated using the size-frequency method (Hamilton & Hynes, 1969; Hynes & Coleman, 1968) and corrected for cohort production intervals (CPI) (Benke, 1979). Infor-mation on CPIs was derived from the literature (Brabender, 2014). Secondary production for Oligochaeta was estimated using a P/B ratio of 5 (Benke & Huryn, 2007) as the coarse taxonomic level and the poor condition after ethanol preservation prevented the deter-mination of individual weights. We propagated the uncertainty of seasonally varying mesohabitat areas, and CPI estimates through these calculations by generating a vector of 1,000 mesohabitat-weighted values and used this to calculate the mean and the 95% percentile confidence intervals (CI) for each predator and
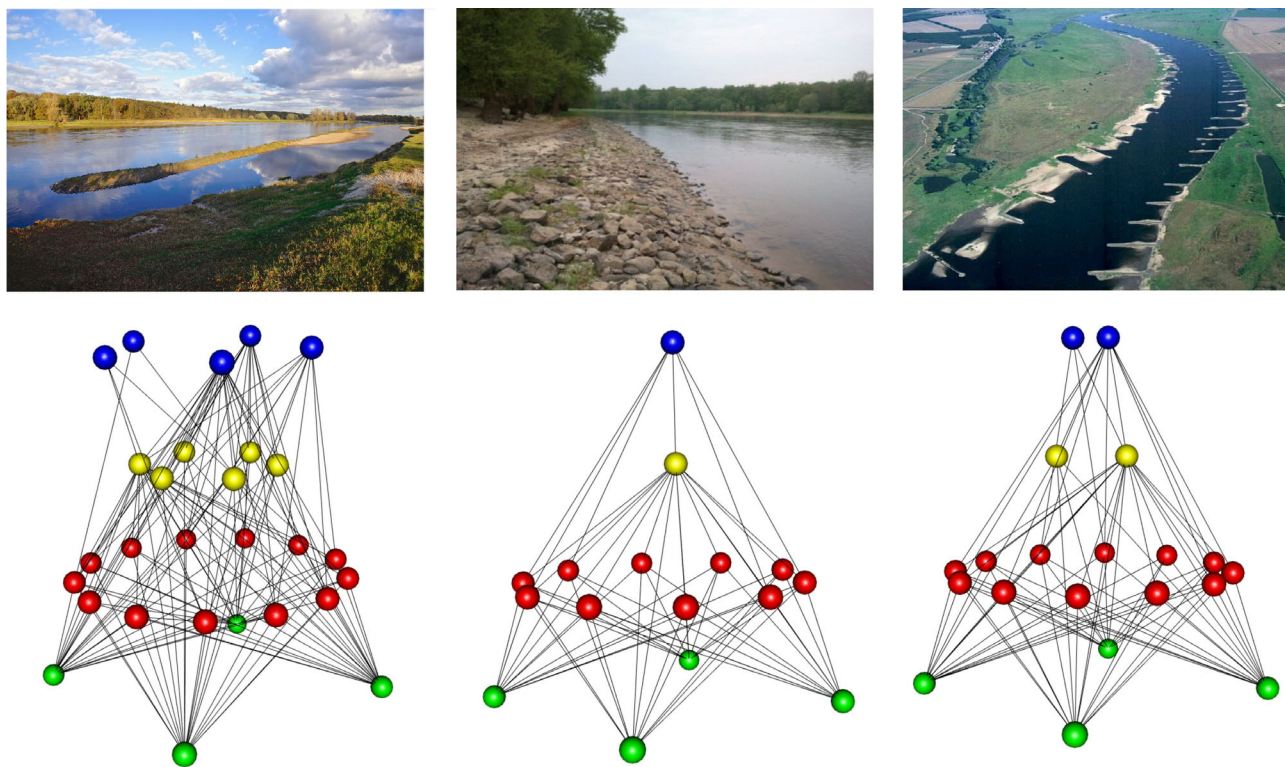

FIGURE 1 Binary food webs of the off-bankline revetment (left), rip rap (middle), and wind dike (right). Spheres represent consumers connected via trophic links. Sphere color depicts the trophic position with resources at the base of the food web (green), followed by primary consumers (red), omnivorous species (yellow) and predators (blue) [Color figure can be viewed at wileyonlinelibrary.com]

engineering structure. A complete description of the sampling procedure and how secondary production was estimated are provided in Brabender et al. (2016).

