Restoration of urban salmon habitat has limited effects on a key ecosystem function in British Columbia, Canada

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Abstract: Pacific salmon (*Oncorhynchus* spp.) have the potential to act as umbrella species (i.e., species whose protection safeguards other biodiversity) in urban streams of western North America. Compared with streams with less anthropogenic development, urban streams have warmer temperatures, higher nutrient loads, and flashier hydrographs from impervious surroundings, as described by the urban stream syndrome. These conditions are likely to affect ecosystem functions that are key to biodiversity and ecosystem services. Ecosystem restoration is frequently undertaken to improve habitat conditions in urban streams, with the goal of supporting highly valued fish populations. Here we ask, does restoration on behalf of Pacific salmon improve urban stream habitat by naturalizing organic matter decomposition rates? We hypothesized that 1) decomposition rates would differ between more urbanized reaches and less-disturbed reaches, and 2) sites receiving more-intensive restoration would have decomposition rates more similar to less-urbanized sites, partly because restoration would mitigate the environmental changes associated with the urban stream syndrome. Using structural equation models, we characterized the relationships between physical habitat, surrounding impervious surface, restoration intensity (a metric of the scale and frequency of restoration interventions), and cotton strip decomposition rates for streams in Vancouver, British Columbia, Canada. We found that streams surrounded by more impervious surface tended to have faster decomposition rates (standardized path coefficient $= 0.38$, the strongest direct effect on decomposition out of all the variables we considered). Reaches with more-intense restoration showed altered physical habitat characteristics compared with less-restored urban reaches. However, restoration intensity did not predict decomposition rates. Human impacts on freshwater ecosystems occur through pathways at broad spatial scales, and our results suggest that local efforts focusing on physical habitat restoration for umbrella species may not be the most effective way to address changes to ecosystem functioning.
Key words: organic matter decomposition, umbrella species, Pacific salmon, impervious surface, urban stream syndrome, cotton strips, canopy cover, water temperature

INTRODUCTION

Urbanization around streams can influence ecosystem functioning through myriad pathways, from effects on aquatic communities and physical ecosystem structure to connectivity with terrestrial ecosystems. These effects can lead to a consistent pattern of higher water temperatures, higher concentrations of nutrients and contaminants, and flashier hydrographs in streams caused by surrounding impervious surface and channel modifications, collectively referred to as the urban stream syndrome (Walsh et al. 2005). The higher water temperatures and nutrient loads in urban streams compared with streams in less-developed watersheds affect the rates of many ecosystem processes, such as organic matter decomposition and primary production (Sudduth et al. 2011, Woodward et al. 2012, Follstad Shah et al. 2017). Simultaneously, urbanization alters stream morphology through channelization and diversion (Paul and Meyer 2001, Elmore and Kaushal 2008), reduction of large woody debris (Finkenbine et al. 2000), and decreased channel complexity (Paul and Meyer 2001, Walsh et al. 2005). These physical and chemical changes can shift the total and relative abundance of species,

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functional groups, and key functional traits that contribute to ecosystem functions (Collier and Clements 2011, Classen-Rodríguez et al. 2019, Marques et al. 2019). Ecological restoration of urban streams aims to apply interventions, such as daylighting, natural channel design, barrier removal, and habitat restoration, to return freshwater populations, communities, or processes back toward a less altered state (Bernhardt and Palmer 2007).

Pacific salmon (*Oncorhynchus* spp.) are highly valued species that are the target of many restoration activities in the Pacific Northwest. These species have the capability to act as umbrella species for stream ecosystems. Umbrella species are those species targeted for conservation action whose protection also provides benefits to co-occurring species (Kalinkat et al. 2017). Umbrella species are often charismatic or culturally important, and their ecological characteristics (e.g., extensive range, large body size) provide benefits to a wider ecosystem, resulting in large areas being conserved. In addition, they are often sensitive to disturbance, requiring that conserved areas do not become degraded, and have overlapping habitat requirements with co-occurring species (Kalinkat et al. 2017). The life history and traits of Pacific salmon make them excellent candidates for designation as umbrella species because they are some of the largest freshwater predators in the ecosystems they inhabit, they migrate over large distances, they are sensitive to human disturbances, and they co-occur with macroinvertebrates and other freshwater organisms (Branton and Richardson 2014, Warkentin et al. 2019). Although potential freshwater umbrella species generally receive less attention than terrestrial species (Branton and Richardson 2011, Kalinkat et al. 2017), restoration projects targeting their habitat could mitigate environmental degradation in human-altered streams (Barnas et al. 2015, Walsh et al. 2020a).

Because the definition of umbrella species focuses on conservation of biodiversity, past assessments of potential freshwater umbrella species have focused on taxonomic richness (Bifolchi and Lodé 2005, Branton and Richardson 2011, 2014, Gilby et al. 2017). Focusing solely on richness, however, neglects the functional consequences of community composition and abundance. Diverse communities often have higher rates of ecosystem functions, and higher-functioning ecosystems also typically support more biodiverse assemblages (Grace et al. 2016, Heilpern et al. 2018). There is a need for studies that examine how habitat restoration targeting umbrella species in degraded urban ecosystems may affect ecosystem function, which is increasingly considered an important metric in ecosystem health assessments because it integrates biotic and abiotic pathways (Gessner and Chauvet 2002, Ranta et al. 2021).

Organic matter decomposition is a key ecosystem function that links terrestrial and aquatic portions of watersheds. Loss of detritivore diversity has been found to decrease rates of decomposition (Gessner et al. 2010). Considering that the urban stream syndrome is associated with lower invertebrate diversity, decomposition may be an effective tool for monitoring urban streams. Some urban streams have demonstrated increased rates of decomposition (Chadwick et al. 2006, Yule et al. 2015), whereas others have shown decreased rates (Chadwick et al. 2006, Classen-Rodríguez et al. 2019, Rossi et al. 2019), either of which can modify the flow of energy in aquatic food webs. Meanwhile, restoration efforts have been found to increase rates of ecosystem functions, including leaf-litter decomposition (Lepori et al. 2005, Frainer et al. 2018). When monitoring restoration outcomes, measuring decomposition has the added benefit of standardized assays that are relatively easy to implement and do not require the long hours of specimen identification required by other biodiversity assessments (Tiegs et al. 2013).

To investigate the potential of Pacific salmon as umbrella species in urban streams, we asked the following question: Do restoration efforts aimed at conserving these species benefit the wider ecosystem by naturalizing organic matter decomposition rates? In the context of the urban stream syndrome, we predicted that more-urbanized sites would have higher water temperatures, higher nutrient concentrations, and altered habitat. We then hypothesized that 1) decomposition rates would be either higher (because of temperature, nutrients, and some habitat alterations) or lower (because of contaminants and other habitat alterations) in more-urbanized reaches compared with less-disturbed reaches, and 2) sites with more restoration would have decomposition rates more similar to less-urbanized sites because restoration would mitigate environmental degradation.

