Article

Forested Riparian Zones Provide Important Habitat for Fish in Urban Streams

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Abstract: Riparian zones form a boundary between aquatic and terrestrial ecosystems, with disproportionate influences on food web dynamics and ecosystem functioning in both habitats. However, riparian boundaries are frequently degraded by human activities, including urbanization, leading to direct impacts on terrestrial communities and indirect changes that are mediated through altered connectivity with adjacent aquatic ecosystems. We investigated how riparian habitat influences fish communities in an urban context. We electrofished nine urban site pairs with and without forested riparian buffers, alongside an additional 12 sites that were located throughout the river networks in the Oslo Fjord basin, Norway. Brown trout (*Salmo trutta*) were the dominant fish species. Riparian buffers had weak positive effects on fish densities at low to moderate levels of catchment urbanization, whereas fish were absent from highly polluted streams. Subtle shifts in fish size distributions suggested that riparian buffers play an important role in metapopulation dynamics. Stable isotopes in fish from buffered reaches indicated dietary shifts, pointing to the potential for a greater reliance on terrestrial-sourced carbon. Combining these results, we postulate that spatially-mediated ontogenetic diet shifts may be important for the persistence of brown trout in urban streams. Our results show that using a food web perspective is essential in understanding how riparian buffers can offset impacts in urban catchments.

Keywords: aquatic-terrestrial linkages; salmonids; food webs; stable isotopes; urban stream syndrome; urbanization; nature-based solutions; blue-green infrastructure

1. Introduction

Streams and their adjacent riparian zones form tightly coupled networks in landscapes, which are characterized by intimate ecosystem and food web linkages across the land-water interface [1–3]. For instance, stream and terrestrial ecosystems are bound by reciprocal flows of organic matter and prey [3–5]. Reciprocal linkages include inputs of terrestrial detritus that help to fuel aquatic food webs, and emerging winged adults of aquatic

insects as an important prey source for riparian consumers, such as spiders, ground beetles, and birds [6–9]. Riparian zones are biodiversity hotspots, providing essential habitat refugia for terrestrial and aquatic biota in the face of global change drivers, such as landscape disturbances and extreme weather events [2,10]. Streams and riparian habitats are important societally through the provision of key ecosystem services to humans (e.g., water purification, carbon storage, and fishing) [11,12]. However, human pressures from land use, such as urbanization, frequently degrade stream–riparian networks, with adverse impacts on cross-habitat linkages and ecosystem services [7,11,13].

Urbanization is a driver of global environmental change that disproportionately impacts freshwater ecosystems [14,15]. Streams draining urban catchments are often highly degraded, characterized by biodiversity losses and altered ecosystem functioning [16–18]. The ubiquity of these responses has led to the "urban stream syndrome" being a key focus of cross-disciplinary research [19]. Urban areas are often highly modified, including hugely transformed riparian zones that are typified by vegetation removal, imperviousness and soil degradation, channel modification (e.g., culverting, bank fixation, and channelization), and in-stream habitat deterioration, including greatly altered chemical, hydrological, and thermal dynamics [13,16]. These changes have led to the decoupling of the stream from terrestrial food webs [7] and declines in key organismal groups, including stream fishes.

Fish community responses to urbanization are less understood than for other biota [20], although there is evidence that urban land uses are associated with losses of sensitive species and increases in tolerant species leading to community homogenization [21–23]. Altered physical habitat, declines in water quality, and the loss of riparian cover have all been suggested as key proximate drivers of urban impacts on fish communities [20]. Many fish are also top predators in streams, and their loss may have profound effects on urban stream food webs by altering energy flows and destabilizing trophic interactions [24]. A decrease of fish in urban streams can reduce the amenity values for human populations and may lead to declines in recreational fishing, an important ecosystem service contributing to physical activity, stress-alleviation, and social interaction [25]. Consequently, there is an urgent need for management approaches for improving fish communities and environmental quality in urban stream–riparian networks, with increasing focus on the utility of forested riparian buffers to help conserve and rehabilitate degraded habitats [26].

Despite best management practices advocating a catchment wide approach for improving water quality and longitudinal connectivity in streams and rivers [27], there is a growing consensus that local remediation efforts, such as forested riparian buffers, offer multiple co-benefits in urban environments [28,29]. Riparian vegetation is particularly important for fish, as it affects light regimes, thermal dynamics, water quality, as well as habitat and food availability [30]. However, urban land use and riparian degradation frequently covary, which means that few studies have disentangled the relative importance of catchment urbanization from riparian land use [19,31,32]. Environmental contingencies, such as those arising from catchment-wide pressures, generate uncertainties that may explain why few regulations exist for forested buffers in stream–riparian networks. This challenge requires targeted case studies that focus on key food web compartments to develop the general framework that is needed for implementing forested buffers in human-impacted landscapes. Here, we wanted to investigate how top consumers (fish) in urban stream food webs respond to forested riparian buffers.

In our study, we investigated the effects of forested riparian buffers on fish communities in the urbanized Oslo Fjord basin (Norway). We sampled 30 sites over gradients of riparian land use and catchment urbanization. The stream sites ranged from having natural woody riparian vegetation to being completely devoid of a vegetated riparian zone. Sites were distributed within the river network, so the effect of catchment urbanization (e.g., urban impacts and altered longitudinal connectivity) could be assessed. Nested within the 30 were 18 site pairs, each with an upstream unbuffered reach and a nearby downstream site with a forested riparian buffer. We wanted to know whether forested riparian buffers

confer benefits to stream fishes and if positive influences are environmental contingent (i.e., dependent on upstream catchment degradation).

Thus, we specifically tested three hypotheses:

1. Size distributions of fish differ with the presence of a riparian buffer. Our *a priori* expectation was that larger-sized fish would be more abundant in buffered sites compared to unbuffered, as there is more available habitat in terms of water depth and cover against predators.

2. Fish densities are positively related to improved riparian condition after accounting for upstream human impacts. To test this hypothesis, we applied the conceptual framework that was introduced by Burdon et al. [33], suggesting that responses to riparian buffers are determined by the extent of a local transition (i.e., improved riparian condition) and its interaction with the environmental context (i.e., the level of upstream catchment degradation).

3. The presence of a forested riparian buffer alters the energy flow paths to stream fishes. We predicted that the "brown" food web channel (i.e., driven by allochthonous carbon sources with cascading effects throughout the food web) would be more dominant in buffered sites. To test this, we analyzed carbon stable isotopes (δ^{13}C) from stream fishes. Stable isotopes (e.g., nitrogen and carbon) are widely used to elucidate food web properties due to predictable changes in isotopic signatures between consumers and resources, where consumer tissues are enriched in the heavy isotope relative to the food resources in their diet [34].