2.3 | Construction of food webs

We used stable isotope analysis (δ^{13}C, δ^{15}N) of macroinvertebrate consumers and their putative food resources and mixing model analysis to quantify the proportion of assimilated resources (Supporting information Figure S1). Samples for consumers and resources were collected in May (summer) and October (autumn) 2011 and March 2012 (spring) from the transition zone, dike field, and stones at each engineering structure. Total annual standing stocks of organic matter resources, including biofilm, BOM, and phytoplankton, were quantified along with the macroinvertebrate sampled as outlined in Brabender et al. (2016). Standing stocks of terrestrial POM (t-POM) were not quantified during the study, and we instead took values from the literature for similar-sized rivers (Benfield, 1997) (Table 1). Detailed information on sampling processing and isotope analysis, as well as mixing model analysis for macroinvertebrate primary consumers, are provided elsewhere (Brauns et al., 2019). For this study, we quantified the proportion of assimilated prey for omnivorous or macroinvertebrate predators initially at the mesohabitat-scale at each engineering structure. We first estimated consumers' trophic positions relative to a mesohabitat -specific baseline derived from stable isotope values of all non-predatory macroinvertebrates, that is, Chironominae, mussels, and snails for each engineering structure and season (Vander Zanden & Rasmussen, 1999). Consumers with a trophic position >2.4 were considered omnivorous or predatory. In preparation for the mixing model analysis, we tested for outliers in the stable isotope data using simulated mixing polygons (Smith, Mazumder, Suthers, & Taylor, 2013) and excluded consumers in less than 5% of the iterations from further analysis. The contribution of prey to the diets of omnivorous or predatory macroinvertebrates was estimated using the MixSIAR model (Stock & Semmens, 2013) with concentration dependence (Phillips & Koch, 2002) and without residual error terms (Parnell

et al., 2013). We ran models for each predator separately by mesohabitat, engineering structure and season and used trophic discrimination factors specific for aquatic invertebrates, that is, 0.1 ± 2.2‰ for δ^{13}C and 2.6 ± 2.0‰ for δ^{15}N (Brauns et al., 2018). Without information on specific dietary preferences for each predator, we assigned all macroinvertebrates from trophic level 2 as potential prey items and included them in the mixing models. For example, snails were included as they are either directly accessible to specialized predators (Brönmark & Malmqvist, 1986) or indirectly via scavenging on dead prey items. We acknowledge that assigning all available primary consumers as potential prey may overestimate realized predator links, but we deemed this potential bias smaller than assigning prey subjectively to their predators. After running mixing models, we used posterior estimates of the proportional contribution of each prey to a given predator's diet to calculate the mean and Bayesian 95% confidence intervals (in the following referred to as credible intervals).

Taxon-specific annual ingestion rates were estimated by first calculating the absolute amount of consumer production attributed to a given resource (PR_{ji}, g DM m^{-2} y^{-1}) as:

$$PR_{ji} = P_j \times R_i \quad (1)$$

where P_j = annual secondary production of consumer j (g DM m^{-2} y^{-1}) and R_i = relative proportion of resource i to consumers diet as calculated from mixing model.

We estimated assimilation efficiencies (AE, %) based on the nitrogen content of the resources after Pandian and Marian (1986) as:

$$AE_i = 9.29 + 8.82 \times N_i \quad (2)$$

where N_i = nitrogen concentration of resource i (%) measured during stable isotope analysis.

Annual ingestion of each taxon (CR_{ji}, g DM m^{-2} y^{-1}) was calculated as:

$$CR_{ij} = \frac{PR_{ij}}{(AE_i \times NPE)} \qu(3)$$

	Off-bankline revetment	Rip rap	Wing dike
Consumers	17 (12–23)[a]	12 (9–14)[a]	15 (13–17)[a]
Links	134 (131–136)[a]	60 (58–61)[b]	81 (79–82)[c]
Mean trophic level	2.32 (2.31–2.33)[a]	2.30 (2.28–2.31)[b]	2.28 (2.27–2.29)[b]
Resource standing stocks			
Animal	1.3×10^4	5.7×10^3	9.0×10^2
Biofilm	201	73	150
BOM	1,354	356	362
Phytoplankton	2.3×10^8		
t-POM	1,151		

TABLE 1 Binary metrics for food webs and total annual standing stocks of resources (mg DM m^{-2}) at the studied engineering structures

Note: Numbers in parentheses are bootstrap percentile 95% confidence intervals. Different lowercase superscript letters indicate significant differences among engineering structures (non-overlapping confidence intervals).

where NPE denotes net production efficiency that was assumed to be 0.5 (Cross et al., 2013).

