The relative importance of abiotic, biotic, and spatial factors in structuring the stream macroinvertebrate metacommunity in a temperate rainforest

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Abstract

1. We investigated how local abiotic and biotic variables versus regional spatial and dispersal variables influenced the structure of a stream macroinvertebrate metacommunity (multiple assemblages linked by dispersal), and whether this varied by dispersal mode.
2. We collected 143 benthic macroinvertebrate samples and associated abiotic and biotic data related to local habitat and species interactions across three river basins on the Olympic Peninsula (Washington, USA). We assessed macroinvertebrate assemblage composition in relation to environmental and spatial variables using mixed effects linear regression and partial redundancy analysis.
3. We found that water temperature, substrate grain size, bankfull width, and salmonid density were the local factors significantly associated with macroinvertebrate assemblage composition. Local variables explained 19.7% of the variation in taxonomic composition, while overland spatial distance explained 7.4% ($p = 0.014$). Local variables were more important for aerially dispersing taxa than for aquatically dispersing taxa.
4. Our results indicated that local abiotic and biotic variables acted together with dispersal and overland distance to shape the macroinvertebrate metacommunity composition across river basins. The relative importance of local habitat variables and spatial processes depended on the dispersal mode, with evidence of dispersal limitation for aquatic dispersers.
5. Our study underscores the role of dispersal in influencing the effect of the local habitat on metacommunity organization, even at small spatial scales. We emphasize the need to apply metacommunity theory to stream management, such as incorporating distance between reaches and organismal dispersal traits in bioassessment models.
6.

1. Introduction

Stream macroinvertebrates are vital players in stream ecosystems, as they form critical trophic links by converting aquatic microbes and detritus to dissolved organic matter, fine particulate organic matter, and living biomass, which allows for the release and transfer of nutrients and energy through the food web (Covich et al. 1999; Macadam and Stockan 2015). Benthic macroinvertebrates also serve as prey for stream vertebrates, including fish, salamanders, and birds (Covich et al. 1999; Hamidoghli et al. 2014) and act as ecosystem engineers via bioturbation (Mermillod-Blondin 2011; Statzner 2012). Many macroinvertebrate taxa are highly sensitive to environmental change (Hauer and Lamberti 2006) and are thus often used as bioindicators of stream ecosystem health (Li et al. 2010).

The aquatic and riparian environment can shape stream macroinvertebrates through complex and often interacting processes that impact macroinvertebrate food availability, habitat, and mortality. For example, the amount of periphyton available as a food source for scraper-grazer and collector-gatherer macroinvertebrates can be limited directly by water velocity and temperature (Rasmussen et al. 2011; Wang et al. 2018; Toskey et al. 2024) as well as indirectly by canopy cover through shading (Elsaholi 2011). Water temperature, also tightly linked with elevation and latitude, directly controls macroinvertebrate enzymatic rates, with colder streams generally hosting less diverse assemblages composed of longer-lived (i.e., univoltine) organisms. (Bonacina et al. 2023). Substrate composition can impact habitat quality through controlling the amount of interstitial space available as refuge from predators and scour (Natsumeda and Iguchi 2019), with larger-sized substrate (i.e., pebbles and cobbles as opposed to fine sediments) generally associated with greater availability of refuges, as well as food resources and dissolved oxygen (Pereira et al. 2017).

In addition, hydrologic conditions have a close but complex relationship with macroinvertebrate assemblages (Álvarez-Cabria et al. 2010); current velocity, associated with gradient, stream size, and channel unit type, can limit food availability through scouring of benthic biofilms (Townsend et al. 2012) and can dislodge and wash macroinvertebrates downstream (Collier and Quinn 2003), although the current also delivers dissolved oxygen and food (i.e., seston) to filter feeding macroinvertebrates (Lancaster and Downes 2010). Predators, like insectivorous fish and birds, are a source of mortality for macroinvertebrates. Their association, however, may not necessarily be negative, as a high abundance of macroinvertebrates is potentially able to sustain a high abundance of predators (Leeseberg and Keeley 2014). Predator abundance is also the result of a complex group of interacting ecological relationships and can be closely tied, either directly or indirectly, to all the aforementioned environmental variables, mediated through their invertebrate prey.

These local abiotic and biotic environmental relationships do not act alone, but are joined by broader-scale regional processes to influence macroinvertebrate assemblages (Vannote et al. 1980; Vinson and Hawkins 1998; Heino 2013a; Brown et al. 2018). According to metacommunity theory (Hubbell 2001; Leibold et al. 2004), the composition of an assemblage or community (i.e., the group of organisms that occur together in a single location) can vary strongly between locations (Schmera et al. 2017) and is likely driven by a combination of local (i.e., abiotic habitat suitability and biotic species interactions) and regional (i.e., habitat connectivity and dispersal ability) mechanisms (Leibold et al. 2004; Vellend 2010). These local and regional mechanisms act in conjunction with environmental and demographic stochasticity (Hubbell 2001; Vellend et al. 2014), the latter of which tends to be high in disturbance-shaped ecosystems like streams (Haghkerdar et al. 2019). Exploring the relative roles of local abiotic and biotic variables versus regional spatial and dispersal variables based on metacommunity theory is particularly suited to streams, given their hierarchical structuring from relatively isolated headwaters to highly connected downstream reaches (Heino and Mykrä 2008; Brown and Swan 2010; Heino 2013a; Altermatt et al. 2013; Schmera et al. 2018).

The study of stream ecology has been heavily shaped by a suite of conceptual frameworks, including the River Continuum Concept (RCC) (Vannote et al. 1980; Brown and Swan 2010; Schmera et al. 2018). This framework considers rivers as continuous, linear gradients of increasing size and flow and connects stream size to taxonomic and functional community structure, determined largely by species sorting (i.e., environmental factors act as filters, allowing for survival only at environmentally suitable sites). More recently, a new class of spatially focused paradigms, including the network position hypothesis (NPH), has emerged and draws strongly from the principles of metacommunity ecology. These dendritic network perspectives consider river systems as branching collections of headwater streams connected by larger mainstem channels and, like metacommunity theory, emphasize the roles of both dispersal and environmental heterogeneity in determining species distribution (Fagan 2002; Brown and Swan 2010; Cañedo-Argüelles et al. 2015; Tonkin et al. 2018).