2. Materials and Methods

2.1. Study Area and Study Design

The Norwegian capitol Oslo is located at the Inner Oslo Fjord (59′55 N, 10′45E). It is the most populous city in Norway with a current population of almost 700,000 inhabitants, and it is the fastest growing major city in Europe [35]. The population has increased by 20% between 2007 and 2018 [36] and large parts of the city are undergoing redevelopment to provide more residential areas by replacing previously industrialized areas. A major city planning strategy from the 1930s was to establish blue-green corridors throughout the city, connecting the inner Oslo Fjord to the surrounding upland forested areas along the stream channels. Oslo has a history of catchment modifications [37–39], thus representing a suitable urban environment for testing our hypotheses.

We investigated fish communities in 30 stream sites across Oslo and specifically addressed the effects of forested riparian buffers as a part of the BiodivErSA-funded CROSSLINK project (Figure 1) [27]. Eighteen of the sites were paired with and without forested riparian buffers at the scale of the sampling reach (i.e., nine pairs, each consisting of an upstream "unbuffered" and a downstream "buffered" site). The site pairs were always relatively close together (mean distance: 350 m) to ensure a similar stream size in terms of discharge with the upstream reach not having a riparian buffer. Paired sites were located in urban impacted landscapes. The buffered sites were selected to fulfill some key requirements: minimum buffer length exceeded 50 m upstream from the downstream end of the sampling reach, and the buffer width was 2–3 x the wetted stream width dominated by larger trees on both sides of the stream. Common tree species (Diameter at Breast Height, DBH > 5 cm) forming riparian buffers included the deciduous *Alnus incana*, *Fraxinus excelsior*, and *Acer platanoides*, whereas unbuffered sites were mostly open and dominated by grass, shrubs, and small trees [29]. Unbuffered sites usually only had a few trees (DBH > 5 cm) along the stream banks. The buffer widths ranged from 10–150 m and buffer lengths from 80–750 m. The additional sites were situated along the river continuum in the same systems, from headwaters to they entered the Oslo Fjord. "Reference" sites were typically located in the forested upstream catchment and constituting pristine, least impacted sites, while "Longitudinal" sites were located lower down in the stream-network, being subjected to accumulated levels of urbanization and with different configurations of the riparian buffer (Figure S1, Supplementary Materials).
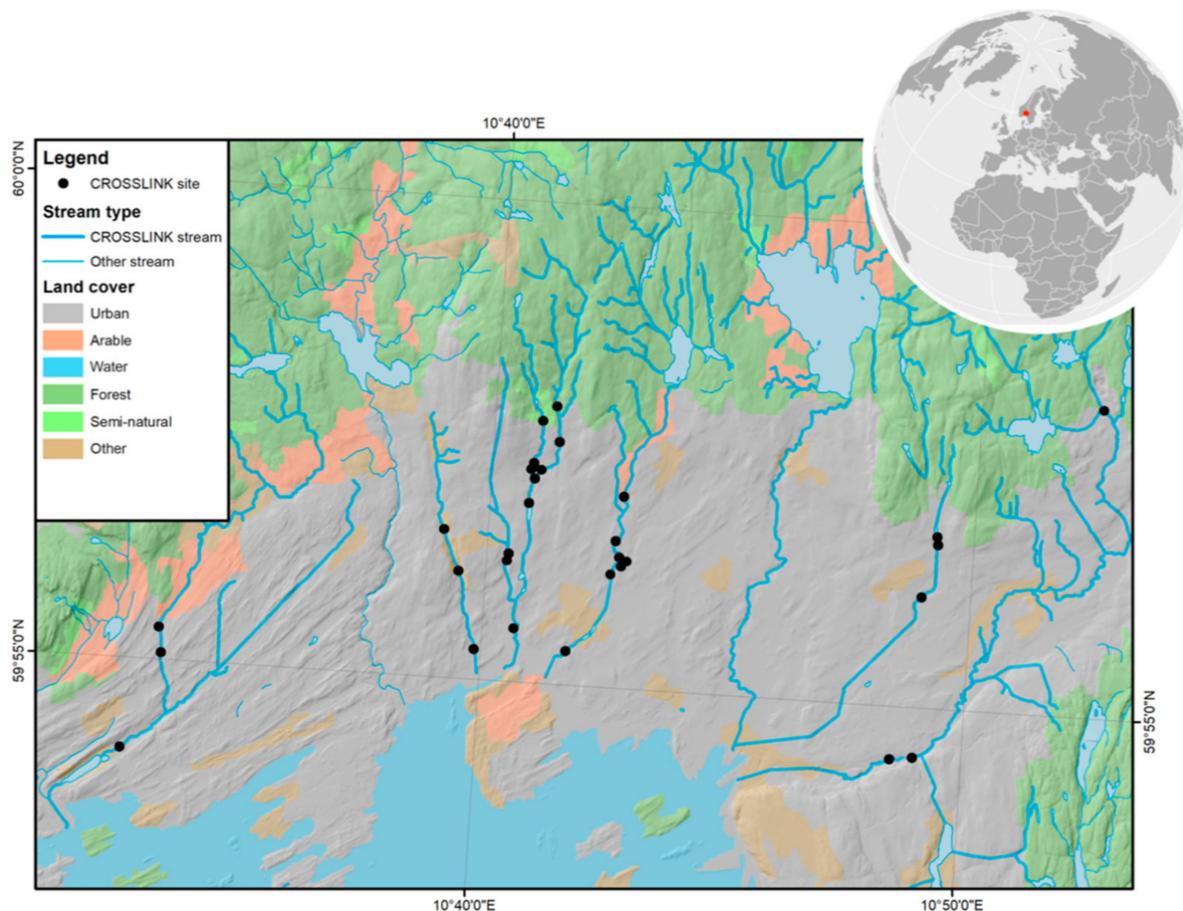
Figure 1. Location of study sites along the stream-riparian networks in the Oslo Fjord basin, Norway.

To ensure consistency, the sampling reaches were wadeable, 1st–3rd order (i.e., approximately 2–5 m wide), and with a stable streambed (i.e., not frequently hydrodynamically disturbed) that is dominated by gravels and cobbles. The standardized length of our study sites was 30 m. The starting point of our surveys was the downstream end of each site, which, in the case of buffered sites, was located as far as downstream within the woody riparian buffer simultaneously having the largest lateral extent. For unbuffered sites, this meant that the location was chosen as far downstream in an unshaded/slightly shaded network position as possible.