To evaluate if engineering structures affect the efficiency at which consumers control their resources, we calculated interaction strength between macroinvertebrates and their resources as species impact (SI) (Cross et al., 2011; Wootton, 1997):

$$SI = \frac{CR_{ij}}{B_i} \qquad (4)$$

where B_i is the total annual resource biomass (mg DW m^{-2}, Table 1).

Our estimates of ingestion rates and interaction strengths are subjected to two major sources of uncertainty, that is, species-specific and seasonal variation of dietary proportions and variation in secondary production due to spatial variation and different life cycles. Uncertainty in estimates of ingestion rates for each consumer was quantified by first generating a vector of 1,000 secondary production values drawn from a uniform distribution delimited by the upper and lower 95% percentile CI. Similarly, a vector of 1,000 dietary proportions was drawn from a uniform distribution delimited by the upper and lower 95% credible interval across the three seasons for each consumer-resource pair. We calculated means and 95% bootstrapped confidence intervals of ingestion rates and interaction strength for each consumer based on these values. We furthermore used these values to calculate total ingestion rates and interaction strength and values for consumer communities separated into native and non-native species for each engineering structure.

We did not include fish in this study as the studied engineering structures are <10 km apart and are within the migration distance of fish. Hence, we cannot exclude the possibility that fish caught at one engineering structure had initially foraged at another engineering structure, which would bias any quantification of site-specific top-down pressure by fish. Moreover, our study adopts a fully quantitative approach, which requires reliable estimates of annual biomass. Given that such estimates are difficult to obtain, especially for large predators such as catfish and pike, we assumed top-down effects from fish on macroinvertebrates were comparable among engineering structures.

2.4 | Food web analyses

We compared the distribution of interaction strength among engineering structures by ranking trophic links with the respective cumulative percentage interaction strength. We converted the 1,000 estimates of ingestion rates into presence-absence data to calculate means and 95% bootstrapped CI of the number of consumer-resource links, number of consumers as well as trophic levels. We compared bootstrap percentile 95% CI among engineering structures and interpreted means with non-overlapping CI as significantly different. Binary food webs were drawn based on the presence/absence of resources in the diet of consumers using the "foodweb" package (Perdomo, 2015) in R (R Core Team, 2013).

We compared how robust the food webs of the three different engineering structures were against a simulated extinction of consumers. For each food web, we simulated species loss by sequentially removing consumers from the food web and calculating the cumulative percentage of the total and secondary extinctions (Dunne, Williams, & Martinez, 2002). We quantified the robustness of food webs against species loss by calculating the percentage of species to be removed to lose 25%, 50%, and 75% off all consumers, that is, robustness measures $R25$, $R50$, and $R75$ (Dunne et al., 2002; Jonsson, Berg, Pimenov, Palmer, & Emmerson, 2015). A low robustness value implies that only a small percentage of consumers' needs to be primarily lost to collapse to 25%, 50%, or 75% of initial consumers' richness.

The amount of secondary extinctions depends on the sequence at which consumers are removed from the food web (Dunne et al., 2002). We thus simulated two extinction scenarios and randomly removed consumers based on the descending number of trophic positions. The scenario of losing predators first follows predictions of food web theory that species at higher trophic levels are among the first to disappear following habitat loss (Ryall & Fahrig, 2006). We excluded basal resources from the analysis as they are unlikely to get lost from the river food web. The analysis was based on mean annual data and was conducted using the "bipartite" package (Dormann, Gruber, & Fruend, 2008).

3 | RESULTS

3.1 | Food web structure

The food webs collectively encompassed 279 trophic links among four basal resources, 22 primary consumers, and six predators (Supporting information, Table S1). However, consumer community composition differed among engineering structures. For example, *Calopteryx splendens* and *Coenagrion* sp. (Odonata) were dominant members of the predator community at the off-bankline revetment and were replaced by *Erpobdella octoculata* (Hirudinea) at the rip rap and wing dike (Supporting information, Table S1). Similarly, specialists for slow-flowing and macrophyte-rich sections of rivers such as *Cloeon dipterum* (Ephemeroptera) and *Anabolia nervosa/furcata* (Trichoptera) were only found at the off-bankline revetment.