Factoring in this hierarchical structuring of rivers and metacommunity theory, the NPH predicts that environmentally heterogeneous and isolated headwater communities should be influenced chiefly by local abiotic and biotic variables, and downstream communities should be controlled by a combination of local abiotic and biotic variables as well as regional spatial and dispersal processes (Brown and Swan 2010; Schmera et al. 2018). Within streams, benthic macroinvertebrate assemblages are useful for studying the role of local variables (Southwood 1977) and dispersal (Li et al. 2021a), given their high taxonomic diversity and varying dispersal modes and abilities (e.g., weak aquatic versus strong aerial dispersers). Aquatic dispersal is theoretically high enough in well-connected habitats to allow species tracking of environmental gradients (i.e., environmental filtering) but potentially insufficient to reach more isolated habitats, which would cause dispersal limitation (Heino and Peckarsky 2014; Heino et al. 2015b). In contrast, aerial dispersal (the primary mechanism of dispersal of most adult aquatic insects, which are typically winged and terrestrial at this stage) is theoretically high enough to allow species to reach relatively isolated headwaters and thus track local abiotic and biotic gradients (i.e., species sorting), but in well-connected mainstem reaches may dominate local processes (i.e., mass effects, whereby high dispersal overrides species sorting, allowing species to survive in otherwise poorly-matched habitat), which can mask species-environmental relationships (Heino and Peckarsky 2014; Heino et al. 2015b).

While many recent studies on macroinvertebrate ecology have taken this metacommunity context into account (Winemiller et al. 2010; Padial et al. 2014; Heino et al. 2015a), we believe the majority of these studies have overlooked elements of the aquatic food web. Quantifying organisms in the aquatic food web at trophic levels both lower and higher than macroinvertebrates (i.e., primary producers such as algae and predators such as insectivorous fish) is key to understanding the local-level species interactions that shape macroinvertebrate assemblage composition. Increasingly, freshwater ecologists find that even for small streams in relatively densely canopied second-growth forests, primary production plays a vital role in shaping benthic macroinvertebrate assemblage composition and abundance (e,g., Entrekin et al. 2020). Yet most stream macroinvertebrate metacommunity ecology studies have focused exclusively on abiotic variables, omitting biotic variables and underlying species interactions, which can underlie important mechanisms of metacommunity assembly (Heino 2013b).

In this study, we aimed to deduce the relative importance of local abiotic and biotic factors versus regional (dispersal mode, overland distance, and reach position) factors in structuring benthic macroinvertebrate taxonomic and functional trait assemblage compositions across multiple watersheds in a temperate rainforest. We used abundance and trait data of macroinvertebrates and corresponding environmental data and geographical coordinates to test the following set of questions and hypotheses:

(i) Question 1: How do macroinvertebrate taxonomic and functional diversity and abundance vary with the local abiotic and biotic habitat variables in temperate rainforest streams, and which local abiotic and biotic habitat variables are the most important in explaining macroinvertebrate assemblage composition?

Hypothesis 1: Macroinvertebrate taxonomic diversity and abundance will increase with substrate grain size, bankfull width, distance from headwaters, canopy cover, sestonic algal biomass, benthic algal biomass, and salmonid (predator) biomass and decrease with water temperature, gradient, maximum flow speed, and elevation. Macroinvertebrate assemblage composition will change with the same above variables linked to physical habitat quality and species interactions.

(ii) Question 2: To what extent is the benthic macroinvertebrate metacommunity in a temperate rainforest structured by local abiotic and biotic habitat variables versus regional (spatial and dispersal) variables?

Hypothesis 2: Macroinvertebrate metacommunity composition is driven by a combination of local (abiotic and biotic) and regional (dispersal and overland distance) factors, with local factors explaining more variance than regional factors.

(iii) Question 3: Does the relative role of local habitat versus spatial variables vary by dispersal mode (i.e., aerial versus aquatic dispersers)?

Hypothesis 3: For aquatic dispersers, spatial factors explain more of the variance in metacommunity composition, indicating dispersal limitation. For aerial dispersers, local abiotic and biotic factors explain more of the variance in metacommunity composition, indicating sufficient dispersal to track environmental variability.

2. Methods

2.1 Study Site

Our study was conducted in the Olympic Experimental State Forest (OESF; (Minkova and Foster 2017) on the western side of the Olympic Peninsula in Washington state, USA (Figure 1). The OESF is a predominantly second-growth temperate rainforest in the Pacific Coastal Ecoregion and typically receives annual precipitation ranging from 203 to 355 cm, most of which occurs as rainfall during the winter (Naiman et al. 2000). We collected data from 29 reaches along 16 small streams (generally two reaches per stream) of orders one through three across three river basins. The stream channels were highly incised and bordered by riparian tree stands dominated by 30- to 50-year-old Red alder (*Alnus rubra)*, Western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), Douglas fir (*Pseudotsuga menziessii*), Pacific silver fir (*Abies amabilis*), and Western redcedar (*Thuja plicata*) (Washington State Department of Natural Resources (WADNR) 1997). The small streams sampled within this study host a fish community composed of Coho salmon (*Oncorhynchus kisutch*), coastal cutthroat (*Oncorhynchus clarkia clarkii*), steelhead/rainbow trout (Oncorhynchus *mykiss*), lampreys (*Lampetra* spp.), and sculpins (*Cottus* spp.) (Martens et al. 2019).

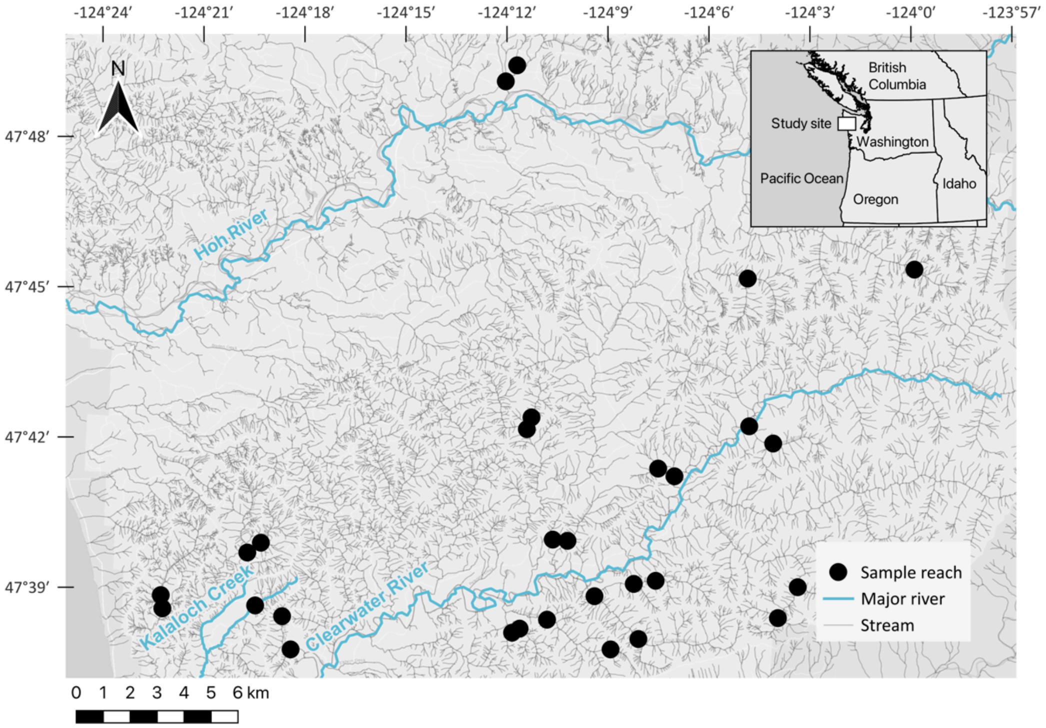

Fig. 1 Map of the sampling reaches and the stream network spanning three river basins in the Olympic Experimental State Forest in Washington State, USA