2.2. Assessment of Riparian Habitat Conditions, Stream Width and Catchment Land Uses

The riparian habitat characteristics were assessed during field surveys along each study site using standardized field protocols. We used the Riparian Condition Index (RCI) that was introduced by Burdon et al. [28], which contains 13 variables to assess the quality of the riparian zone. The variables include channel shading, buffer width, buffer intactness, vegetation composition of buffer and adjacent land, groundcover of buffer and adjacent land, as well as bank stability, soil quality (denitrification potential and drainage), livestock access, land slope, and rills/channels. Briefly, observers rank aspects of the riparian zone from poor (1) to excellent (5) for each of the bank to indicate the quality and integrity of the riparian zone (Table S1, Supplementary Materials). The scores were summed to provide an index of riparian habitat quality (RCI). For the analysis of total riparian condition, the scores of the two banks (left and right) of the same site were averaged to provide a single value for riparian condition at each site.

We recorded cross-sectional measurements of wetted channel width at 5-6 transects that were distributed in a stratified random approach throughout each individual 30 m long study site and calculated stream area.

Data on upstream land use cover for stream catchments of each study site were obtained from the CORINE Land Cover Inventory [40].

2.3. Water Quality Data

We collected water samples in bottles during two different seasons (autumn 2017, summer 2018). The water samples were collected from below the water surface (i.e., 10 cm) in the channel thalweg at the downstream end of each site. Site pairs were sampled on the same day. Water samples were stored cold and refrigerated upon return to the laboratory. The water samples were analyzed in NIVAs accredited laboratory following international standards (https://www.niva.no/en/services/laboratory-services, accessed on 26 November 2020). Water samples were analyzed for total nitrogen (NS 4743:1993), ammonium (NH_4N; [41]), nitrite- and nitrate-nitrogen ($NO_2N + NO_3N$; NS 4745:1991), total phosphorus (NS 4725:1984), dissolved reactive phosphorus (PO_4P; NS 4724), specific conductivity, and pH (NS-EN ISO 10523). Specific conductivity was collected at the time of sampling while using a handheld instrument (WTW pH/Cond 3410i, Weilheim, Germany). For further details on water quality sampling, see [28].

2.4. Fish Survey and Stable Isotope Sampling

Thirty sites were sampled at base flow conditions in summer 2018. We electrofished sites at 230 V using a Terik Technologies FA4 generator (Levanger, Norway) to estimate the species composition and fish population density in each reach. All reaches were sampled using two independent runs with successive removals. The catch efficiencies were always sufficiently high to calculate population densities using the formulae from Serber & Le Cren [42]. The densities were both calculated per m stream and per m^2 (Table S2, Supplementary Materials). Fish were measured (length in cm and weight in g) and identified before up to ten individuals of each species were fin-clipped for stable isotope analysis and returned to the stream upon completion of sampling. Samples for stable isotope analysis were stored on ice upon return to the laboratory. Fish were collected in accordance with ethical and legal standards. Oslo Municipality provided approval.

2.5. Stable Isotope Analysis (SIA)

The stable isotope samples were frozen and then freeze-dried (LyoDry compact, Mechatech systems LTD, Bristol, UK) for a minimum of 48 h at $-45\,^{\circ}$C. Freeze-dried samples were ground to a homogenous powder and individually encapsulated into tin capsules. The encapsulated samples were analyzed for their carbon and nitrogen ratios using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the Stable Isotope Facility (University of California, Davis, CA, USA). For our data analyses, we focus on δ^{13}C stable isotopes to track resource use of stream fish related to the presence/absence of a forest buffer (see below [43,44]).

2.6. Data Analysis

Our study investigated the effects of forested riparian buffers on fish communities in an urban context and tested whether positive impacts of woody vegetation are environmental contingent. To do this, we analyzed data from the CROSSLINK project on riparian integrity, fish communities, food web responses (carbon stable isotopes, δ^{13}C), and catchment-wide human impacts (upstream land use and water quality) from the Oslo Fjord catchment.

1. Effects of vegetated riparian buffers on size distribution of stream fish were inspected visually using histogram plots and summary statistics (i.e., mean $\pm$ SD, median, skewness) for each site type (i.e., reference, buffered, unbuffered, and longitudinal sites).

2. To study a context dependent influence of forest buffers on fish, we first tested the relationship between the Riparian Condition Index (RCI) and fish abundance (i.e., number of fish per site).

Any variability that is caused by unknown factors has the potential to reduce the statistical power and sensitivity of biomonitoring indicators when comparing responses across human impact gradients [45]. Thus, the inherent weaknesses of observational data combined with inappropriate statistical analyses have limited the utility of field monitoring data for detecting and managing environmental stressors [46,47]. For riparian habitat, whilst poor conditions are expected to limit fish numbers, the same does not apply for good conditions, since other human impacts (e.g., water quality, hydrological connectivity) and natural phenomena (e.g., hydrodynamic disturbance, biotic interactions) introduce variability in the abundances of fish observed at different sites with similar riparian conditions. We used quantile regression to test whether fish abundances were limited by riparian conditions and if other factors introduce variability in the relationship between riparian habitat and fish abundances. Quantile regression is a statistical method used to estimate the conditional quantiles of a response variable distribution in a linear model to provide a more complete view of possible causal relationships between variables that are involved in ecological processes [48]. Quantile regression can be used to estimate the rate of change for any quantile (or percentile) of a response variable to a limiting factor [45,49]. Regression quantiles are ascending sequences of planes that are above an increasing proportion of sample observations as the values of the quantiles (*t*) increase [48]. This property of regression quantiles enables the estimation of the rate of change (slope) for any quantile of the data, and not just along the central tendency, as in ordinary least squares (OLS) regression [45]. We predicted that the upper percentiles of fish abundances would be limited by the riparian condition, whereas the lower percentiles could be limited by a suite of measured and unmeasured factors. In combination, these predictions would form a wedge-shaped relationship between the riparian condition and fish abundances. We estimated quantile regression coefficients and 90% confidence intervals for the 0.05, 0.25, 0.5, 0.75, and 0.95 percentiles using the *quantreg* R package. Hypothesis tests and CI were bootstrapped using the *xy* method with 200 replications. We also tested the relationship between riparian condition and fish abundances using a generalized linear mixed effects model (GLMM) assuming a Poisson distribution for count data. The GLMM differed from quantile regression by assessing the central tendency, as in ordinary least squares (OLS) regression, but accounts for the non-independence of Site as a random factor. The GLMM was fitted using the *glmer* function in the *lme4* R package.