The food web at the off-bankline revetment had significantly more trophic links, and the mean trophic level was significantly higher than at the rip rap or wing dike (Table 1, Figure 1). Comparing food web robustness among engineering structures revealed that simulated rates of secondary extinctions were comparable (Figure 2). Extinction rates varied more with extinction scenario, and species removal by descending trophic position produced lower total extinctions than random removal (Figure 2).

3.2 | Interaction strength

Total ingestion rates were eight times lower at the rip rap and six times lower at the wing dike than at the off-bankline (Table 2). This was almost entirely due to significantly higher ingestion rates of native species at the off-bankline that exceed native species ingestion at the rip
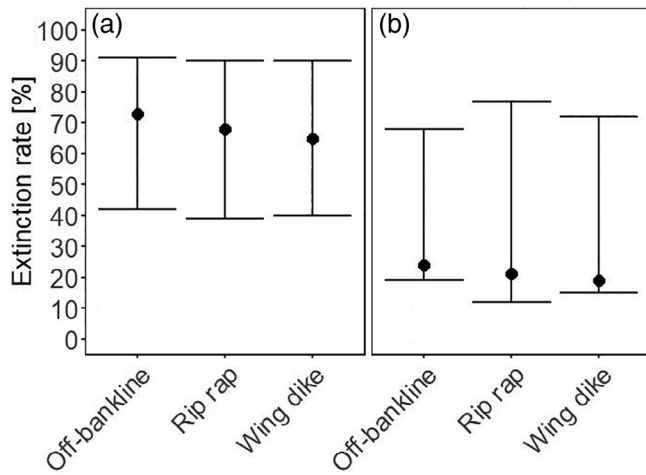
FIGURE 2 Total extinction rate following the removal of 25% (lower whisker), 50% (dot) and 75% (upper whisker) of consumers from binary webs at the studied engineering structures. Extinctions scenarios were (a) random loss and (b) removal with descending trophic position

rap by 27 times. On the other hand, ingestion by non-native species was significantly higher at the rip rap than at the other two engineering structures. When considering ingestion rates by resource, the largest differences occurred between off-bankline revetment and rip rap. Total ingestion rates of biofilm and BOM were more than an order of magnitude higher at the off-bankline revetment than at the rip rap. Most of these differences were due to Chironominae that contributed substantially to total ingestion at the off-bankline revetment (Table S1) but less to total ingestion at the rip rap. Similarly, *Radix balthica* (Gastropoda) contributed more than 20% to total ingestion at the off-bankline but was absent from the rip rap and wing dike.

Interaction strengths between consumers and biofilm and BOM were one order of magnitude higher at the off-bankline revetment than at the rip rap and wing dike (Table 3). Total strength of predator–prey interactions did not significantly differ among engineering structures. In contrast, interaction strength between native consumers and animal prey was one order of magnitude higher at the off-bankline revetment (Table 3). Predator–prey interaction strength of non-native species was significantly higher at the rip rap than the wing dike and off-bankline revetment but did not differ significantly between the two latter structures.

The cumulative distribution of interaction strengths for rip rap was less skewed than that of the off-bankline revetment and the wing dike (Figure 3). A total of 8% of all links contributed to >50% of total interaction strength at the rip rap. At the wing dike, 5% and off-bankline, less than 1% of all links contributed to >50% of total interaction strength, respectively (Figure 3).

4 | DISCUSSION

Our qualitative and quantitative analysis of large lowland river food-webs revealed substantial variation in food-web structure, energy

TABLE 2 Total ingestion rates (g DM m^{-2} y^{-1}) and ingestion rates for communities separate into native and non-native species for each resource

	Off-bankline revetment			Rip rap			Wing dike		
	Total	Native	Non-native	Total	Native	Non-native	Total	Native	Non-native
Animal	14 (10–18)[a]	4 (3–6)[a]	9 (5–12)[a]	14 (8–19)[a]	0 (0–0)[b]	13 (8–19)[a]	2 (1–2)[b]	0 (0–0)[b]	2 (1–2)[b]
Biofilm	454 (145–758)[a]	450 (156–743)[a]	14 (4–24)[a]	42 (18–66)[b]	13 (5–21)[b]	29 (5–51)[a]	33 (5–61)[b]	31 (4–59)[b]	1 (0–2)[b]
BOM	648 (319–979)[a]	622 (307–957)[a]	17 (6–29)[a]	41 (18–65)[b]	13 (5–21)[b]	28 (6–49)[a]	101 (12–185)[b]	96 (10–183)[b]	2 (1–3)[b]
Phytoplankton	131 (39–223)[a]	128 (43–214)[a]	4 (1–6)[a]	22 (9–36)[b]	10 (4–16)[b]	13 (1–24)[a]	58 (7–107)[a]	53 (5–104)[a,b]	2 (1–3)[a]
t-POM	97 (29–165)[a]	92 (24–162)[a]	6 (3–8)[a]	42 (21–64)[a]	12 (6–17)[b]	31 (12–50)[b]	51 (7–95)[a]	51 (6–94)[a,b]	2 (1–3)[c]
Σ	1,357 (879–1,823)[a]	1,303 (842–1,779)[a]	49 (34–66)[a]	162 (112–208)[b]	48 (33–63)[b]	114 (69–160)[a]	238 (109–376)[b]	226 (99–353)[c]	9 (6–11)[c]