METHODS

To answer our research question, we assessed organic matter decomposition rates as a measure of ecosystem function in 9 streams along an urbanization gradient with both restored and unrestored stream reaches in and around Vancouver, British Columbia, Canada. We surveyed water quality and habitat characteristics (e.g., physical and chemical properties) to understand how urbanization and restoration may alter physical stream habitat, and we quantified the surrounding impervious surface to understand the effects of urbanization on decomposition rates. Rather than using the abundance of umbrella species (i.e., Pacific salmon species) as a predictor of decomposition rates, we used restoration intensity (a metric of the scale and frequency of restoration interventions; Chazdon et al. 2024) because regardless of the effectiveness of restoration for salmon returns, restoration could still provide benefits to the wider ecosystem. We measured restoration intensity at both the local scale (directly surrounding sites where decomposition was measured) and across the watershed (reflecting that environmental conditions at broader spatial scales contribute to determining ecosystem processes measured locally). We used a series of linear mixed-effects models (LMMs) and piecewise structural equation modeling (SEM) to assess how urbanization and restoration affect decomposition and habitat variables while accounting for confounding effects from elevation.

Study area and sites

The City of Vancouver is located on the west coast of British Columbia, Canada, and has a human population of >2.5 million people, which has led to many streams exhibiting conditions associated with the urban stream syndrome. Summer base flows and water velocity are both lower in Vancouver streams compared with less urban streams, and impervious surfaces have also caused higher turbidity and NO_3^- loads, along with lower dissolved O_2 (Finkenbine et al. 2000, Ruan et al. 2019). Vancouver's streams historically provided passage to spawning anadromous salmonids, including the Chinook Salmon *Oncorhynchus tshawytscha* (Walbaum, 1792), Coho Salmon *Oncorhynchus kisutch* (Walbaum, 1792), Sockeye Salmon *Oncorhynchus nerka* (Walbaum, 1792), Pink Salmon *Oncorhynchus gorbuscha* (Walbaum, 1792), Chum Salmon *Oncorhynchus keta* (Walbaum, 1792), Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* (Richardson, 1836), and Rainbow Trout *Oncorhynchus mykiss* (Walbaum, 1792), but in many streams, salmon populations dwindled and disappeared with increasing urban development (Chen et al. 2017, Finn et al. 2021). Since approximately the 1970s, the cultural and economic values of salmon have led to a surge in efforts by governments, and most notably citizen Streamkeepers, to restore urban streams (Pacific Streamkeepers Federation n.d.). Restoration interventions in Vancouver have ranged in scale from low-cost, volunteer-based riparian plantings and cleanups and higher-cost professional culvert upgrades to major stream re-engineering, such as daylighting and channel reconstruction (Table S1).

We selected 9 streams on Vancouver's North Shore (Brothers, Cypress, Eagle, Gallant, McDonald, Mosquito, Parkside, Rodgers, and Westmount creeks) and 1 in the City of Vancouver (Still Creek) (Fig. 1), representing a gradient of urbanization and restoration (Table 1). All streams except Westmount Creek had salmonids present, and communities included stocked salmon in 3 of the streams (Table 1). All of the streams passed through urbanized areas with dense housing in their lower reaches. The upper reaches of the North Shore streams passed through forested areas or low-density housing. We chose 2 to 5 sites in each stream at which to deploy cotton strips based on total stream length, the location of existing temperature loggers, proximity to restoration projects, and site accessibility, and we measured water chemistry at 1 to 3 of these sites in each stream (see below). All but 1 stream had at least 1 site within a restored reach. The chosen sampling reaches represented a combination of restored and unrestored reaches within watersheds, enabling comparisons among non-urbanized, urbanized restored, and urbanized unrestored reaches

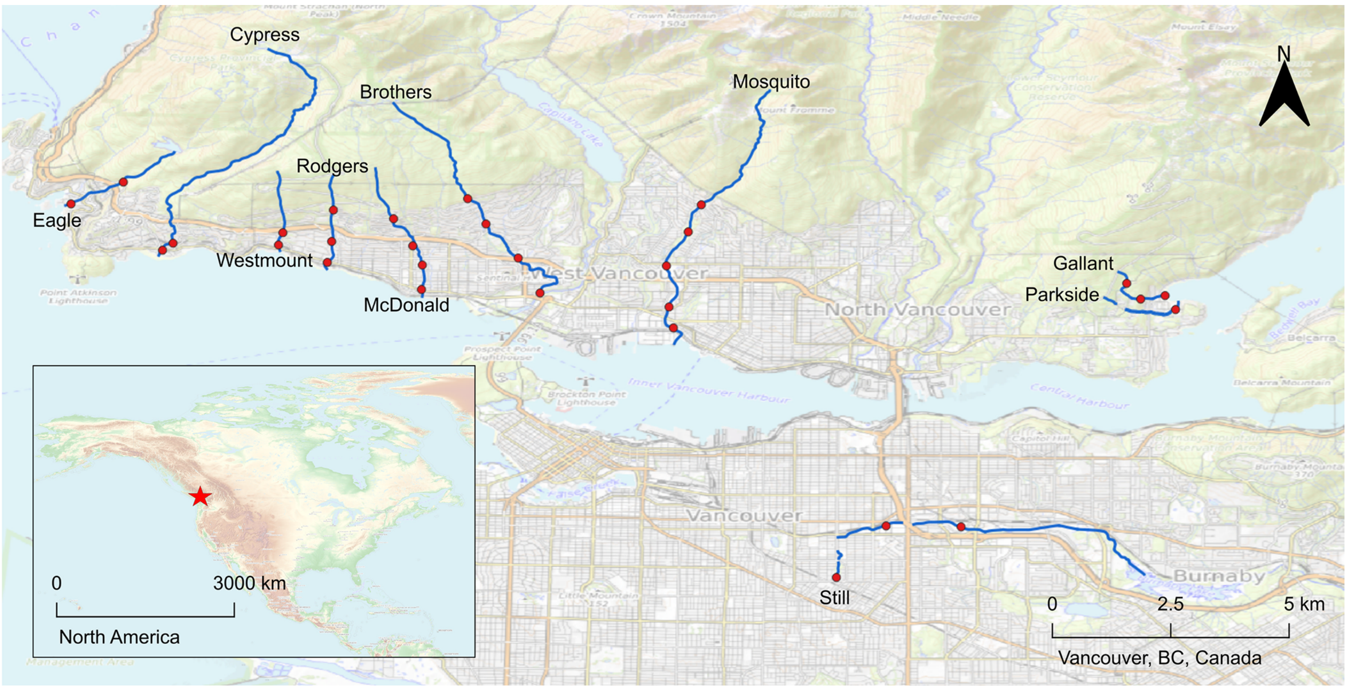

Figure 1. Map of 10 study streams and 29 sampling sites, marked with red circles, around the metropolitan Vancouver area, located in British Columbia, Canada, marked with a red star on the inset map of North America (data sources: Government of British Columbia, GeoBC Branch 2025 [stream networks]; OpenTopoMap 2026 [basemap]).