Our second approach adopted the conceptual framework that was introduced in Burdon et al. [28] and applied to our buffered/unbuffered site pairs. We used General Linear Models (GLM) to test the influence of riparian condition (RCI), upstream human activities (i.e., upstream catchment degradation "urbanization"), and their interaction on fish densities. This approach enabled us to test responses of fish communities to changes in riparian conditions, whilst accounting for upstream catchment degradation. We calculated the *log response ratio*, a common effect size metric that was calculated as log proportional change in the means of treatment and control group (e.g., buffered vs unbuffered), for fish density and RCI, with the former being the response variable (dFISH) and the latter a predictor (i.e., the magnitude of change from an "unbuffered" to a "buffered" riparian state, dRCI). In our model, we included fish density calculated per m stream, because our estimates of fish density calculated per area (m^2) revealed that stream reach area was not independent of buffer/no buffer and it was likely to under-estimate population effects (Figure S2, Supplementary Materials). We used Principal Components Analysis (PCA) to describe *upstream catchment degradation "urbanization"* (i.e., environmental context). The PCA decomposed log-transformed water quality variables (i.e., total inorganic nitrogen, ammonium, nitrite- and nitrate-nitrogen, total phosphorus, dissolved reactive phosphorus, specific conductivity, and pH) and logit-transformed upstream land-use cover variables (i.e., % of the catchment area covered by urban, arable cropping, forest, natural features, water, wetlands, and other) into site scores (Axis 1, hereafter referred to PC1), explaining 56% of total variation (Table S3, Supplementary Materials). We scaled the PC1 scores by a constant (the min value) to help aid the interpretation of interactions.

3. Effects of forest buffers on food web properties were elucidated based on carbon stable isotopes (δ^{13}C). We run linear mixed-effect models (LMM) to test whether buffers influence differences in fish-δ^{13}C signatures whilst accounting for body size, and if buffers influence the relationship of body size with fish-δ^{13}C signatures. One site pair (Mærradals-bekken; cf. Table S2, Supplementary Material) was stocked with hatchery fish that were fed during their rearing and thus might confound our expectations of isotopic signatures in natural populations of brown trout. Thus, we excluded this outlier site pair from our analyses. The LMMs included a *varIdent* function to enable different variances per stratum for site type [50], and we used site "pairs" as a random effect to account for non-independence of site pairs. The LMM was fitted with the *lme* function using the *nlme* package. We used the function *testInteractions* in the *phia* R package to test whether the size-δ^{13}C relationship was significant in each site type. All tests were conducted in R [51].

3. Results

3.1. Fish Communities and Forested Buffers in Urban Streams

We collected a total of 1085 fish and a total biomass of 16,942 g from 24 sites across Oslo (no fish were present at six sites): 136 individuals in forested reference sites (a total biomass of 1321 g, n = 4), 239 individuals in unbuffered sites (total biomass of 4041 g, n = 6), 388 individuals in buffered sites (total biomass of 6665 g, n = 6), and 322 individuals in longitudinal sites (total biomass of 4915 g, n = 8). A total of 4 fish species were caught with brown trout (*Salmo trutta*) being the dominant species (N = 1026; Table S4, Supplementary Materials). The trout population in the streams was mainly composed of 0+, 1+ and 2+ year classes, based on the length measurements and the maximum size of the trout that were caught by electrofishing ranged from 13.3 to 28.1 cm in the individual streams. There were no differences in the mean size between site types, including the comparison between site pairs ($F_{3,9}$ = 0.752, *p* = 0.5476), nor was there a general difference in the abundance of young of the year (YoY). However, we found a greater number of fish of the intermediate size class (~10 cm) in the buffered sites (Figure 2). This was evidenced by the greater median size in buffered sites, whereas the unbuffered sites had a more right-skewed size distribution that was driven by the larger sized individuals (Figure 2).