2.2 Field Data Collection

We collected samples and made measurements of biotic and abiotic variables linked to the aquatic food web, microhabitat, and position in the stream network along each stream reach. We collected biotic samples in each stream reach from downstream to upstream, including salmonid biomass, sestonic algae, benthic macroinvertebrates, and benthic algae (Figure 2). We measured sample-level abiotic (approximately 10-cm microhabitat scale) variables with each benthic macroinvertebrate sample, including canopy cover and water temperature (Figure 2). Simultaneously and alongside the salmonid sampling, we measured reach-level abiotic variables, including median substrate grain size, bankfull width, elevation, gradient, and maximum water velocity (Figure 2). We selected this suite of biotic and abiotic factors based on our literature review and opportunistic sampling constrained by resources and personnel.

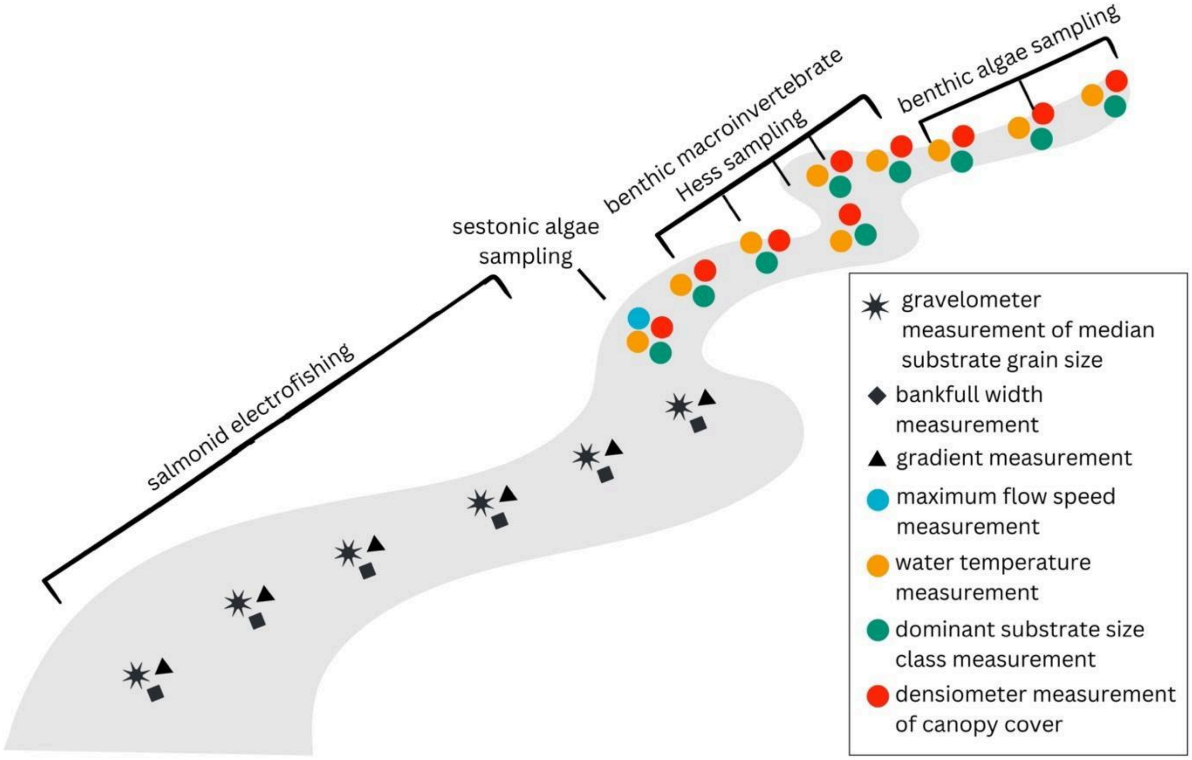

Fig. 2 Diagram of field sampling of the local abiotic and biotic variables in an example stream reach

We deployed block nets at the upstream and downstream ends of a 100 m stream length to estimate live salmonid biomass. We then conducted multiple-pass removal electrofishing with at least three passes and analyzed within the program Capture (Martens and Connolly 2014). Lengths and weights of individual fish were recorded, and the average weight per species and life stage was used to convert the estimated number of fish to biomass. Approximately 10 m upstream of the electrofishing reach, we sampled sestonic algae by filling two 1-L amber bottles in the stream thalweg (Parker 2020). Approximately 10 m farther upstream, we used a Hess sampler (mesh size = 363 µm, diameter = 0.33 m) to collect five samples of benthic macroinvertebrates, each sample from a different riffle, which we then rinsed through a 363 µm mesh sieve and preserved in the field with 70% ethanol (Parker 2019). We collected each of three to five composite benthic algal samples approximately 10 m upstream from the last benthic macroinvertebrate sample by removing periphyton with a brass-bristled brush scrubbed over a 24- × 36-mm area demarcated by a slide frame from three representative cobbles from one riffle and then rinsing with deionized water into an amber bottle (Parker 2020). We placed the sestonic and benthic algal samples in a cooler with ice until they were filtered approximately two to eight hours after collection.

In association with each benthic macroinvertebrate sample, we measured canopy cover using a hand-held densiometer (Lemmon 1956), water temperature using an encased thermometer (Parker 2019), and dominant substrate size class using a ruler to measure the coarse categories of clay (0.001 – 0.003 mm), silt (0.004 – 0.062 mm), sand (0.063 – 2 mm), pebble (2.1 – 64 mm), cobble (64.1 – 256 mm), boulder (> 256 mm), and bedrock (Parker 2019). Every 20 m along the 100 m electrofishing reach, we measured median substrate grain size using a gravelometer in intervals along a transect, bankfull width (the width of the stream when the channel is full), and gradient by dividing the difference in surface water elevation by the horizontal watercourse distance. We also measured elevation and latitude/longitude using a handheld Global Positioning System (GPS) unit and maximum water velocity by placing a propeller current meter in the thalweg at a narrowing of the stream (Minkova and Foster 2017).