Table 1. Profile of study streams with presence of the potential umbrella species (*Oncorhynchus* spp.), degree of urbanization (i.e., measured as mean % impervious surface), and restoration intensity (a metric of the scale and frequency of restoration interventions) undertaken across the watershed. To quantify restoration intensity, projects were assigned as either lightly assisted (and given a score of 1 point), moderately assisted (2 points), or heavily assisted (3 points), with category definitions explained in Table 2, and the restoration intensity metric represents the sum of all projects in a watershed. Mean catch per unit effort is presented for a subset of the study streams, sampled in July 2021, as well as the number of salmon stocked in the streams by enhancement programs (Gemmell 2023). Common names of species are all salmon except Cutthroat, Rainbow, and Steelhead, which are trout.

Stream	Species of salmonid	Mean catch per unit effort	Stocked (no.)	Mean impervious surface (%)	Restoration intensity
Brothers Creek (BRT)	Chinook, Chum, Coho, Cutthroat, Pink, Rainbow, Steelhead	0.144	No (0)	27.90	16
Cypress Creek (CPS)	Chum, Coho, Cutthroat, Pink	0.432	Yes (6147)	24.63	3
Eagle Creek (EAG)	Chum, Coho, Cutthroat	0.537	Yes (1401)	12.98	12
Gallant Creek (GLT)	Cutthroat	Not assessed	No (0)	9.04	10
McDonald Creek (MCD)	Chum, Coho, Cutthroat, Steelhead	0.144	No (0)	35.27	26
Mosquito Creek (MSQ)	Coho, Chum, Pink	0.110	No (0)	26.25	60
Parkside Creek (PRK)	Coho, Cutthroat	Not assessed	No (0)	10.91	15
Rodgers Creek (RGR)	Chum, Coho, Cutthroat, Pink	0.400	Yes (2970)	19.81	15
Still Creek (STL)	Chum	Not assessed	No (0)	62.67	29
Westmount Creek (WTM)	None	Not assessed	No (0)	30.79	0

(Table S2). A total of 30 sites were chosen for this experiment (Fig. 1) in collaboration with local partners, although we later discarded 1 site because of the loss of sampling equipment.

Decomposition and temperature measurements

We used a cotton strip assay as a standardized method for measuring organic matter decomposition in the study streams. We prepared cotton strips following methods from Tiegs et al. (2013) with Fredrix® Unprimed Cotton Duck Canvas 15113 (Tara Materials, Inc., Lawrenceville, Georgia). We created 8-cm-long, 27-thread-wide cotton strips with fringe that was 3-mm long on the long edges and 4 to 5 threads wide on the short edges. We deployed the cotton strips on 22, 23, and 28 May 2021 (early-summer study period) and 28 and 29 July 2021 (mid-summer study period). We deployed 4 cotton strips/site in each study period. To secure the strips in the stream, we used two 20-cm^2, 10-kg cement blocks with open centers (Basalite® Concrete Products, Surrey, British Columbia, Canada) per site. We attached 2 cotton strips to each block by first securing a large zip tie around the block and then attaching the cotton strips with smaller zip ties. Some sites had existing HOBO® Pendant Temperature/Light Loggers (UA-002-08) or HOBO TidbiT Temperature Loggers (UTBI-001), otherwise we attached our own HOBO Pendant UA-002-08 loggers (both models made by Onset® Computer Corp., Bourne, Massachusetts) to 1 concrete block/site, again using a small zip tie. We placed 1 block in a pool and the other in a riffle, except in particularly uniform reaches in which case we placed both blocks in either pools or riffles. Blocks were placed within 5 m of each other within a site and situated to ensure they would remain fully submerged under water. For 2 sites we later moved the blocks because of high-flow events and in response to further input from stakeholders.

We retrieved the cotton strips at the end of the early-summer study period on 24 and 25 June and at the end of the mid-summer study period on 24 and 25 August. When retrieving cotton strips, we gently brushed the strips with a paintbrush to remove organisms and particles. We then lowered the strips into Falcon tubes containing 70% ethanol for 30 s to remove microbial communities before wrapping each strip in aluminum foil. We froze the strips until the end of the collection period, at which time we placed them in a drying oven at 40°C for 90 h. We also dried 8 control cotton strips, which we did not deploy in streams, but which we soaked in ethanol for 30 s prior to drying.

We measured the tensile strength of the cotton strips on an Instron® 5469 Universal Testing Machine (Instron, Norwood, Massachusetts). After drying, we prepared cotton strips for tensile strength measurement by painting 2 cm at the ends of the cotton strips with Acrylic Mediums Gloss Gel 5708 (Liquitex®, London, UK) to prevent them from slipping out of the machine grips. The machine was equipped with a 2-kN load cell and 50-kN large clamps (Instron #2716-020). We set the rate of advancement to 2 cm/min and calculated the decomposition rates as the % tensile loss per degree day (TLDD) with Eq. 1 (Tiegs et al. 2013):

$$\mathrm{TLDD} = \frac{100\left(1 - \frac{TS_e}{TS_r}\right)}{\mathrm{DD}}, \qquad \text{(Eq. 1)}$$

where TS_e is the final tensile strength of the cotton strip, TS_r is the mean tensile strength of the control strips, and DD is degree days (see below for DD calculations). Where this calculation resulted in a negative number, TLDD was assigned as 0.

We used data from the temperature loggers to calculate DD: the mean temperature for each day the loggers were deployed, summed over the deployment period. Three of the pre-existing temperature loggers malfunctioned during the deployment period: 1 in Brothers Creek (BRT02) and 2 in Mosquito Creek (MSQ01 and MSQ04; see Table S2 for site name definitions). Because we found a high correlation between DD and elevation, we predicted DD for those sites based on a linear relationship from other sites on the same stream.

Water chemistry

We sampled water chemistry to understand whether the study streams were affected by the higher nutrients and pollutants that are commonly associated with the urban stream syndrome (Walsh et al. 2005). We took water chemistry samples for pH, total NH_3, and P during the early-summer study period on the same days as instrument deployment at 1 to 3 of the cotton-strip-assay deployment sites for each stream depending on its length, with 1 site near the outlet, the middle, and the headwaters to be representative of changes along the stream length. We collected samples for pH and P measurements into 250-mL high-density polyethylene containers. We collected samples for NH_3 measurements into 100-mL amber glass bottles and used sulfuric acid (H_2SO_4) as a preservative. We filled 1 bottle of each type at a total of 21 sites. Water chemistry analysis was performed by ALS Environmental® (Burnaby, British Columbia, Canada). Water samples were kept in a cooler with ice packs and delivered to the lab by the end of the sampling day. NH_3 was measured by flow-injection analysis with fluorescence detection after reaction with ortho-phthaldialdehyde, and P (soluble reactive P, including orthophosphate) was measured colorimetrically after filtering through a 0.45-μm-membrane filter in the lab.