### 3.2. Context Dependent Influences of Forested Buffers on Stream Fish

We assessed if improved riparian conditions (i.e., forested buffers) can influence fish abundances and densities and whether a positive effect was contingent on the environmental context (i.e., upstream catchment degradation described as "urbanization"). An initial test showed that the riparian condition is important for fish numbers, with a significant positive influence of the Riparian Condition Index (RCI) on fish abundances ($F_{1,15}$ = 23.4, *p* < 0.001, Table S5, Supplementary Materials). However, plotting the data indicated a "wedge-shaped" relationship (Figure 3), which we tested using quantile regression. The upper percentiles (0.95, 0.75) showed a significant positive influence of riparian condition (*p* < 0.05), but the non-significant relationship for lower percentiles indicated the potential for other factors to limit fish abundances (*p* > 0.05). Several sites with a high RCI scores had low fish abundances, or, in some cases, no fish present (Figure 3, Table S2, Supplementary Materials). Subsequently, we tested the interaction between the change in fish densities (log response ratio between paired buffered/unbuffered sites, LRR), the improvement of riparian condition (LRR), and upstream human activities (PC1). We found evidence for an interaction between catchment urbanization and riparian integrity, where the positive influence of forested buffers on fish densities at low and moderate pollution (PC1) becomes neutral at high pollution (Figure 4, Table 1).
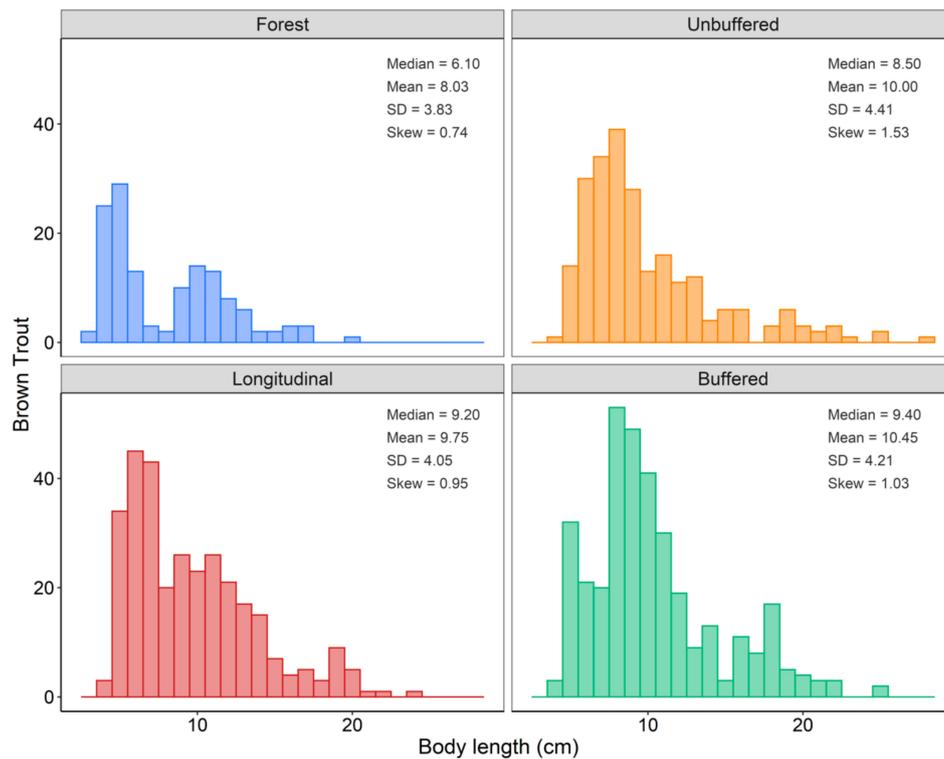
Figure 2. Histogram plots showing the distribution of brown trout (Salmo trutta) body lengths (cm) among the four site types: Pristine or least-impacted 'Reference' sites (=Forest) that were typically located further upstream due to urbanization in lower reaches, site pairs with an 'Unbuffered' upstream site and a downstream 'Buffered' site with a woody riparian buffer on both banks, and 'Longitudinal' sites that were typically located further downstream from the other site types to capture cumulative impacts of urban land uses. Mean and SD, median, and skewness of each site type are given in each panel.
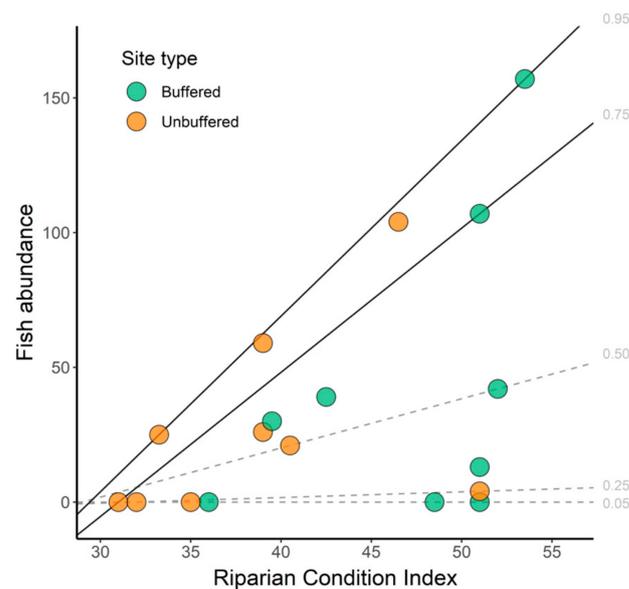
Figure 3. Slopes from estimated quantile regression coefficients for the 0.05, 0.25, 0.50, 0.75, and 0.95 percentiles. Solid lines indicate significant relationships ($p < 0.05$), whereas dashed lines indicate non-significant relationships ($p < 0.05$). The results show a "wedge-shaped" pattern of variation in fish abundances relative to the Riparian condition Index (RCI), where good riparian condition places an upper constraint on fish numbers, but other factors limit fish densities, even with good riparian habitat.
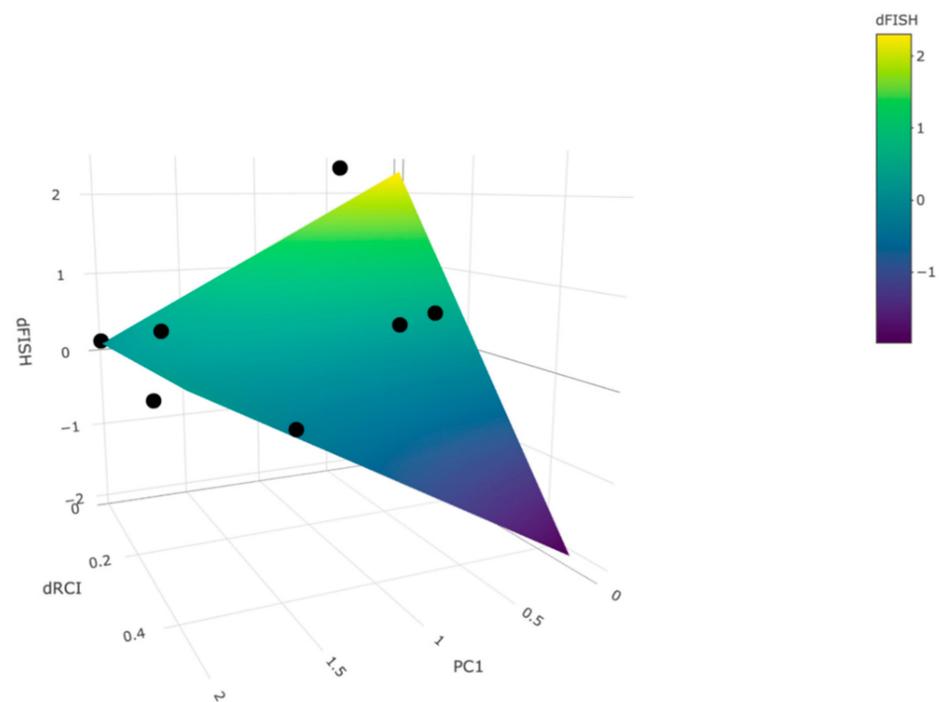
Figure 4. Context dependent fish responses to forest buffers in the Oslo Fjord basin. Increasing urbanization (PC1) weakened the potential for riparian buffer (dRCI) to have a positive effect on fish densities (dFISH). PC1 explains 56% variation in catchment-wide human impacts. Each point represents a site pair (unbuffered and buffered sites) in the Oslo Fjord basin.

Table 1. Results from the General Linear Models (GLM) testing the influence of riparian condition (RCI), upstream human activities (i.e., upstream catchment degradation "urbanization"), and their interaction on fish densities. The model use log response ratios to describe the magnitude of change in the response (dFISH) and predictor (dRCI) variables between site-pairs (i.e., unbuffered upstream sites and downstream, buffered sites) whilst controlling for the existing level of ecological impairment (i.e., upstream PC1). PC1 is the Axis 1 sites scores from a Principal Components Analysis (PCA) explaining 56% variation in catchment-wide human impacts. CI, 95% confidence interval.

| Response	Predictors	Estimates	CI	*p*
dFISH	(Intercept)	2.43	0.14–4.71	0.04
	dRCI	−9.54	−20.32–1.24	0.07
	PC1	−1.16	−2.74–0.41	0.12
	dRCI * PC1	5.07	−1.93–12.06	0.12
	Observations		9	
	Nagelkerke R^2		0.62	