2.3 Laboratory Analyses

Upon return from the field, we filtered all algal samples through GF/F filters and then froze the filters. Within approximately 24 hours of collection, we poured each benthic macroinvertebrate sample over a 363-µm sieve and transferred it to a bottle with a final concentration of 95% ethanol and 5% glycerol to ensure long-term preservation. Within one to seven days of field collection, we extracted the light pigments from the sestonic and benthic algal samples by placing the GF/F filters into 90% acetone and freezing for 24 hours. After extraction, we brought samples to room temperature and then measured chlorophyll-*a* (chl-*a*) concentration, as a proxy for algal biomass, with a fluorometer using the acidification method (Arar and Collins 1997). Finally, within three years of collection, we used a dissecting microscope (10× magnification) to enumerate and identify all benthic invertebrates to the lowest feasible taxonomic level, usually genus, following a dichotomous key (Merritt et al. 2019).

2.4 Data Analysis

2.4.1 Calculation of metrics

We calculated three metrics from our benthic macroinvertebrate samples that we assessed in relation to environmental and spatial variables: i) taxonomic biodiversity and abundance, ii) functional habit (i.e., movement/existence mode; sprawler, swimmer, clinger, and burrower), and iii) functional feeding group (i.e., collector–gatherer, collector–filterer, scraper/grazer, shredder, and predator) composition (Merritt et al. 2019). To obtain one value for each reach-level metric, we averaged the values of each reach-level environmental variable that we measured multiple times per reach (i.e., sestonic algal chl-*a* concentration, benthic algal chl-*a* concentration, median substrate grain size, bankfull width, elevation, and gradient). We included the variable river basin to capture any geologic or hydrologic variation specific to each of our three river basins. We then created a matrix of overland (Euclidian) distances between reaches with the distm function of the 'geosphere' package (Hijmans 2021). We considered only Euclidian distance, as not all our sample reaches were connected via the watercourse, given that the sample reaches were spread across three separate river basins. Moreover, Euclidian distance may be more relevant than watercourse distance to the dispersal pathways of macroinvertebrate assemblages dominated by macroinvertebrates with winged adult stages (i.e., insects) (Kärnä et al., 2015; Li et al., 2021;

Tonkin et al., 2018; but see Hou et al., 2022). To confirm that our sampling adequately represented the riffle-dwelling benthic macroinvertebrate assemblage at each reach and in the whole study system, we created a species accumulation curve using the specaccum function and estimating the actual size of the taxon pool and using the specpool function, both in the 'vegan' package (Oksanen et al. 2022). We performed all statistical analyses in R (R Core Team 2022), created plots using the 'ggplot2' package (Wickham 2016), and used $\alpha = 0.05$ as the significance threshold.

2.4.2 Abiotic and biotic drivers of macroinvertebrate biodiversity and abundance

To assess benthic macroinvertebrate taxonomic biodiversity and abundance metrics in relation to environmental variables (Hypothesis 1), we created a linear mixed effects regression model for each of the following diversity and abundance metrics: taxa richness, Shannon's H biodiversity (Magurran 2004), Pielou's evenness (Pielou 1966), and abundance using the lme function of the 'nlme' package (Pielou et al. 2022). We log-transformed macroinvertebrate abundance so that the model residuals were normally distributed, and we mean-centered all fixed effects in each model to account for minor multicollinearity caused by including interaction terms (Iacobucci et al. 2016). In the global model, we included each of the eleven environmental variables and the interactions between average benthic algal chl-*a* concentration and canopy cover, sestonic algal chl-*a* concentration and canopy cover, and sestonic and benthic algal chl-*a* concentrations as fixed effects. We included only these three specific interactions based on a priori hypotheses, rather than including all possible interactions to avoid overfitting the models. We also included reach nested within stream basin as random effects. As no variables were correlated at or above $r = 0.7$, we did not remove any variables due to cross-correlation (Figure S1). For each biodiversity and abundance metric, we compared second-order Akaike's Information Criteria (AIC_C) among all possible model iterations using the dredge function of the 'MuMIn' package (Bartón 2022). We then averaged all top-ranked models with $\Delta AIC_C \leq 2$ for each biodiversity and abundance metric (Zuur 2009; Grueber et al. 2011).

2.4.4 Abiotic and biotic drivers of macroinvertebrate assemblage composition

We determined the most important abiotic and biotic variables driving differences (Bray-Curtis dissimilarity) in macroinvertebrate assemblage composition (Hypothesis 2) using partial Redundancy Analysis (RDA). Partial RDA is an ordination technique that is a constrained (direct) gradient analysis based on linear regression that allows for partitioning out the variance in assemblage composition explained by spatial versus environmental (abiotic and biotic) predictor variables (Borcard et al. 1992; Cottenie 2005; Peres-Neto et al. 2006; Tuomisto and Ruokolainen 2006; Soininen 2014). For three partial RDAs, the response variables were composed of 1) Hellinger-transformed taxonomic count data, 2) untransformed functional habit group count data, and 3) untransformed functional feeding group count data. We used a Hellinger transformation on the taxonomic count data to down-weight the effect of rare species (Legendre and Gallagher 2001; Legendre and Legendre 2012). To model spatial autocorrelation and composition (representing the regional component of the explanatory variables) with linear predictors, we used Principal Coordinate Analysis of Neighbor Matrices (PCNM) (Borcard and Legendre 2002) of overland distances between reaches and retained the eigenvectors with positive eigenvalues. The local abiotic and biotic habitat variables formed the remainder of the explanatory variables. We assessed multicollinearity among local variables with the variance inflation factors, all of which were under 5. Using the rda function, we performed a partial RDA on all reaches and then selected the relevant abiotic and biotic variables to retain in the model with a forward selection procedure (Blanchet et al. 2008). We assessed the significance of each local variable with a permutation test using the function anova.cca on the partial RDA results (Legendre et al. 2011). These analyses used the 'vegan' package (Oksanen et al. 2022).

2.4.5 Metacommunity composition by dispersal mode

We assessed the compositional structure of taxa, which we separated into aerial dispersers (winged adults) and aquatic dispersers (unwinged adults) (Hypothesis 3) (Heino 2013b). For each partial RDA, the response variables were composed of Hellinger-transformed taxonomic count data. To estimate the portion of the variation in metacommunity composition explained by variation in local (abiotic and biotic) variables, we used the adjusted redundancy statistic (R^2_{adj}), which controls for the number of samples and explanatory variables (Peres-Neto et al. 2006).