Habitat measurements

For the early-summer study period, we measured habitat and stream characteristics for each site in the 3 weeks following instrument deployment. We measured wetted width (to the nearest 0.1 m) across existing channel flow and bankfull width (to the nearest 0.1 m) by estimating the furthest extent the channel could carry water at highest flow. We measured depth (to the nearest 1 cm) and flow velocity (to the nearest 0.03 m/s [0.1 ft/s]) with an FP111 Flow Probe (Global Water Instrumentation, Gold River, California) in representative pools and riffles. Using a 1-m^2 quadrat divided into 25 squares, we characterized the substrate for 1 pool and 1 riffle at each site into categories of impermeable surface, rocks (diameter >20 cm), gravel (diameter 2.5–20 cm), fine gravel (diameter <2.5 cm), sand, mud, living plants, leaf litter, biofilm, and woody debris by counting how many squares were covered by each material. We estimated % pool and riffle cover (to the nearest whole %) for a stream reach encompassing the cement blocks (up to 5 m long). We quantified canopy cover above the stream reach by counting the squares with open canopy on a Convex Model A spherical crown densiometer (item no. 43887; Forestry Suppliers®, Inc., Jackson, Mississippi), from which we calculated canopy cover (to the nearest whole %). We also classified the riparian vegetation into type (forest, field, meadow, and housing) and dominant species of tree, shrub, and ground cover (Table S3). For a limited selection of habitat and stream characteristics that were predicted to change over the season (wetted width, depth, and velocity), we repeated these measurements for the mid-summer study period on the same day as cotton strip collection.

To measure local urbanization influence at each site, we used Google® Earth Pro (version 7.3.3; Google, LLC, Mountain View, California) to calculate a weighted average of the % impervious surface of a 400-m^2 quadrat around the site (data source: https://open-data-portal-metrovancouver.hub.arcgis.com, accessed August 2021).

Restoration metrics

Our definition of umbrella species focuses on whether restoration targeted at Pacific salmon habitat also provides benefits to co-occurring species by improving ecosystem function. Therefore, we created a catalog of restoration projects motivated by concern for salmon habitat in the study streams. We collected information on restoration from news articles, public records, and Streamkeeper databases (Table S1). We identified sources through Google searches with variations of key words related to restoration, salmon, and the name or location of each study stream, using new combinations until searches resulted in no new restoration interventions. Additionally, we contacted Streamkeeper groups for each study stream to obtain records of restoration projects that were not available to the public. We cataloged a total of 80 restoration projects that were undertaken between 1978 and 2020 in the study streams (described in Table S1, including data sources). For our metric of restoration intensity, projects were assigned as either lightly assisted (and given a score of 1 point), moderately assisted (2 points), or heavily assisted (3 points) in line with the suggested classification in Chazdon et al. (2024) (Table 2). This scoring system allows for a case-by-case assessment of restoration projects based on the degree of intervention used to promote ecosystem recovery on behalf of Pacific salmon. The score per site was the sum of all the project scores that occurred within an ~400-m^2

area surrounding each study site, and the score per watershed was the sum of the project scores for the entire stream. Restoration intensity per site ranged from 0 to 21 and per watershed ranged from 0 to 62.

We developed a parallel metric of restoration effort to test the robustness of our results. To calculate restoration effort, we assigned 1 point to each restoration project for a component within the stream and 1 point for a component in the riparian zone, and we multiplied points by the length of the project (in years). Restoration effort per site ranged from 0 to 15 and per watershed ranged from 0 to 33. We assessed the correlation between restoration effort and restoration intensity metrics in each watershed with Spearman's rank-order correlation and found that they were highly correlated (r_s = 0.91) but provided different information (Table S2). Because restoration effort is primarily a vote-counting method, whereas restoration intensity incorporates qualitative information about restoration activities, our results here focus primarily on restoration intensity; however, we present and discuss differences between restoration intensity and restoration effort.

Assessing correlations among explanatory variables

We examined the correlation between habitat variables by calculating Spearman's rank-order correlation in R (version 4.4.1; R Project for Statistical Computing, Vienna, Austria) using RStudio® Integrated Development Environment for R (version 2023.06.1+524; Posit® Software, PBC, Boston, Massachusetts). First, we cleaned and processed data with packages *tidyr* (version 1.3.1; Wickham 2024) and *dplyr* (version 1.1.4; Wickham et al. 2023). To assess the correlation between variables measured separately in early and late summer (e.g., stream depth, width, and velocity), we chose a positive association as the alternative hypothesis. For other correlation tests we used a 2-sided test. To address our hypotheses, we needed to account for the fact that lower-elevation sites are much more urbanized (Spearman's $r_s = -0.51$, $p = 0.004$) and that non-urbanized sites have not undergone restoration.

Assessing urban influence on stream conditions

To assess whether streams surrounded by higher amounts of local impervious surface exhibited key characteristics of the urban stream syndrome, we first sought to understand the relationship between elevation and stream temperature by fitting an LMM with the *lme4* package (version 1.1-35.5; Bates et al. 2015) with mean temperature over the deployment period as the response variable, elevation as a fixed effect, and sampling period and watershed as random effects (model 1 in Table S4). To address the effects of urbanization and restoration on stream temperature, we then used the residuals from the 1st model as the response variable in a linear model with local impervious surface, restoration intensity (or effort), and their interaction as fixed effects (models 2 and 3 in Table S4). We repeated this procedure for total NH_3, dissolved P, and pH (but because these variables were only measured once, we omitted

Table 2. Summary of restoration intensity metric category definitions, based on classifications from Chazdon et al. (2024).

Restoration intensity	Types of restoration	Number of projects in category
Lightly assisted	Installing incubation boxes, cleaning up in the stream and riparian areas, and removing invasive plants	6
Moderately assisted	Upgrading culverts (adding baffles and shotcrete, creating a natural bottom), adding diversion pipes to augment summer flow, adding fish ladders, adding timber guides, building box culverts, removing invasive plants and adding native riparian plantings, adding boulders and logs into the stream, installing debris fences and anchors, and cleaning instream blockages	42
Intensively assisted	Restoring the stream mouth (adding a series of pools and drops, redefining the estuary path), constructing rearing ponds, constructing or lengthening side channels, excavating plunge pools and adding boulders to raise the water level, bank stabilization and creek reconstruction to reduce sediment loads, removing channelization of the stream, daylighting the stream, widening the stream, reconstructing the stream bed and adding habitat complexity, converting or restoring the riparian habitat to wetlands and meadows, installing bioswales, construction of weirs and rebuilding intakes, and removing gravel from the stream	32

sampling period; see models 4 through 12 in Table S4). For each response variable, if the LMM with elevation did not show evidence for an effect of elevation, determined as a p-value <0.05, then rather than using the residuals, we expanded the model to include the main effect of elevation plus an interaction between impervious surface and restoration intensity. For LMMs, we used the *MuMIn* package (version 1.48.4; Bartoń 2024) to calculate marginal (fixed effects only) and conditional (entire model) R^2 values and the *lmerTest* package (version 3.1–3; Kuznetsova et al. 2017) in R to calculate F statistics and p-values associated with fixed effects.