3.3. Effects of Forested Buffers on Urban Stream Food Webs

To test our hypothesis (3) that the "brown" food web channel (i.e., driven by allochthonous carbon sources) would be more dominant in buffered sites, we analyzed $\delta^{13}C$ from a total of 244 biological samples (i.e., fin clips) that were collected from stream fishes during the field surveys (*Salmo trutta*: n = 219, *Salvelinus fontinalis*: n = 24, *Phoxinus phoxinus*: n = 1). Overall, fish from buffered sites generally encompassed a narrower $\delta^{13}C$ range (from −27.5 ‰ to −23.3 ‰) than fish from unbuffered sites (from −30.4 ‰ to −24.5 ‰) and shifted towards more enriched $\delta^{13}C$—i.e., the detrital-driven "brown" food web channel (median buffered: −25.5 ‰ vs. median unbuffered: −26.8 ‰; Figures 5 and 6). Interestingly, $\delta^{13}C$ from our forested reference sites showed a bimodal distribution with a smaller peak at −29.0 ‰ and the larger peak at −25.5 ‰. The isotopic composition of fish from longitudinal sites showed the largest variability and ranged from −30.8 ‰ to −22.9 ‰.
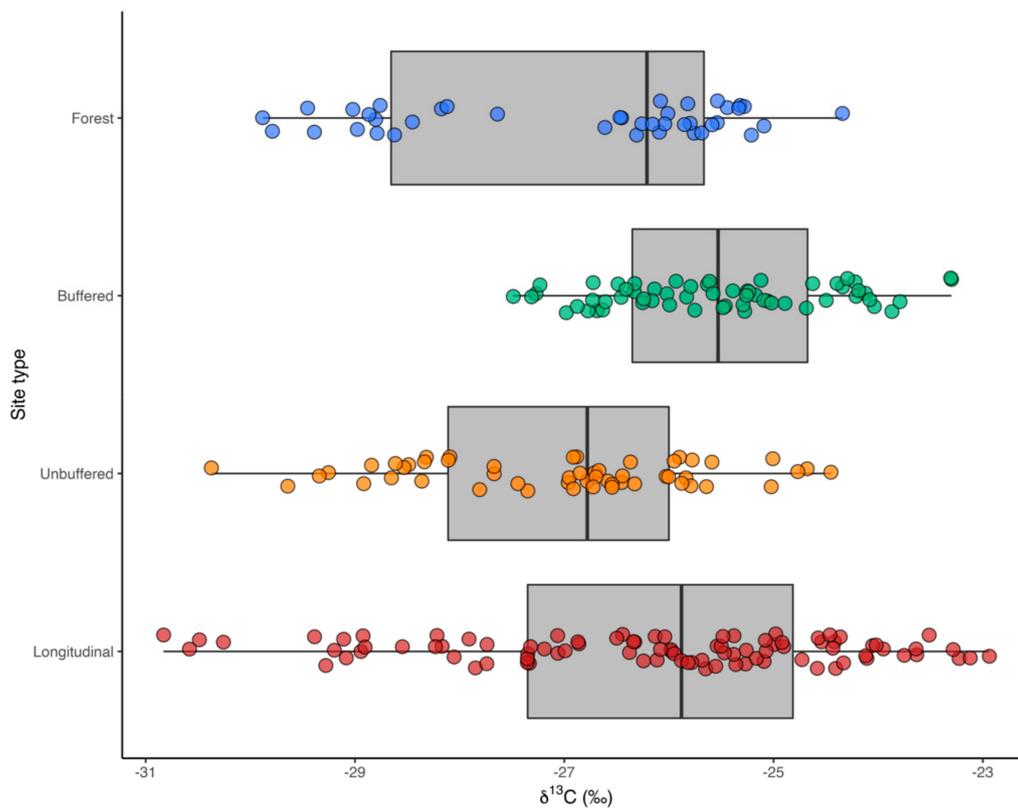
Figure 5. Distribution of δ^{13}C signals across the four site types in Oslo, Norway: forested reference sites (n = 4; isotope samples: 40), unbuffered (n = 6; isotope samples: 53), buffered (n = 6; isotope samples: 60) and longitudinal (n=8; isotope samples: 91) sites across Oslo. In each box plot, the center line indicates the median, the box limits indicate the upper and lower quartiles, the whiskers indicate the 1.5× interquartile range.

We saw evidence for two food web pathways leading to the largest brown trout in our streams. These pathways differed between the buffered and unbuffered sites after accounting for fish size in our statistical models (Figure 6, Table 2). One pathway characterized by depleted δ^{13}C values typical of algal-derived carbon was predominant in the unbuffered sites, while the enriched δ^{13}C values, characteristic of terrestrial-derived carbon, was more representative of the buffered sites. The relationship between fish length and δ^{13}C was statistically significant for both buffered and unbuffered sites ($p < 0.001$), but differed in their slopes (Figure 6, Table 2). This shift in isotopic signatures between the buffered vs. unbuffered sites was accompanied by the greater number of intermediate-sized fish (~10 cm) in the buffered sites making forest buffers a source of these fish (Figure 2, Figure 6). The larger bodied fish (> 17 cm) showed less fidelity to buffers and a convergence in isotopic signatures (Figure 6).
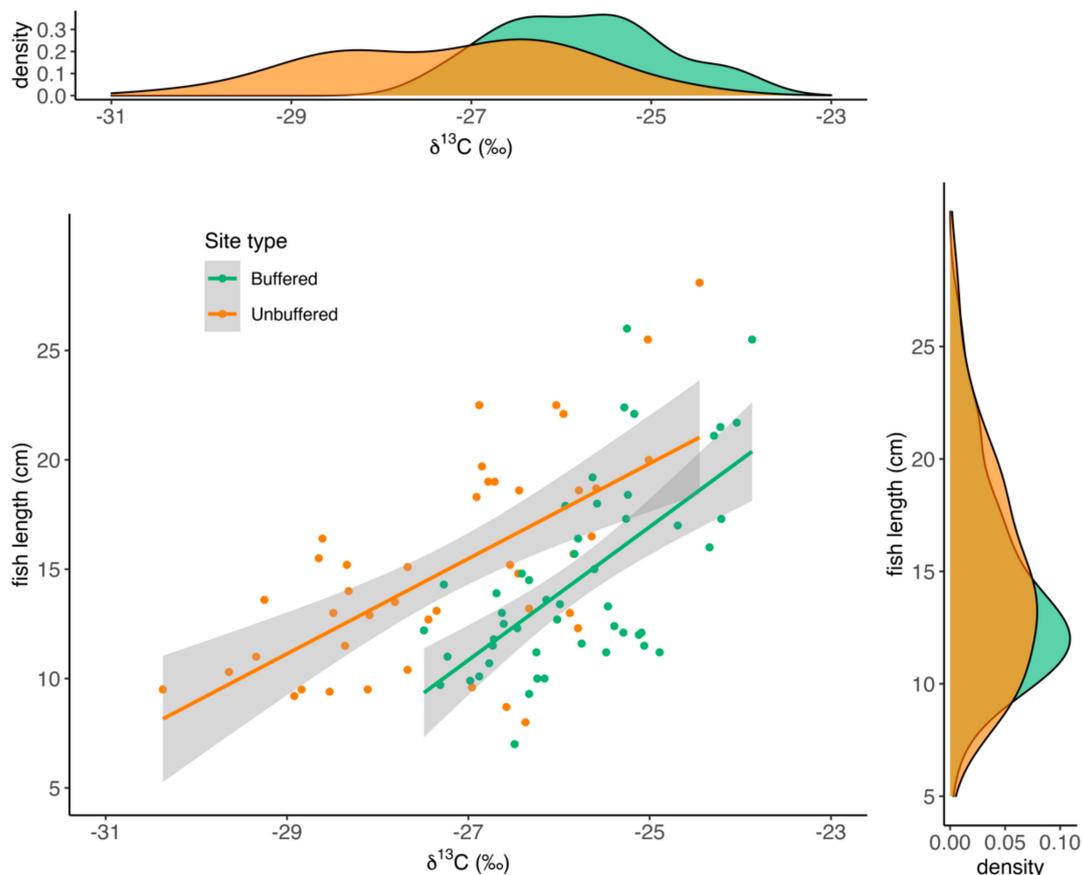
Figure 6. Relationship between isotope signatures (δ^{13}C) and fish body size (cm) whilst accounting for site type (unbuffered and buffered, N = 93 biological samples). Separate regression lines for buffered (green) and unbuffered (orange) sites. The density plots along margins show differences in the distribution of values (top, δ^{13}C; right, fish length) between the buffered and unbuffered sites.