Note: Numbers in parentheses are bootstrap percentile 95% confidence intervals. Different lowercase superscript letters indicate significant differences among engineering structures (non-overlapping confidence intervals).

Abbreviations: BOM, Benthic organic matter; t-POM, terrestrial particulate organic matter.

TABLE 3 Total interaction strength (y^{-1}) and interaction strength exerted by native and non-native species

		Resources				
		Animal	Biofilm	BOM	Phytoplankton	t-POM
Off-bankline	Total	1.1×10^{-3} (7.7×10^{-4}–1.3×10^{-3})^a	2.3×10 (7.2×10^{-1}–3.8×10)^a	4.8×10^{-1} (2.4×10^{-1}–7.2×10^{-1})^a	5.7×10^{-7} (1.7×10^{-7}–9.6×10^{-7})^a	8.5×10^{-2} (2.5×10^{-2}–1.4×10^{-1})^a
	Native	3.3×10^{-4} (2.3×10^{-4}–4.3×10^{-4})^a	2.2×10 (7.7×10^{-1}–3.7×10)^a	4.6×10^{-1} (2.3×10^{-1}–7.1×10^{-1})^a	5.6×10^{-7} (1.9×10^{-7}–9.3×10^{-7})^a	8.0×10^{-2} (2.1×10^{-2}–1.4×10^{-1})^a
	Non-native	6.6×10^{-4} (3.9×10^{-4}–9.2×10^{-4})^a	6.8×10^{-2} (2.2×10^{-2}–1.2×10^{-1})^a	1.3×10^{-2} (4.3×10^{-3}–2.2×10^{-2})^{a,c}	1.6×10^{-8} (5.6×10^{-9}–2.7×10^{-8})^a	4.9×10^{-3} (2.9×10^{-3}–7.0×10^{-3})^a
Rip rap	Total	2.4×10^{-3} (1.4×10^{-3}–3.4×10^{-3})^b	5.7×10^{-1} (2.4×10^{-1}–9.0×10^{-1})^b	1.2×10^{-1} (5.2×10^{-2}–1.8×10^{-1})^b	9.7×10^{-8} (3.8×10^{-8}–1.5×10^{-7})^b	3.7×10^{-2} (1.9×10^{-2}–5.5×10^{-2})^a
	Native	1.7×10^{-5} (4.7×10^{-6}–2.9×10^{-5})^b	1.8×10^{-1} (7.2×10^{-2}–2.8×10^{-1})^b	3.7×10^{-2} (1.5×10^{-2}–5.9×10^{-2})^b	4.3×10^{-8} (1.8×10^{-8}–6.8×10^{-8})^b	1.0×10^{-2} (5.1×10^{-3}–1.5×10^{-2})^b
	Non-native	2.3×10^{-3} (1.4×10^{-3}–3.4×10^{-3})^b	4.0×10^{-1} (7.4×10^{-2}–6.9×10^{-1})^a	7.9×10^{-2} (1.8×10^{-2}–1.4×10^{-1})^a	5.5×10^{-8} (6.3×10^{-9}–1.0×10^{-7})^a	2.7×10^{-2} (1.0×10^{-2}–4.3×10^{-2})^b
Wing dike	Total	7.2×10^{-4} (4.7×10^{-4}–9.8×10^{-4})^a	2.2×10^{-1} (3.4×10^{-2}–4.0×10^{-1})^b	2.8×10^{-1} (3.2×10^{-2}–5.1×10^{-1})^{a,b}	2.5×10^{-7} (3.2×10^{-8}–4.6×10^{-7})^a	4.4×10^{-2} (6.2×10^{-3}–8.3×10^{-2})^a
	Native	1.9×10^{-6} (6.6×10^{-7}–3.1×10^{-6})^c	2.1×10^{-1} (2.7×10^{-2}–3.9×10^{-1})^b	2.6×10^{-1} (2.6×10^{-2}–5.1×10^{-1})^{a,b}	2.3×10^{-7} (2.1×10^{-8}–4.5×10^{-7})^a	4.4×10^{-2} (5.3×10^{-3}–8.2×10^{-2})^a
	Non-native	7.2×10^{-4} (4.7×10^{-4}–9.8×10^{-4})^a	7.1×10^{-3} (2.9×10^{-3}–1.1×10^{-2})^b	5.9×10^{-3} (2.4×10^{-3}–9.4×10^{-3})^a	8.7×10^{-9} (2.9×10^{-9}–1.4×10^{-8})^a	1.5×10^{-3} (5.5×10^{-4}–2.4×10^{-3})^c