After selecting variables that were not highly correlated, we performed principal component analyses (PCAs) to explore multivariate stream habitat characteristics and to create composite variables describing stream habitat with the *stats* package in R.

Assessing drivers of cotton strip decomposition

Finally, we examined potential direct and indirect effects of urbanization and restoration on TLDD using piecewise SEMs with the *piecewiseSEM* package (version 2.3.0.1; Lefcheck 2016) in R. This approach allowed us to control for the pervasive effect of elevation, which is associated with both water temperature and land-use patterns, and to assess how any perceived effects of restoration could be related to urbanization, given that only developed sites were restored. We chose the piecewise SEM approach because it accommodates random effects, which were important because we had multiple sites per watershed and multiple decomposition measurements per site. Thus, our SEM consisted of 4 LMMs. We scaled and centered our data, then modeled TLDD as a function of surrounding (i.e., local) impervious surface, restoration intensity, elevation, the 1st principal component of the habitat characteristics PCA, and placement in a pool vs a riffle, with site as a random effect. The 1st principal component axis was modeled as a function of elevation and restoration intensity, with watershed as a random effect. Local impervious surface was modeled as a function of elevation, and restoration intensity was modeled as a function of both elevation and impervious surface, with both models including watershed as a random effect to account for the fact that non-urbanized sites are not restored. We checked whether the assumptions of each component model were met with the *DHARMa* package (version 0.4.6; Hartig 2024) in R. See Appendix S1 for additional details on our model formulation and selection procedure. We further assessed SEM fit by considering Fisher's C and the marginal and conditional R^2 values of each component model in the SEM.

To explore how choices about the method for measuring restoration affected our conclusions, we constructed 3 additional SEMs. The 1st used site-specific restoration effort instead of restoration intensity. The 2nd used a modified subset of restoration effort, where we considered only instream habitat restoration and excluded projects that focused on fish passage (such as fish ladders) and the construction of spawning habitat outside of the main stream channel (such as ponds). The 3rd additional model used % tensile loss per day (TLND; not temperature-adjusted) as opposed to TLDD as the response variable of interest. In our main model we used TLDD as our metric of decomposition because TLDD allows for a standardized comparison across sites with different water temperatures and because temperature-adjusted decomposition rates are commonly found in other studies. However, modeling TLND allowed us to more explicitly examine the effect of temperature on decomposition rates. In the TLND SEM, we included a component model with DD as a function of elevation and local impervious surface and with watershed as a random factor, and we included DD as an explanatory variable in the component model of TLND.

RESULTS

Stream characteristics

Most of the study streams had a cascade morphology (characterized by a steep, narrowly confined channel with turbulent flows and large cobble or boulders; Montgomery and Buffington 1997) and were forested with red alder (*Alnus rubra* Bong.) and western redcedar (*Thuja plicata* Donn ex D. Don) as the dominant tree species (both native to the region). Streams had a mean wetted width of 5.0 m (range 0.7–9.5 m), depth of 23 cm (range 7–54 cm), and velocity of 0.34 m/s (range 0.1–3.6 m/s) in early summer. Variables that were measured separately for each sampling period tended to be very highly correlated, for example depth ($r_s = 0.55$, $p = 0.002$), wetted width ($r_s = 0.86$, $p < 0.001$), and temperature accumulated over the sampling period ($r_s = 0.50$, $p = 0.003$), with the notable exception of stream velocity ($r_s = -0.16$, $p = 0.8$).

Temperature and nutrients

Mean water temperature during cotton strip deployment had a strong negative relationship with elevation (LMM $F_{1,50.18} = 27.47, p < 0.001$; Table S5, Fig. 2A) and no further association with local impervious surface, restoration, or their interaction (when considering restoration intensity: $F_{3,54} = 0.02$, $p = 0.7$; when considering restoration effort: $F_{3,54} = 1.28$, $p = 0.3$; Table S5). We confirmed that the effect of elevation on temperature was not biased by low-elevation streams being more urbanized (which is shown in Fig. S1) by repeating the LMM only with the portion of sites that were surrounded by ~20% impervious surface or less (which spanned an elevational gradient of 14–394 m a.s.l.), obtaining nearly identical results ($F_{1,13.73} = 9.51$, $p = 0.008$; estimated coefficient for the effect of elevation $= -0.009$ for both full and reduced datasets; Table S6). Neither total NH_3 ($F_{1,12.72} = 0.01$, $p > 0.9$, marginal $R^2 < 0.001$; Table S7) nor P ($F_{1,12.63} = 0.05$, $p = 0.8$, marginal $R^2 = 0.001$; Table S8) were associated with elevation; thus, we expanded the LMMs

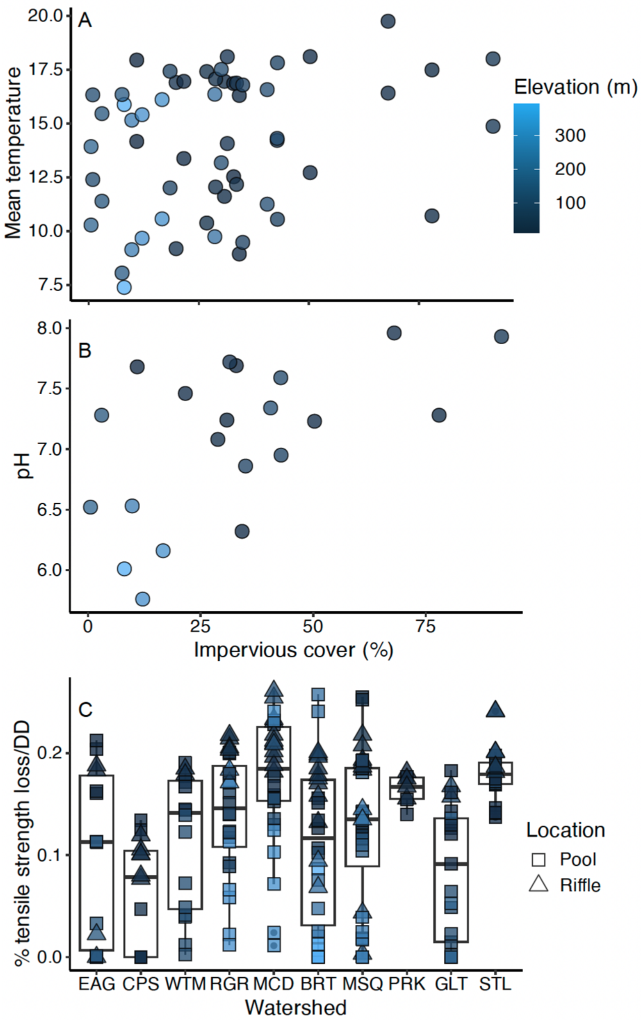

Figure 2. Key physical conditions and decomposition rates varied with elevation within and among watersheds in the Vancouver metropolitan area, British Columbia, Canada, in summer 2021. Mean water temperatures during cotton strip deployment periods (A) and early-summer pH (B) both tended to be higher at sites surrounded by more impervious surface, which themselves were concentrated at low elevations. Decomposition rate, measured as the % of a cotton strip's tensile strength lost per degree day (DD) during the deployment period, varied among streams and often with elevation within streams. In panel C streams are presented from west to east in the study area. EAG = Eagle Creek, CPS = Cypress Creek, WTM = Westmount Creek, RGR = Rodgers Creek, MCD = McDonald Creek, BRT = Brothers Creek, MSQ = Mosquito Creek, PRK = Parkside Creek, GLT = Gallant Creek, STL = Still Creek.