Table 2. Results from the mixed models testing the influence of riparian buffer on carbon stable isotopes (δ^{13}C) in fish, whilst accounting for fish body size, and testing if buffers influence the relationship of body size with fish δ^{13}C signatures. R_m^2, marginal R^2; R_c^2, conditional R^2.

Response	Predictors	numDF	denDF	F-Value	*p*-Value	R_m^2	R_c^2
δ^{13}C	(Intercept)	1	81	10,809	<0.001	0.611	0.907
	Site type	1	4	6.564	0.062		
	Body size (mm)	1	81	118.0	<0.001		
	Site type: Body size	1	81	8.75	<0.001		

4. Discussion

Urbanization is a driver of global environmental change leading to multiple impacts on watersheds, including the decoupling of the stream from semi-terrestrial and terrestrial food webs [7] and declines in key organismal groups, including stream fishes [21–23]. Although best management practices have advocated a catchment-wide approach for improving habitat quality in streams and rivers, there is a growing recognition that local restoration efforts, such as forested riparian buffers, offer multiple co-benefits in urban environments [28]. Forested riparian buffers provide crucial terrestrial habitat, help to reverse the "urban stream syndrome", and offer a nature-based solution to offset the impacts of climate change [28,29]. We sought to explore the effects of forested riparian buffers on stream fish in the heavily urbanized Oslo Fjord basin, Norway.

4.1. Effects of Forest Buffers on Stream Fish in an Urban Context

We found, in concordance with other studies, weak positive effects of forested riparian vegetation on fish populations [32,52]. A positive effect on fish abundances seemed to be limited by other factors, as a number of sites with a high Riparian Condition Index (RCI) had low fish densities, or, in some cases, no fish present (Figure 3). The "wedge-shaped" relationship between RCI and fish abundances highlights this assumption [53]. We expected that other human impacts from urbanization, such as source pollution interferes with, and, in some cases, completely disrupts, stream-riparian buffer interactions, thereby limiting their potentially positive effects on fish populations. Urban land uses have been shown in several studies to be detrimental to fish populations [21–23,54,55] as well as other aquatic biota [16,17,56–58]. Given the presence of point-source and diffuse pollution in our urban streams with measured impacts on indicators of stream health [29], it is highly likely that water quality is a major limiting factor for populations of fish species, like brown trout. A test of the "environmental context" hypothesis [28] supported our assumption, as higher fish densities in the presence of a forested riparian buffer declined when the upstream catchment became too heavily degraded (both in terms of water quality and upstream land use, PC1). Given that some streams were fishless in our study (at the upper end of our urbanization gradient, PC1), we ended up with a relative low number of sites for our analyses and, hence, a limited statistical power. However, we believe that our ability to detect a positive effect using this modest dataset provides a useful indicator of the potential value of riparian buffers in an urban context.

More sites across different urban contexts are needed to verify our findings, given highly populated watersheds frequently experience multiple pressures and stressors in addition to biogeographical differences in fish assemblages. However, the benefits of additional replication with independent sites are constrained due to the finite spatial extent of urban areas and the differing intensities of urban land-uses. Increasing the sample size would require careful attention to context-driven differences in responses. For instance, in the Oslo Fjord catchment, we would not have been able to add further sampling sites without potentially confounding the study design by choosing low-impact peri-urban sites or alternatively, risking pseudo replication by increasing the number of non-independent study sites.

Another complementary approach that could help to disentangle context-driven (e.g., different combinations of stressors) effects on aquatic biota are experiments using mesocosms [59]. Mesocosms can reduce environmental complexity while maintaining essential background conditions of natural systems and providing the inferential power of replicated experiments. Most stream-side mesocosm experiments have focused on disentangling stressor interactions in agricultural landscapes [60–62], but this approach can also be used to investigate urban stressors [63]. Future studies in urban streams can further utilize the advantages of mesocosm experiments to quantify stressor impacts on aquatic biota and the mechanisms underpinning potential solutions that are related to riparian vegetation (e.g., thresholds for riparian vegetation types after which the positive effect of riparian buffers are lost).

Our data also suggest that measures of population densities per meter stream length is a better indicator than a measure per sampling area of the positive effects of riparian zones. We attribute this to the fact that riparian zones have a number of modifying effects on stream morphology [28], one being an increase in stream width as compared with non-buffered stream reaches [64–66] (Figure S2, Supplementary Materials). Hence, using an area-based measure is likely to under-estimate population effects.

4.2. Forest Buffers foster Tangled Stream-Riparian Food Webs in Urban Areas

Our findings add to the oft-quoted principle that "you are what you eat" by suggesting "you are *where* you eat". We posit that the absence of a forest buffer resulted in a dietary shift towards the putative algal-driven "green" food web channel, as indicated by more ^{13}C depleted stable isotopes in fish. We speculate that trout were more dependent on smaller