3. Results

3.1 Environmental and taxonomic descriptive metrics

Of the eight abiotic and three biotic variables we measured across all reaches, distance from headwaters varied the most, and water temperature varied the least (Table S1). No correlation between abiotic and biotic variables exceeded $r = 0.70$ (Figure S1). Our 142 benthic macroinvertebrate samples from 29 reaches across three river basins contained 114 taxa (Table S2). The top five most abundant taxa across all samples were *Baetis* spp., Chironomidae, *Cinygmula*, Oligochaeta, and Acari. These taxa comprised 19.7%, 17.0%, 15.1%, 9.1%, and 5.0% of the individuals in our samples, respectively.

3.2 Abiotic and biotic drivers of macroinvertebrate biodiversity and abundance

Taxonomic richness significantly increased with sestonic algal chl-*a* ($p < 0.05$; Table 1). Taxonomic diversity (Shannon's H) was not significantly related to any of the variables we tested ($p > 0.05$; Table 2). Pielou's evenness significantly increased with gradient ($p < 0.05$; Table 3).

Macroinvertebrate abundance significantly increased with bankfull width and sestonic algal chl-*a*, especially at low levels of canopy cover ($p < 0.05$; Table 4, Figure S2). Sestonic algal chl-*a* concentration had the greatest effect size, about 1.5 times each effect sizes of i) bankfull width and ii) the interaction of sestonic algal chl-*a* concentration and canopy cover (Figure S3).

Table 1. Taxonomic richness model-averaged estimates of fixed effect coefficients and associated p-values based on 142 samples from 29 reaches spanning three river basins on the Olympic Peninsula in Washington state, USA, in 2020.

Local variable	Coefficient	p-value	
Sestonic algal chl-*a* concentration	129.59	0.013	*
Bankfull width	0.29	0.443	
Canopy cover	-0.01	0.781	
Water temperature	-1.09	0.211	
Sestonic algal chl-*a* concentration x canopy cover	-1.68	0.633	
Benthic algal chl-*a* concentration	0.25	0.489	
Benthic x sestonic algal chl-*a* concentration	-5.34	0.647	

Gradient	-0.04	0.813
Substrate grain size	0.00	0.817
Salmonid biomass	0.02	0.834
Distance from headwaters	0.00	0.818
Maximum flow speed	0.00	0.945
Elevation	0.00	0.897

Table 2. Shannon's H model-averaged estimates of fixed effect coefficients and associated p-values based on 142 samples from 29 reaches spanning three river basins on the Olympic Peninsula in Washington state, USA, in 2020.

Local variable	**Coefficient**	**p-value**
Benthic algal chl-*a* concentration	0.00	0.838
Sestonic algal chl-*a* concentration	0.22	0.925
Canopy cover	0.00	0.439
Benthic x sestonic algal chl-*a* concentration	-1.13	0.331
Benthic algal chl-*a* concentration x canopy cover	0.00	0.352
Gradient	0.02	0.494
Elevation	0.00	0.845
Sestonic algal chl-*a* concentration x canopy cover	0.06	0.704
Salmonid biomass	0.00	0.798

Table 3. Pielou's Evenness model-averaged estimates of fixed effect coefficients and associated p-values based on 142 samples from 29 reaches spanning three river basins on the Olympic Peninsula in Washington state, USA, in 2020.

Local variable	**Coefficient**	**p-value**	
Sestonic algal chl-*a* concentration	-0.65	0.2416	
Canopy cover	0.00	0.226	
Gradient	0.02	0.006	*
Sestonic algal chl-*a* concentration x canopy cover	0.10	0.204	
Benthic algal chl-*a* concentration	0.00	0.779	
Benthic algal chl-*a* concentration x canopy cover	0.00	0.537	
Salmonid biomass	0.00	0.660	
Water temperature	0.00	0.776	

Table 4. Log of abundance model-averaged estimates of fixed effect coefficients and associated p-values based on 142 samples from 29 reaches spanning three river basins on the Olympic Peninsula in Washington state, USA, in 2020.

Local variable	**Coefficient**	**p-value**	
Sestonic algal chl-*a* concentration	19.66	< 0.001	*
Bankfull width	0.12	0.013	*
Canopy cover	0.00	0.947	
Gradient	-0.02	0.578	
Sestonic algal chl-*a* concentration x canopy cover	-1.22	0.003	*
Substrate grain size	0.00	0.567	
Benthic algal chl-*a* concentration	0.01	0.725	
Water temperature	0.00	0.871	
Maximum flow speed	0.00	0.878	
Elevation	0.00	0.884	

3.4 Abiotic and biotic drivers of macroinvertebrate assemblage composition

Overall, water temperature, substrate grain size, bankfull width, gradient, maximum flow speed, distance from headwaters, elevation, sestonic algal chl-*a* concentration, and salmonid biomass were retained as local predictors after forward selection of the taxonomic assemblage model (partial RDA, $p = 0.011$; Figure 3). Water temperature, substrate grain size, bankfull width, and salmonid biomass were significant predictors of taxonomic assemblage composition ($p = 0.012$, $p = 0.009$, $p = 0.004$, $p = 0.009$, respectively). In the functional habit group assemblage composition model, water temperature, substrate grain size, bankfull width, distance from headwaters, elevation, and salmonid biomass were retained as local predictors after forward selection. However, none were significant ($p > 0.05$). Similarly, in the functional feeding group model, water temperature, distance from headwaters, and salmonid biomass were retained as local predictors after forward selection, although none were significant ($p > 0.05$).