to include impervious surface and restoration intensity. For NH_3 the resulting model explained a large proportion of variance (conditional $R^2 = 0.43$), but most of the variance was associated with the watershed random effect rather than the fixed effects (marginal $R^2 = 0.05$, all p-values for interaction and main effects >0.3; Table S7). Results were nearly identical for P (Table S8). By contrast, pH was strongly negatively associated with elevation ($F_{1,9.86} = 93.04$, $p < 0.001$; Table S9, Fig. 2B). In the linear model with the residuals as a response variable, there were no associations of pH with local impervious surface, restoration intensity, or their interaction ($F_{3,17} = 0.87$, $p > 0.4$; Table S9).

Multivariate characterization of stream habitat

We found high correlations between several pairs of habitat variables, particularly those within the categories of water chemistry, microhabitat, and temperature, which informed our decisions about which habitat variables to include in the PCA. We used only the June measurements of depth and wetted width, and we excluded bankfull width completely because it was highly correlated with wetted width (from early-summer measurements, $r_s = 0.93$, $p < 0.001$). The first 2 principal component axes of the PCA explained 43% of the variation in the dataset (Figs 3, S3). The 1st principal component (PC1) explained 22% of the variance in the dataset, with strong positive loadings from % pool, streambed sand, and biofilm, whereas streambed rocks, June stream velocity, and overstory density had strong negative loadings. The 2nd principal component (PC2) explained 21% of the variance in habitat, with strong positive loadings from wetted width, June stream depth, June stream velocity, and rocks and with strong negative loadings from fine gravel and mud streambed cover.

A PCA of habitat characteristics at 21 sites where water chemistry measurements were collected was very similar (explaining 47% of the variation in the smaller dataset; Fig. S3). In this PCA pH had a positive loading on PC1, with higher pH in sites with slow-moving, sandy pools, and a weaker, negative loading on PC2 (Fig. S4).

Overall effects of urbanization and restoration on decomposition rates

To investigate the relationship between urbanization, restoration of Pacific salmon habitat, and decomposition, we fit a piecewise SEM. Model fit was only moderate (Fisher's $C = 17.80$, $p = 0.02$; see Appendix S1 for discussion of model fitting). Our SEM structure was nearly saturated, complicating the calculation of χ^2 and C; however, we did not remove model components to increase directed separation because all paths were relevant to our specific hypotheses. Conditional R^2 values were high (>0.60) for each of the 4 component models, and marginal R^2 (attributed to fixed effects only) ranged from 0.13 for the PC1 model to 0.43 for the TLDD model.

Decomposition rates (i.e., TLDD) of 212 cotton strips collected from the study sites across the study periods varied from 0 to 2.97%/DD with a mean of 1.59%/DD (Fig. 2C). In our piecewise SEM (Table S10, Fig. 4), local impervious surface had a direct, positive effect on decomposition (standardized coefficient = 0.38 ± 0.12 SE, $p = 0.004$), whereby

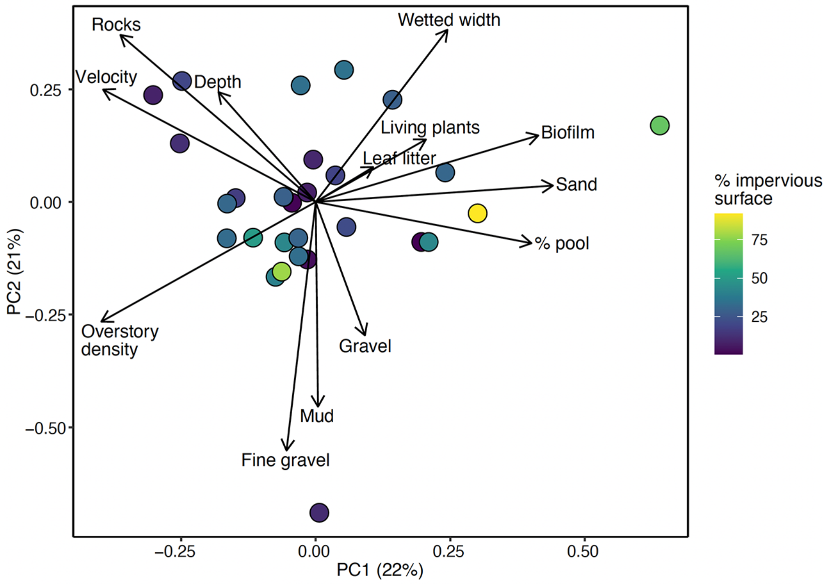

Figure 3. Principal component (PC) analysis of habitat variables measured at 29 stream sites in the Vancouver metropolitan area, British Columbia, Canada, with complete data from the early-summer 2021 study period. Vectors show magnitude and direction of habitat variables on the PC axes.