Note: Numbers in parentheses are bootstrap percentile 95% confidence intervals. Different lowercase superscript letters indicate significant differences among engineering structures (non-overlapping confidence intervals).

flow, and interaction strengths associated with three engineering structures differing in habitat availability. Food webs at highly altered shores were simplified, exhibiting lower consumer-resource interaction strengths, and had a high share of non-native species. In contrast, the food web at the semi-natural shore, dominated by native species, was more complex and more efficient in controlling resource standing stocks. Surprisingly, this did not result in a substantially higher food web robustness against species loss at the semi-natural shore compared to the altered shores.

4.1 | Food web structure

Following our expectations, the food web at the semi-natural off-bankline revetment was significantly more complex and had food chains significantly longer than at hydromorphologically altered shores. Our results are not supported by or even contradict several predictions from classical food web theory concerning food web topology. Following the productive space hypothesis (Schoener, 1989; Spencer & Warren, 1996), larger habitats should only support more complex food webs if resource availability is higher. Such productive habitats should support more complex food webs than less productive habitats of a given size. Organic matter standing stocks differed partially among engineering structures, but interaction strengths above 1 indicate that consumers were not resource-limited at any engineering structure. Moreover, the size of the engineering structures was comparable even if food web complexity differed substantially. In line with the dynamic stability hypothesis (Pimm & Lawton, 1977), one would expect shores with lower spatio-temporal dynamics to have longer food chains or greater complexity, which this study could not confirm. Instead, the presence of complex, 3-dimensional habitats and consumers requiring such habitats seem to be more important drivers of food chain length than habitat size, productivity, or spatial dynamics. The differences in food web topology encountered in our study may be attributed to the lack of structural complexity following the absence of macrophyte habitats at the wing dike and the rip rap (Figure 1). In riverine environments, submerged, and emerged macrophytes exhibit a high complexity and favor specific communities consisting of Ephemeroptera, Odonata, and Trichoptera (Cogerino, Cellot, & Bournaud, 1995) as found in this study at the off-bankline revetment. Our results are in good agreement with the predictions of Briand and Cohen (1987), who demonstrated that habitat complexity determines food-chain length with complex 3-dimensional habitats having longer food chains than simple 2-dimensional habitats.