grazing invertebrates, including chironomids in unbuffered stream reaches (Figure 7). However, more C^{13} enriched stable isotopes in fish from buffered sites pointed to the potential for greater reliance on terrestrial-sourced carbon (i.e., the "brown" food web channel). We speculate that the generally larger sized detritivores (shredders such as limnephilid caddisflies utilizing allochthonous CPOM) makes them a more favorable food for trout [67]. Trout are known to be size-specific predators and the higher overall energetic benefits of preying on large food items, within (in the upper end) the prey handling size range of an individual, have been shown in a number of studies [68].
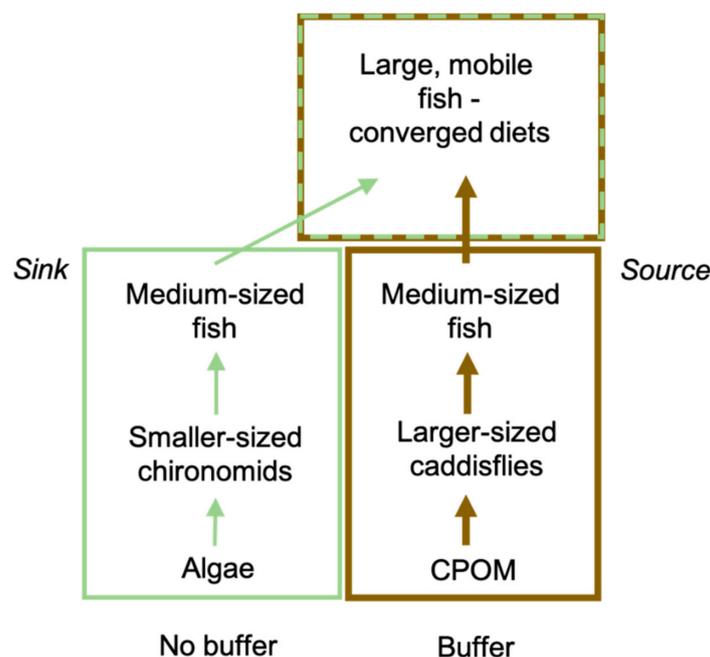
Figure 7. Conceptual model showing the two food web channels to the top: the algal-driven "green" food web channel in unbuffered sites (left) and the "brown" food web channel relying on terrestrial-sourced carbon (right). The peak in abundances of intermediate-sized fish in reaches with forest buffers suggest that buffered sites are a source of fish at this life stage. Larger fish from both site types converged on a diet consistent with detrital and terrestrial food sources.

Forested riparian buffers may have increased the proportions of terrestrial invertebrates in the diet of trout. Fluxes of terrestrial invertebrates falling to the water surface constitute a secondary allochthonous source of energetically beneficial prey for stream fish and their availability is directly linked to the presence of overhanging riparian vegetation [7,69]. Allochthony has been shown to help stabilize food webs in the face of environmental stress [70] and support food webs after restoration [71]. We believe that our results further suggest that forest buffers may help to stabilize urban stream food webs by providing a detrital "slow" energy channel in addition to the "fast" energy channel based on algae [72,73].

We also found evidence for subtle shifts in trout size distributions which suggesting that riparian buffers play an important role in metapopulation dynamics: intermediate-sized fish (~10 cm) were more abundant in buffered reaches as compared to the upstream unbuffered sites. This size class might be more sensitive to the presence of overhead cover [74], as their intermediate size makes them more susceptible to visual predators, which include bird species (*Phalacrocorax* spp.) [75]. The presence of riparian buffers may have encouraged the intermediate-sized fish to have greater site fidelity, whilst the larger sized fish were more mobile with larger home ranges [76–78].

Our statistical analyses showed that the $\delta^{13}C$ of trout was influenced by the interaction between site type and fish body size. The larger bodied fish (>17 cm) in our study

showed a convergence in isotopic signatures indicative of a similar diet in this size class (Figures 6 and 7). We posit that these larger fish had more similar diets due to their larger home ranges and less fidelity to a single site type. Alternatively, their diets may have become more similar due to the size structure of prey assemblages, with a preference for larger-bodied caddisflies and terrestrial invertebrates available in the drift at both site types. Either way, it seems likely that prey from riparian buffers are important for these larger fish due to their more ^{13}C enriched isotopic signatures.

Combining our abundance results with the stable isotopes signatures of brown trout, we postulate that spatially-mediated ontogenetic diet shifts may be important for the persistence of trout in urban streams [24]. The detrital "slow" energy channel that is provided by the presence of woody riparian vegetation appears to be an important feature of trout metapopulation dynamics, because these habitat types supported the highest abundances of intermediate-sized fish, and stable isotopes of larger fish from both site types converged on a carbon isotopic signature consistent with detrital and terrestrial food sources. The peak in abundances of intermediate-sized fish in reaches with forest buffers suggest that buffered sites are a source of fish at this life stage. However, future research should test the relative importance of ecosystem size (e.g., wetted channel width), habitat refugia (i.e., overhead cover and reduced predation risk), and resource availability (i.e., aquatic detritivores and terrestrial inputs of prey) in driving the abundances of trout in urban streams. Our findings emphasize that using a food web perspective is essential for better understanding how riparian buffers can offset impacts in urban catchments. This is consistent with studies highlighting the need to incorporate measures of ecosystem functioning into environmental assessments to better understand pressure–response relationships [79–81].

We observed an interesting pattern in fish carbon isotopic signatures at our forest reference sites. The forest sites showed a bimodal distribution with a smaller cluster at −29‰ indicating a strong reliance on putative autochthonous food sources (Figure 5). This cluster was dominated by fish that were sampled from the same study site. This site was influenced by an upstream lake, meaning that phyto- and zooplankton drifting into the study reach likely enabled a more depleted ^{13}C isotopic signature to be expressed in the receiving stream food web.

5. Conclusions

Urbanization impacts stream ecosystems globally, causing biodiversity losses, altered system functioning, and reduced service provisioning. Consequently, there are growing efforts to rehabilitate and restore degraded urban stream-riparian networks [82]. Addressing the "urban stream syndrome" requires multiple mitigation tools. The enhancement and conservation of forested riparian buffers with their multiple benefits offers a cost-efficient solution in already degraded urban freshwater ecosystems as well as a key habitat feature to preserve when new areas are urbanized. Our study demonstrates that riparian buffers have the potential to mitigate the effects of urbanization on fish to a certain degree of environmental impact. However, with increasing urban impacts, the positive influence is de-coupled when habitat conditions become too heavily degraded in terms of upstream catchment deterioration (water quality and land use).

We also advance our knowledge of urban stream ecosystems using a food web perspective to reveal the importance of detrital and terrestrial carbon sources that are provided by riparian buffers. Our results suggest that spatially-mediated ontogenetic diet shifts may be important for the persistence of brown trout in urbanized streams of the Oslo Fjord basin.

The modest improvements that are suggested here may grow in magnitude when added to the broad portfolio of benefits provided by forested riparian buffers [28,29,83–85]. However, maximizing positive outcomes for fish in urban streams requires coordinating the placement of buffers with other management strategies, including controlling and mitigating point-source pollution. To conceptualizing and planning the optimal configuration of forested riparian zones at the catchment scale (i.e., width, length, position in the

stream network), however, requires context-specific considerations and the forecasting of different scenarios. Future urban planning should implement modelling frameworks, such as CoMOLA [86,87], to optimize the spatial allocation and extent of riparian zones along urban stream networks to promote biodiversity, ecosystem functioning, and services to enhance human well-being, thus ultimately helping to create sustainable and livable cities of the future.

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