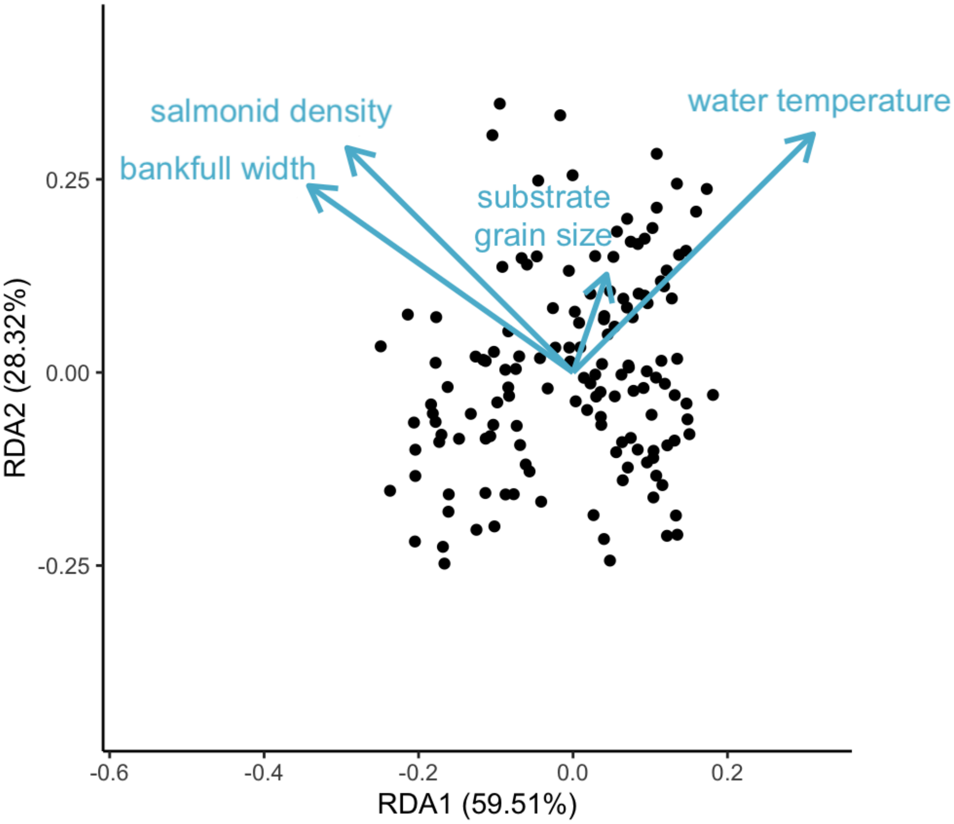

Fig. 3 Ordination plot of the constrained redundancy analysis (RDA) of macroinvertebrate metacommunity taxonomic composition at each reach with vectors of significantly correlated abiotic and biotic variables ($p < 0.05$). The horizontal axis is the first redundancy analysis axis (RDA1), and the vertical axis is the second redundancy axis (RDA2)

3.5 Relative roles of local abiotic and biotic versus spatial drivers of macroinvertebrate metacommunity composition

Variance in macroinvertebrate taxonomic metacommunity composition (i.e., taxonomic composition dissimilarity) was explained by both local variables and overland spatial distance, which explained 19.7% and 7.4% of the variation, respectively (model $p = 0.014$). The top five taxa driving the overall macroinvertebrate assemblage composition were *Cinygmula* (Heptageniidae), *Baetis spp.* (Baetidae), Chironomidae, Oligochaeta, and Leuctridae.

3.6 Metacommunity composition by dispersal mode

For aerially dispersing taxa, 21.1% of the variation in assemblage composition was explained by local abiotic and biotic variables, and 6.3% was explained by overland spatial distance (Euclidean distance; model $p = 0.009$) (Figure 4). The top five taxa driving the assemblage composition of aerial dispersers were *Cinygmula*, Chironomidae, *Glossosoma* (Glossosomatidae), Leuctridae, and *Ephemerella* (Ephemerellidae). For aquatically dispersing taxa, 7.4% of the variation in assemblage composition was explained by local abiotic and biotic variables, and 6.4% was explained by overland spatial distance (model $p = 0.001$) (Figure 8). The top five taxa driving the assemblage composition of aquatic dispersers were Oligochaeta, Acari, Collembola, Tricladida, and Harpacticoida.

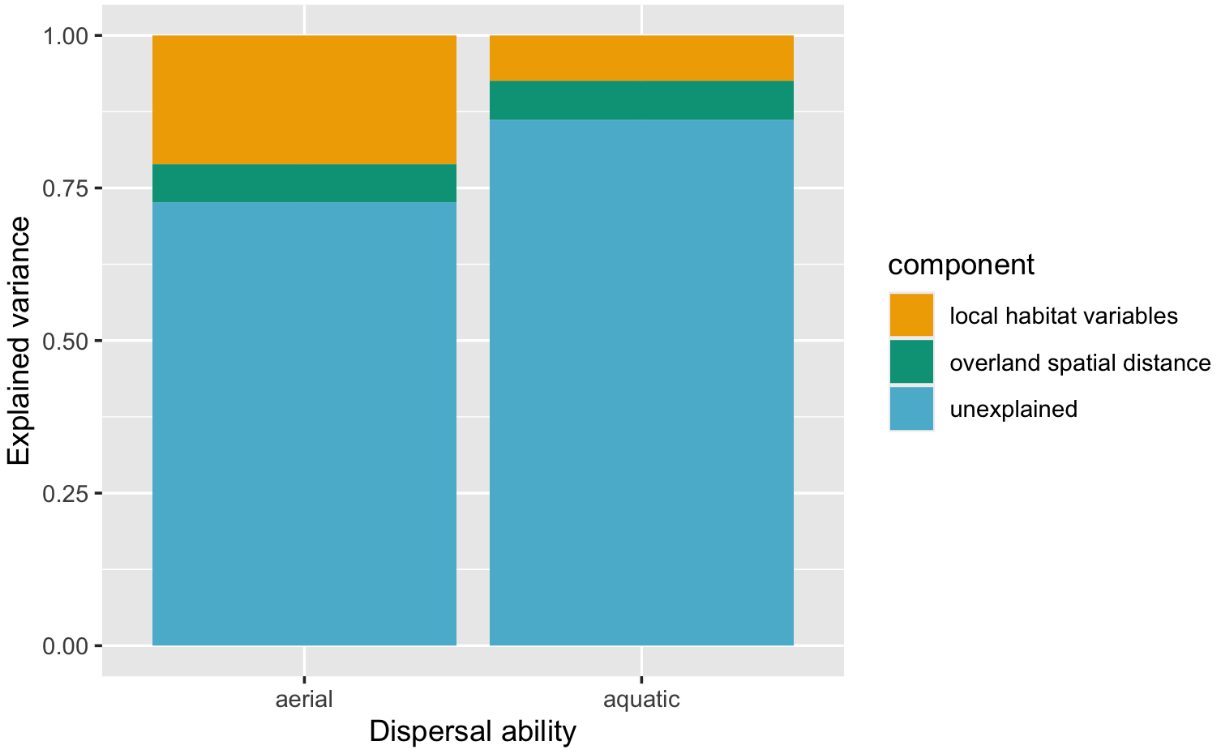

Fig. 4 Variance partitioning of the macroinvertebrate metacommunity composition for strong aerial and aquatic dispersers

4. Discussion

4.1 Abiotic and biotic drivers of macroinvertebrate biodiversity, abundance, and assemblage composition

We found that substrate grain size was a significant driver of macroinvertebrate assemblage composition, as we hypothesized and as has been found by others (Rezende et al. 2014; Leszczyńska et al. 2017). Substrate grain size has been shown to influence the flow velocity and shear stress, retention of organic material (Rabeni and Minshall 1977; Eedy and Giberson 2007), periphyton biomass, and oxygen saturation of stream bottoms (Coleman and Hynes 1970; Strommer and Smock 1989; Traunspurger et al. 2015; Majdi et al. 2017). Additionally, more physically complex stream substrate like cobble and pebble substrate serves as oviposition habitat (Hoffmann and Resh 2003), and refugia from flow (Winterbottom et al. 1997; Duan et al. 2008) and predation (Flecker and David Allan 1984; Ruetz et al. 2006), thereby hosting higher abundance and biodiversity of macroinvertebrates compared to less physically complex substrate (e.g., sand, silt, bedrock). Anthropogenic disturbance, including forest harvest (Gomi et al. 2005) that can increase the amount of fine sediment in streams may thus lead to a change in macroinvertebrate assemblage composition. Conversely, the low levels of instream wood, that can trap sediments, in these streams resulting from past timber harvest practices (Martens et al. 2019) may lead to continually increasing substrate grain size (Pollock et al. 2009), which may, in turn lead to a change in macroinvertebrate assemblage composition.