Two decisions inherent to our approach of constructing food webs require attention as they could influence the findings related to food web complexity. First, we estimated trophic links to macroinvertebrate predators by including all available prey items. This decision, typical for most isotope-based approaches, may overestimate food web complexity as links may be assigned to predators that are not realized. Gut content analysis is a way to overcome this potential bias but suffers from constraints on identifying heavily digested prey items. We applied the isotope approach to all engineering structures, and any potential bias in the number of realized trophic
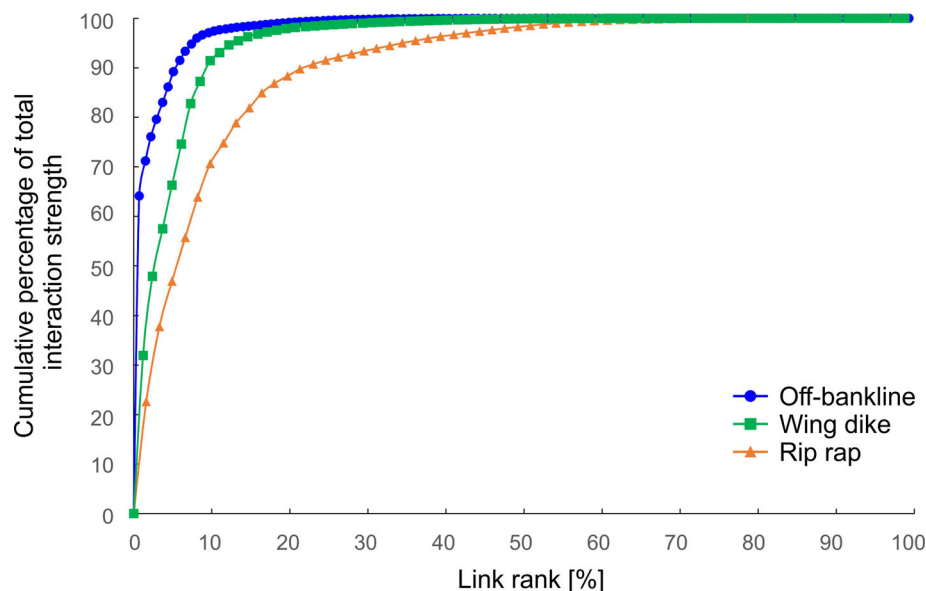
FIGURE 3 The relationship between the cumulative percentage of total annual ingestion and the link rank for food webs at the studied engineering structures [Color figure can be viewed at wileyonlinelibrary.com]

links would apply to all structures. Hence, we are confident that the comparison of food web complexity among the studied engineering structures is robust even if the comparability to other studies may be restricted. Second, we are uncertain about the effects of excluding fish-prey interactions on our estimates of food web complexity. Deciphering the feeding locality of fish in large rivers seems impossible as long as prey communities or their isotopic composition are not substantially different. Our sampling sites were less than 10 km apart, and macroinvertebrates did not differ enough in isotope composition to allow for assigning feeding localities of fish to engineering structures. Hence, further studies are needed to test to what extent human-induced changes in food web complexity propagate through the food web to affect top consumers.

The non-native predator *D. villosus* dominating the highly altered shorelines could not compensate for the loss of complexity associated with native predators. Surprisingly, the loss of trophic complexity did not affect the robustness of food webs against simulated species loss as extinction rates were comparable among sites. This unexpected result may have at least three potential explanations. First, secondary extinction critically depends on the choice of the extinction sequence and how the extinction risk is assigned across consumers (Berg, Pimenov, Palmer, Emmerson, & Jonsson, 2015). We choose a random removal and a "predator first" scenario but to which extent this produces a realistic sequence of species loss from food webs remains unclear. Second, our comparison was restricted to highly altered and semi-natural sites because unmodified natural shores no longer exist at the Elbe River, which is not uncommon in large navigable rivers (Best, 2019; Grill et al., 2019). It is plausible to assume that natural shorelines may harbor more predators and greater food web complexity than the studied semi-natural shore. This is partially due to the lack of large wood or woody debris from the near-natural off-bankline revetment. River wood is a critical component for riverine hydromorphology (Gurnell et al., 2005) and riverine ecosystem functioning. Previous studies at large rivers found large wood to support

more biodiversity, higher secondary production of benthic macroinvertebrates, and more complex food webs (Benke, Van Arsdall, Gillespie, & Parrish, 1984; Benke & Wallace, 2015). Consequently, the overall impact of riverine engineering structures on food webs robustness may be higher than demonstrated in our study. Third, our study design was unreplicated at the level of engineering structures, which prevented us from contrasting the variability of food web robustness within and among engineering structures. We quantified variability from variations among mesohabitats as well as temporal variability and included both in our comparison. This should assure that differences among engineering structures are larger than those attributed to small-scale variability induced by mesohabitats within the structure and the variability stemming from consumers' life cycles. Furthermore, rip raps and wing dikes show only minor variation in habitat availability along the lower Elbe River, and we can thus assume that our results are representative beyond the particular study sites.

4.2 | Interaction strength

The ingestion rates at the off-bankline revetment exceeded those at the other engineering structures. Much of these differences were due to the different contributions of native and non-native species. The significantly higher ingestion rates found at the off-bankline revetment were almost exclusively produced by native species such as Chironominae (Table S1). This result is in line with our previous study, where high secondary production rates of Chironominae contributed to the overall differences between the off-bankline revetment and the other engineering structures (Brabender et al., 2016). Again, differences in habitat availability among sites, particularly the higher share of silt habitats, may be responsible for the differences observed in the current study.