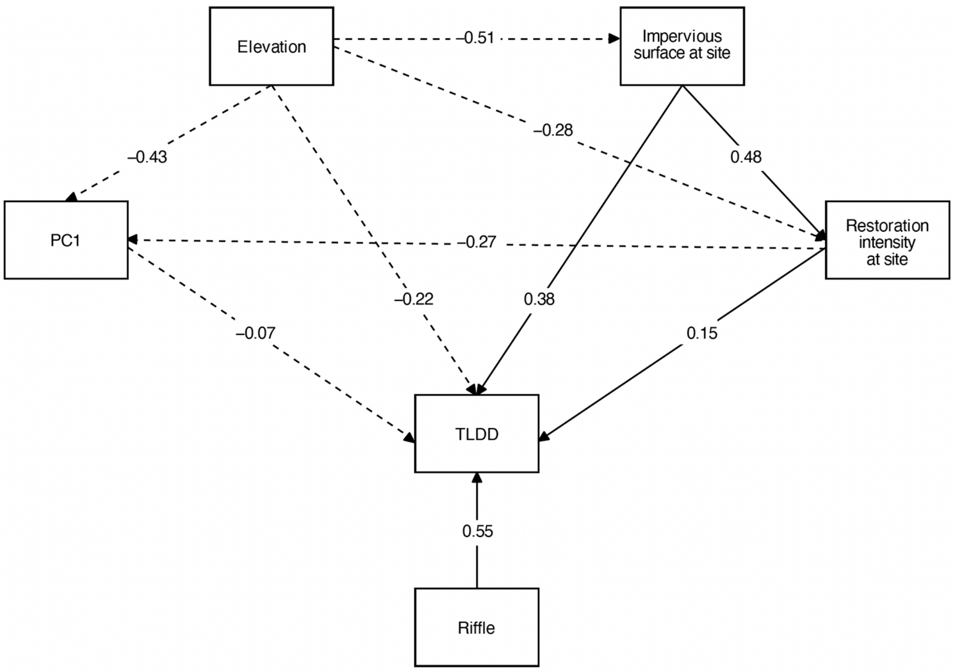

Figure 4. Results of a piecewise structural equation model (SEM) examining the direct and indirect effects of elevation, urbanization (i.e., % impervious surface surrounding a stream site), restoration intensity, location in a riffle or a pool (Riffle), and habitat characteristics (as the 1st principal component [PC1] from a principal component analysis) on cotton strip decomposition rates (measured as tensile strength loss per degree day [TLDD]; $n = 212$) at 29 stream sites in 10 streams in the Vancouver metropolitan area (British Columbia, Canada) across the early-summer (late May to late June) and mid-summer (late July to late August) deployment periods in 2021. Positive associations are indicated by solid lines and negative associations by dashed lines. Numbers in each path show the standardized path coefficients from the SEM. Results of a similar SEM on TLDD with temperature as an additional variable in the model were qualitatively similar (see Fig. S7) and showed a direct and indirect (via temperature) influence of elevation on decomposition.

cotton strips decomposed more quickly in urbanized sites with more impervious surroundings. Contrary to our hypotheses, the intensity of Pacific salmon habitat restoration did not have a strong effect on cotton strip decomposition rates (standardized coefficient [direct effect] = 0.15 ± 0.11 SE, $p = 0.2$). The main mechanism through which stream habitat influenced decomposition rate was via faster decomposition in pool vs riffle location (standardized coefficient [direct effect] = 0.25 ± 0.10 SE, $p < 0.001$). PC1 of the habitat PCA, representing a gradient from high canopy-cover, rocky reaches with fast-moving water to sandy, biofilm-covered reaches, had no apparent effect (standardized coefficient = -0.07 ± 0.11 SE, $p = 0.5$).

As expected, elevation was important in our model of decomposition, but as an indirect rather than a direct effect (Fig. 4). Elevation was negatively associated with local impervious surface (standardized coefficient [direct effect] = -0.51 ± 0.04 SE, $p < 0.001$) and restoration intensity (standardized coefficient [direct effect] = -0.28 ± 0.07 SE, $p = 0.001$). Thus, elevation had an indirect effect on decomposition rate via impervious surface of -0.19, calculated from the component direct effects, whereby cotton strips deployed at lower elevations tended to decompose more quickly because of higher urbanization (Fig. 4).

Piecewise SEM models using restoration effort rather than restoration intensity did not have improved global goodness of fit. Using complete restoration effort (Fisher's $C = 25.49$, $p = 0.001$; Table S11, Fig. S5), the direct effect of elevation became more important for TLDD, with cotton strips at lower elevations decomposing faster (standardized coefficient [direct effect] = -0.23 ± 0.11 SE, $p = 0.05$). Using restoration effort with only stream habitat restoration projects (Fisher's $C = 41.15$, $p < 0.001$; Table S12, Fig. S6) indicated a stronger effect of local impervious surface on restoration effort (standardized coefficient [direct effect] = -0.26 ± 0.09 SE, $p = 0.003$) than the prior 2 models but still no effect of restoration effort on TLDD (standardized coefficient [direct effect] = 0.11 ± 0.10 SE, $p = 0.3$).

Finally, building an alternative piecewise SEM focused on TLND and incorporating direct and indirect effects of temperature demonstrated somewhat improved global goodness of fit (Fisher's $C = 19.81$, $p = 0.1$, but issues remained with calculation of χ^2). As expected, temperature had a strong direct effect on daily decomposition rates and was colder at high elevations and in areas with less local impervious surface, adding indirect effects of those variables on decomposition (Table S13, Fig. S7).

DISCUSSION

We measured organic matter decomposition in urban streams to investigate whether restoration in support of Pacific salmon influences stream ecosystem function and, thus, whether Pacific salmon could be umbrella species for stream ecosystems. Supporting our initial hypothesis, we found that organic matter decomposed faster in streams surrounded by more impervious surface, although it was difficult to disentangle the causal effect of urbanization from an underlying elevational gradient. We also predicted that urbanized sites with more-intense restoration interventions would have similar decomposition rates to less-urbanized sites; however, we found little support for this hypothesis. This result aligns with previous research showing that restoration did not alter leaf-litter decomposition rates in agricultural reaches (Griffiths et al. 2012) or gross primary production, ecosystem respiration, or NO_3^- cycling in urban reaches (Sudduth et al. 2011). Ecosystem functioning may be difficult to restore once degraded. Overall, we did not find strong evidence that restoration of Pacific salmon habitat pushed decomposition rates back toward their presumed baseline, despite the inclusion of some reaches with quite mature restoration projects.

There are multiple pathways through which urbanization is likely to affect decomposition. Here, we used the amount of local impervious surface around a stream as a metric of urbanization. The influence of impervious surface on organic matter decomposition varies in the literature (Chadwick et al. 2006, Imberger et al. 2010, Kielstra et al. 2019). We found a strong, positive relationship whereby even after adjusting for the warmer water temperatures in streams surrounded by higher amounts of impervious surface, these streams had higher decomposition rates per growing degree day. This pattern could be explained by other elements of the urban stream syndrome, such as higher nutrient loads or flashier hydrographs, which typically accelerate decomposition (Woodward et al. 2012). However, after controlling for the effect of elevation, we did not find evidence of higher concentrations of NH_3 and P in more-urbanized than less-urbanized stream reaches, although if there is high biological demand for labile nutrients and they are taken up immediately, variation would be hard to detect using snapshots of dissolved nutrient concentrations. Higher peak flows, another element of urbanization, could lead to differences in decomposition, and there were 3 storm events with precipitation >10 mm during each study period (West Vancouver AUT station; extracted from the Environment and Climate Change Canada Historical Climate Data website: https://climate.weather.gc.ca/index_e.html, accessed 19 July 2025). Another possibility is that more-urbanized reaches have different biological communities, which could additionally contribute to decomposition rates outside the temperature pathway. Surveying biological communities was outside the scope of this project, but we suggest it as a direction for future research.

The effectiveness of umbrella species conservation has most commonly been assessed by comparing overall species richness in areas with varying abundances of the umbrella species (Roberge and Angelstam 2004, Branton and Richardson 2011). In addition to the number and type of restoration interventions, the study streams varied in their salmon stocking status (Table 1), which affects demography and expected adult returns. Disentangling the effects of restoration on salmon status, and then salmon status on communities and ecosystems, would be particularly complex considering the varying origins of salmon in these streams. Thus, rather than assessing the abundance of the umbrella species, we took a more expansive approach by considering how effort expended to protect them, regardless of that effort's success in producing the desired effect on the focal species, could benefit ecosystems in 2 ways. First, we assessed the potential functional benefits to ecosystems rather than focusing solely on biodiversity. Many ecosystem functions are promoted by higher levels of biodiversity; therefore, we expected that conservation of umbrella species would protect ecosystem functions. Second, we chose to more mechanistically examine the potential pathway from umbrella species to ecosystem function by focusing on habitat modification targeted at improving conditions in degraded ecosystems rather than focusing on habitat protection, which assumes that ecosystems are intact and can be maintained that way.