Reaches with a wider bankfull width had significantly higher macroinvertebrate abundance and different assemblage composition than reaches with a narrower bankfull width, as we hypothesized. Bankfull width, a proxy for the hydraulic conditions associated with stream size, has been shown to be a key determinant of benthic macroinvertebrate assemblage composition (Gasith and Resh 1999; Sandin and K. Johnson 2004; Bêche and Resh 2007; Power et al. 2008; Bêche et al. 2009). Such hydraulic variables, including current velocity, volumetric flow, and sheer stress, are critical evolutionary forces and influence macroinvertebrate morphologies and life histories (Nelson and Lieberman 2002). Bankfull width, especially in highly incised streams like those in our study, is also a control of light availability, with greater bankfull width corresponding with greater light availability (Savoy et al. 2021).

As light is an essential driver of photosynthesis, greater light availability allows for higher algal biomass, both in the water column (sestonic algae) and on the stream bottom (benthic algae) (Kiffney et al. 2004; Toskey et al.). Because algae are an essential food resource for macroinvertebrates, macroinvertebrate biomass is tied to light availability and thus canopy cover (i.e., a bottom-up process) (Kiffney et al. 2004; Kaylor and Warren 2017). This aligns with our findings of a significant correlation between macroinvertebrate assemblage composition and the interaction between canopy cover and each of sestonic and benthic algae. We also found a positive correlation between macroinvertebrate richness and abundance and sestonic algal biomass, which comports with the importance of bottom-up processes in structuring macroinvertebrate assemblages, in alignment with our hypotheses and the findings of others (Nery and Schmera 2016).

We found that the biomass of salmonids, major predators of macroinvertebrates in our study streams (Martens et al. 2019; Martens and Devine 2022), was significantly correlated with macroinvertebrate assemblage composition, as we hypothesized. Despite the metacommunity ecology theory that interspecies interactions (e.g., predation) are an important local process contributing to species distribution, most macroinvertebrate metacommunity ecology studies have not incorporated fish predation, either directly or indirectly (Heino 2013b). Some studies that have examined the role of fish in structuring stream macroinvertebrate assemblages have linked fish predation to changes in macroinvertebrate assemblage composition (Flecker and David Allan 1984; Nyström et al. 2001; Peckarsky et al. 2002; Moulton et al. 2010), particularly in functional feeding group composition, primarily through size-based diet selection (Peckarsky et al. 2002). Future research is needed to understand the mechanisms driving the relationship between assemblage or community composition, environmental heterogeneity, and predation.

Over 60% of the variance in macroinvertebrate assemblage composition in our study was left unexplained by the local (i.e., abiotic and biotic) and regional (i.e., spatial and dispersal) variables we measured. This could be due to the omission of important variables (e.g., watercourse distance, wind direction and speed, dissolved nutrients, coarse particulate organic matter, pH, dissolved oxygen, competition, and parasitism) or, per neutral theory (Hubbell 2001) perhaps could have resulted from high environmental stochasticity such as resulting from flood disturbances (Death 2010; Heino et al. 2015b). While no floods were observed by us during the field sampling for this study, the flow regimes typical of these perennial but small streams are characterized by high and variable flows in the late fall through spring and low and stable baseflow in the summer and early fall. Nonetheless, the high degree of unexplained variance was not surprising, as previous studies have found similar levels of unexplained variance (Heino et al. 2004, 2015b; Godoy et al. 2019).

4.2 Relative roles of local abiotic and biotic versus spatial drivers of macroinvertebrate metacommunity composition

Overall, our results indicated that local abiotic and biotic habitat variables act together with regional variables (i.e., dispersal traits and spatial variables) to contribute to, in part, benthic macroinvertebrate metacommunity composition across multiple river basins on the Olympic Peninsula (Figure 5). The greater importance of local variables compared to regional variables suggests that niche-based (local, environmentally driven) processes are a major driver of metacommunity assembly in stream macroinvertebrates. This is a similar finding to results from previous studies, despite considerable context-dependency (Cottenie 2005; Mykrä et al. 2007; Heino 2010; Heino et al. 2012, 2015b; Sarremejane et al. 2017). The greater significance of local variables compared to spatial variables emphasizes the importance of local habitat and highlights the potential of stream restoration to enhance altered macroinvertebrate communities in areas negatively impacted by anthropogenic activities.

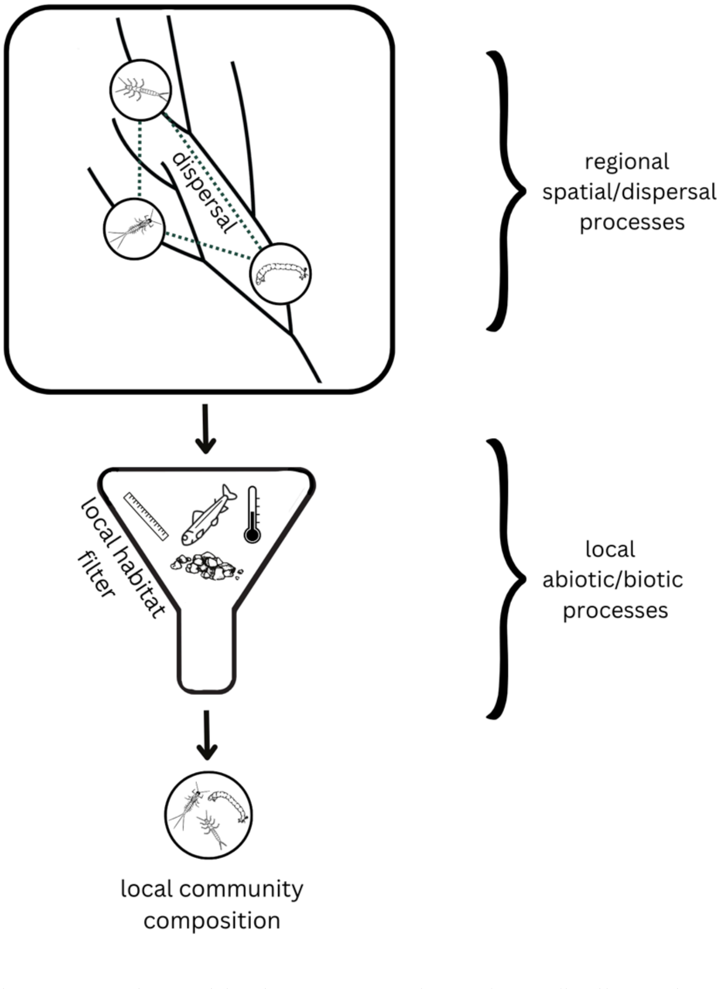

Fig. 5 A conceptual diagram and graphical representation of our findings that support the theory of spatial and dispersal processes as a filter of local assemblage composition, preceding the local