The interaction strength analysis showed that the efficiency at which consumers control riverine organic matter decreased with

decreasing habitat availability and was particularly apparent in the strongly reduced interaction strength between native consumers and BOM and biofilm at the highly altered rip rap and wing dike (Table 3). This was mainly due to differing ingestion rates because resource standing stocks were comparable among engineering structures (Table 1). A similar pattern was observed for a riverine food web subjected to hydraulic alterations, where non-native consumers dominated interaction strength but were inefficient in controlling the primary production of biofilms (Cross et al., 2013).

The distribution of interaction strengths showed a higher proportion of strong interactions at the highly modified rip rap but a higher proportion of weak interactions at the semi-natural off-bankline. Interaction strength in our study was primarily driven by consumers' ingestion rates rather than resource standing stocks, and weak interactions at the off-bankline were due to a dominance of consumers exhibiting low ingestion rates (Table S1). Similar patterns were observed in other studies comparing human-modified with pristine food webs, such as food webs subjected to litter exclusion (Hall, Wallace, & Eggert, 2000) or artificial floods (Cross et al., 2013). Apparently, natural or semi-natural ecosystems with high habitat availability and habitat diversity promote complex food webs with a high proportion of weak interactions (Bellmore et al., 2015). A potential reason for this observation may be that heterogeneous ecosystems provide more niches for specialized consumers with smaller population sizes. Even if the mechanisms remain unclear, our results align with predictions of food web theory that natural food webs have a strongly skewed distribution of interaction strengths (McCann, Hastings, & Huxel, 1998). What is the benefit of the higher share of weak links? Food web theory posits that a larger number of weak links make food webs more robust to external disturbances. However, food web robustness was comparable between the rip rap and the off-bankline despite the differing interaction strength distributions. We hypothesize that ecosystems having food webs with more weak links can still have larger total interaction strength than those with a few strong links. Hence, even if individual consumers do not contribute much to total energy transfer, the consumer community as a whole efficiently controls organic matter resources. This is indeed a desirable feature of food webs, particularly in nutrient-rich ecosystems, where primary production is often not bottom-up limited but needs to be controlled top-down to prevent eutrophication or even harmful algal blooms.

Another interesting finding was that total predator–prey interaction strength was comparable among engineering structures due to the interplay of interaction strengths of native and non-native predators. Altered shorelines exhibited significantly lower interaction strengths for native predators and similar or higher interaction strengths for non-native predators, that is, *D. villosus*. This resulted from higher ingestion rates by non-native predators and two-fold lower prey biomass at the rip rap and the wing dike. Hence, non-native predators compensated for the loss of native predators and led to overall efficient control of prey biomass at highly altered shores. This indicates that non-native predators can be functionally equivalent to native predators if the latter become extinct following

human impacts. This result provides novel evidence on the significance of non-native predators for the structure and matter flows in food webs and sheds new light on the functional role of non-native species in rivers. Given that the establishment of non-native species often interacts with riverine hydromorphological degradation (Johnson et al., 2008; Mercado-Silva, Helmus, & Vander Zanden, 2009), we need to deepen our understanding of the functional role of non-native species and their interaction with human stressors.

5 | CONCLUSION

Most large rivers worldwide are transformed into navigation routes decoupled from their floodplains. They exhibit low habitat heterogeneity with a concomitant loss of native biodiversity and dominance of non-native communities. This community restructuring challenges conventional river management as altered ecosystems may not necessarily be functionally similar to undisturbed ecosystems. Quantifying such changes requires alternative approaches that focus on the functional role of species and consider matter fluxes at the ecosystem scale (Downs & Piegay, 2019; Palmer & Ruhi, 2019; Power, 2001). Our study provided novel evidence that the loss of riverine habitats leads to simplified and inefficient food webs functionally dominated by non-native species. Non-native predators seem to be functionally equivalent in terms of their interaction strength. However, non-native primary consumers could not compensate for the loss of their native counterparts at highly altered shores. Our results demonstrate that human-driven differences in habitat availability in large rivers produce effects beyond a mere reduction of riverine biodiversity and compromises ecosystem functionality and ecosystem services. For example, the low interaction strength between consumers and basal resources encountered at highly altered shores indicates that human-altered rivers may lose the ability to regulate water quality. We are beginning to understand how altered food webs translate into losing ecosystem services (Dee et al., 2017; Dobson et al., 2006), but further studies are needed on how human activities alter the functioning of river ecosystems.

CONFLICT OF INTEREST
The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT
The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials.

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