Contrary to our hypotheses, we did not find evidence that restoration of salmon habitat resulted in different ecosystem functioning when compared with sites where less-intense restoration efforts were undertaken. There could be at least 3 reasons for this lack of evidence. First, it is possible that restoration did not change the stream environment. Our SEM indicated a moderately strong relationship between restoration intensity and PC1 of the habitat PCA, which was characterized by wide, sandy reaches with prevalent pools, leaf litter, and biofilm. This relationship was negative, suggesting that restored reaches were narrower, deeper, rockier, and had faster-moving water. Our SEM also showed that riffles had faster decomposition rates than pools, a finding consistent with previous decomposition studies, including those using cotton strips (Webb et al. 2019, Banks et al. 2023). Thus, this 1st possible explanation seems inconsistent with our data, although anthropogenic factors influencing stream structure and function often operate across broader scales than can be effectively addressed with reach-scale restoration projects (Bernhardt and Palmer 2011) and may have overwhelmed the local changes in specific physical conditions.

A 2nd possible explanation for the lack of restoration effects on decomposition is that salmon may not be effective umbrella species for stream biodiversity; thus, their conservation may only minimally affect biotically mediated ecosystem function. Previous research reported that protecting habitat for predicted umbrella species does not necessarily result in protecting the type of habitat needed by other species of concern (Branton and Richardson 2014, Wang et al. 2021). In our case, a lack of response by other species to restoration for our predicted umbrella species could be related to the types and locations of restoration projects that were undertaken. In the site with the highest restoration intensity (the outlet of McDonald Creek), these efforts focused mainly on the physical structure of salmon habitat and connectivity, including installing fish ladders and installing baffles around culverts. These types of projects are important for increasing salmon populations by reducing barriers to migratory pathways, but they do not necessarily address habitat conditions that contribute to diversity or abundance of other stream biota. The main mechanism through which these lower intensity, migration-focused projects may serve as umbrella interventions for other taxonomic groups is through eventual ecosystem-scale effects of the Pacific salmon returns, for example, through effects on resource provisioning and the nutrient cycle (Walsh et al. 2020b), should the projects have their intended benefits. On the other hand, projects that restore stream habitat rather than only restoring connectivity for fish movement have been shown to affect both the invertebrate assemblages responsible for organic matter processing and decomposition itself (Muotka et al. 2002, Frainer et al. 2018). Habitat restoration often falls under the intensively assisted category, requiring expensive engineering solutions. Thus, although removal of the barriers that currently render many kilometers of stream length inaccessible to salmon (Finn et al. 2021) is a winning strategy from a cost–benefit perspective, salmon may be more effective umbrella species (e.g., over shorter timescales) for biodiversity and ecosystem processes when their protection motivates habitat restoration. We suggest that as barriers are removed and salmon can increasingly regain access to urban streams, more-intensive habitat restoration approaches should have a role in ensuring habitat quality for not only salmon but also invertebrates and microbes that play key roles in stream ecosystem function.

Another related reason that salmon may not be effective umbrella species in our study is the location of restoration projects within the stream network. Several sites with the highest restoration intensities were stream outlets. Restoration of physical structure and downstream reaches is an essential step in restoring salmon access to watersheds, but this does not address the broader-scale anthropogenic impacts happening upstream and propagating downstream in urban watersheds, thus potentially limiting the positive effects of restoration on stream biodiversity. Elsewhere, research has shown that restoration efforts at the headwaters and in small watersheds have the highest impacts on ecosystem processes because benefits from restoration efforts in downstream reaches may be overwhelmed by cascading effects from upstream (Levi and McIntyre 2020). On the other hand, Vancouver's development pattern, where steep slopes and provincial land ownership prevents urbanization at the top of watersheds, presents a unique context for evaluating the scale of urbanization and restoration impacts. In the study area and in other cities with similar topography, headwaters are rarely urbanized, which justifies the restoration focus on downstream reaches.

Finally, a 3rd possible explanation for the lack of restoration effects on decomposition is that even if conservation of Pacific salmon does protect biodiversity, the degree to which this protection promotes ecosystem functioning may be limited in the absence of a strong, positive relationship between biodiversity and ecosystem function or if restoration does not benefit taxa that contribute to decomposition. Restoration could support ecosystem functioning through abiotic pathways alone; however, biodiversity also often promotes organic matter decomposition (Handa et al. 2014). The relationship between biodiversity and decomposition in freshwater ecosystems is not straightforward—abiotic and biotic conditions mediate the strength and slope of diversity–decomposition relationships (Lecerf and Richardson 2010, Beaumelle et al. 2020). For example, a recent study considering the effects of land use on both freshwater biodiversity and cotton strip decomposition found strong effects on the former but not the latter (Koivunen et al. 2023), indicating a nonlinear relationship between biodiversity and decomposition.

Our conclusions about whether Pacific salmon are effective umbrella species for stream ecosystems are likely related to the differing approach of our research compared with past work. We assessed the effectiveness of the umbrella species concept where a restoration scheme has actually been applied as opposed to many studies that assessed the diversity of co-occurring species across the umbrella species' existing range without considering variation between conserved and unconserved habitats. As habitat loss continues globally, it will be important to understand whether the umbrella species concept works where habitat is already degraded or if the primary utility of the concept is to prevent the conversion of intact habitat.

Although Pacific salmon may not have served as umbrella species in the context of decomposition in our study, their presence in urban streams still has many benefits. As charismatic species, Pacific salmon help people connect with the natural world and generate interest in habitat protection and restoration, which is likely to have long-term benefits for ecosystems and their inhabitants far beyond the scale of a local restoration project. It is also possible that restoration benefits for ecosystem function simply take a long time to manifest because of differing recovery times of abiotic and biotic components within the ecosystem; therefore, temporal dynamics are important to consider in further research. Future studies should incorporate biodiversity monitoring to understand whether the effects of restoration are mediated by biological communities that co-occur with the potential umbrella species. In a world where funding for environmental conservation and restoration is limited, there is an urgent need to prioritize actions that provide benefits to more than just 1 taxonomic group. Stream restoration is a key strategy for safeguarding Pacific salmon (Walsh et al. 2020a) and could provide widespread benefits for biodiversity and ecosystem processes if we can identify which particular restoration interventions are effective at promoting ecosystem functioning.

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Author contributions: ARW and CJL conceived the ideas, designed the methodology, and collected the data. ARW performed initial analyses and wrote the 1st draft of the manuscript. CJL performed additional statistical analyses. Both authors revised the manuscript and gave final approval for publication.

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Data and code availability: Data are publicly available on Figshare at https://figshare.com/s/8e08ae22881ec370e6f7. Code used to perform analyses and generate figures is available on GitHub at https://github.com/chelseajlittle/salmon-stream-decomp.

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