environmental filter. Regional spatial/dispersal factors explained 7.4%, and local abiotic/biotic factors explained 19.7% of the variance in macroinvertebrate assemblage composition.

4.2.1 Metacommunity composition by dispersal mode

The relative importance of local and regional variables in our study depended on the dispersal mode. Local abiotic and biotic variables explained greater variation in the metacommunity composition of aerial dispersers than aquatic dispersers. The greater environmental structuring of more strongly dispersing taxa (i.e., aerial dispersers) aligns with the metacommunity theory that environmental filtering (i.e., species tracking of environmental gradients according to habitat suitability) acts after dispersal. That is, our findings support the hypothesis that dispersal traits and spatial variables (e.g., landscape configuration and connectivity) modulate the effect of the local environment on metacommunity composition (Heino 2013b; Grönroos et al. 2013; Heino et al. 2015b; Kärnä et al. 2015; Heino et al. 2017; Tonkin et al. 2018; Li et al. 2019; Ptatscheck et al. 2020; Li et al. 2021a). It is important to note, however, that the aerially dispersing taxa in our study (e.g., Ephemeroptera, Plecoptera, Trichoptera, Diptera, Coleoptera) are generally known as environmentally sensitive organisms, and thus their more robust association with local variables may also be due to this sensitivity, rather than their ability to reach and therefore track environmental gradients (Jacobsen et al. 2003; Madsen et al. 2015). In contrast, the aquatic dispersers in our study (e.g., Oligochaeta, Acari, Collembola, Tricladida, Harpacticoida) are generally considered to be environmentally tolerant organisms, which could contribute to their weaker assemblage composition association with the local variables.

4.3 Field applications of metacommunity theory

Current bioassessment models are typically based purely on environmental filtering, a niche-based approach, and compare the community composition and diversity of a biological indicator (often benthic macroinvertebrates) from assessment sites to model predictions based on reference sites (Bonada et al. 2006). While there have been some arguments made that regional processes such as dispersal do not impact biological indices (Hawkins et al. 2000; Aroviita et al. 2009; Frimpong and Angermeier 2010), our study adds to growing evidence for the need to apply metacommunity theory to increase the accuracy of bioassessments (Heino 2013a; Siqueira et al. 2014; Heino et al. 2017; Cai et al. 2019; Cid et al. 2020; Li et al. 2021b; Liu et al. 2024). Omission of dispersal processes, including network structure, reach isolation, and dispersal ability, from bioassessments can bias the resulting assessment of ecological status. Mass effects can enable organisms to temporarily inhabit suboptimal habitats due to high dispersal rates, thereby altering the community composition such that it is not completely determined by local environmental conditions (Brown et al. 2011), which can cause overestimation of stream condition. Dispersal limitation, on the other hand, can prevent poorly dispersing organisms from reaching more isolated sites regardless of habitat suitability (Siqueira et al. 2014; Heino et al. 2017), which can lead to underestimation of habitat quality. Monitoring smaller regions (e.g., ecoregion or river basin) can aid in reducing the effect of dispersal limitation on biological indices thereby allowing for more direct assessment of habitat conditions (Heino 2013a). However, we found evidence of dispersal limitation within a relatively small spatial extent – a single forest across three drainage basins. This evidence of dispersal limitation even at a small spatial scale may imply that it may still be important to account for dispersal even at the smaller scales typical of many biomonitoring programs.

We recommend that connectivity as well as organismal dispersal ability be incorporated into bioassessment models. Distance between sites, such as watercourse and overland distance, can be included as an explanatory variable, much as we have done in this study. Organismal dispersal ability can be estimated based on mode of dispersal (i.e., aerial versus aquatic) as we have done, or can be more precise, using an open-access dispersal database that links aquatic invertebrate traits to dispersal ability (Sarremejane et al. 2020). Bioassessment practitioners can refer to existing frameworks (e.g., Cid et al. 2020, 2022; Patrick et al. 2021; Li et al. 2021b) to incorporate physical and organismal-based dispersal processes in addition to environmental filtering into predictive models.

4.4 Conclusions

We found that bankfull width was positively associated with stream macroinvertebrate abundance, gradient was positively associated with taxonomic evenness, and sestonic algal biomass was positively associated with abundance and diversity of macroinvertebrates. Water temperature, substrate grain size, bankfull width, and salmonid biomass were the main local abiotic and biotic factors related to macroinvertebrate assemblage composition. Overall, over twice as much of the variation in taxonomic assemblage composition was explained by local variables compared to overland spatial distance. The relative importance of local variables in explaining variance in macroinvertebrate assemblage composition was higher for aerially dispersing taxa than aquatically dispersing taxa. Our study provides further evidence of the importance of accounting for regional dispersal processes when assessing community composition such as for bioassessments, even at relatively small spatial scales.

Statements and Declarations

Author Contribution Statement

Conceptualization: Elsa K Toskey, Stephen M Bollens, Kyle D Martens; Methodology: Elsa K Toskey, Stephen M Bollens, Kyle D Martens, Peter M Kiffney, Gretchen Rollwagen-Bollens; Formal analysis and investigation: Elsa K Toskey, Stephen M Bollens, Kyle D Martens; Writing - original draft preparation: Elsa K Toskey; Writing - review and editing: Elsa K Toskey, Stephen M Bollens, Peter M Kiffney, Kyle D Martens, Gretchen Rollwagen-Bollens; Funding acquisition: Stephen M Bollens, Kyle D Martens, Gretchen Rollwagen-Bollens; Resources: Stephen M Bollens, Kyle D Martens, Gretchen Rollwagen-Bollens; Supervision: Stephen M Bollens

Competing Interests

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethics Approval

All Washington state and U.S. federal permitting requirements were met by the lead agency on this project (Washington State Department of Natural Resources).

Data Availability Statement

The data collected and analyzed in this study are available from the corresponding author upon reasonable request.

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