

Landscape attributes explain salmonid ecological neighbourhoods across a complex river network

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Abstract

1. Defining population neighbourhood boundaries provides a critical spatial framework for understanding ecological processes and informing species-specific conservation and restoration planning. The population neighbourhood boundary demarcates the total quantity of available habitat across life stages where specific ecological processes (e.g., breeding, foraging, migration) occur for all individuals within a population. For mobile species within dendritic freshwater networks, the population neighbourhood boundary can be defined by the upper limit of occurrence (ULO) of an individual within a population.
2. We sought to define contemporary neighbourhood boundaries across a complex river network in southwestern Washington State, U.S.A. by: (1) identifying ULOs for three anadromous fish (*Oncorhynchus* spp.); and (2) quantifying the relationship of the ULO with landscape attributes and local features for these species of profound social and ecological importance.
3. Extensive field surveys covering 669 river km across 2 years documented the ULOs for coho salmon (*Oncorhynchus kisutch*), steelhead trout (*Oncorhynchus mykiss*), and chum salmon (*Oncorhynchus keta*) as well as any local features, such as natural barriers, that influenced the ULOs. Generalised linear mixed models quantified the relationships between the ULOs and landscape attributes derived from remote sensing data.
4. We identified the ULO for 115 coho salmon terminal streams, 97 steelhead streams, and 57 chum salmon streams. Natural barriers determined the ULO in just 5%–16% of the terminal streams, depending on species. Landscape attributes associated with the ULOs varied among species; however, drainage area, elevation, and geology were important landscape predictors for all species. Models for each species had good to excellent predictive performance (percent correct classification: 78%–89%; AUC: 0.87–0.96).
5. We demonstrated that large-scale landscape attributes can accurately and consistently detect species-specific differences in population neighbourhoods across broad and diverse habitats. In comparison, local scale features (e.g., natural barriers) played a minor role in determining the neighbourhood boundaries in our study catchment. The modelled relationships between landscape attributes and the population neighbourhood provide a framework to guide conservation planning and predict benefits of habitat reconnections.

KEYWORDS

aquatic habitat, connectivity, distribution models, Pacific salmon, restoration planning

1 | INTRODUCTION

Understanding the factors that influence the distribution of species through time and across space is a fundamental goal of ecology and crucial information needed to effectively manage and recover populations. Many local populations of species occupy mosaic patches of habitat that shift in suitability over time and space (Brennan et al., 2019; Stanford et al., 2005). Connectivity among habitat patches provides access to new patches of habitat in the face of natural disturbance, facilitates (re)colonisation following local extirpations (Fausch et al., 2002; Hanski & Gilpin, 1991; Schindler et al., 2015), and increases the exploitation of heterogeneous habitats. In contrast, habitat fragmentation has been identified as playing a critical role in the loss of biodiversity (Haddad et al., 2015; Hanski, 2015) and extinctions (Crooks et al., 2017; Fagan, 2002; Ricciardi & Rasmussen, 1999) in both terrestrial and aquatic ecosystems. Community composition, trophic organisation, and species persistence and residency may also be significantly impacted due to habitat fragmentation (Wilson et al., 2016).

The documentation of species distribution and the processes that shape these distributions must be viewed at the spatial and temporal scale relevant to the study question (Wiens, 1989). Conservation and recovery goals are often at the population scale (U. S. Endangered Species Act, 1973), so it is important to understand the spatial extent over which ecological processes affect an entire population. Addicott et al. (1987) formalised the *ecological neighbourhood* concept as a generalised framework for scaling and defined this concept as the area of heterogeneous habitat patches an organism uses during an ecological process. An ecological neighbourhood is determined based on an ecological process, a time period relevant to that process, and an organism's activity during that period. This concept can be applied across spatial and organisational scales, providing a flexible approach for evaluating a broad array of ecological questions (Dunning et al., 1992). For example, the strength of predator-prey interactions can be evaluated based on the extent of spatial overlap between ecological neighbourhoods of relatively sedentary predators and a migratory prey population (DeAngelis & Petersen, 2001). In addition to delineating an ecological neighbourhood based on a single ecological process, ecological neighbourhoods that combine multiple ecological processes such as foraging, seasonal movements, and dispersal (sensu Ball, 2002; Bissonette & Adair, 2008) have been used to identify habitat for management and conservation. Following the approach by Antolin and Addicott (1991), which documented the colonisation and movement among local aphid populations (*Aphis varians* and *Macrosiphum valeriani*), we apply the ecological neighbourhood concept to the population scale, hereafter population neighbourhood, to capture the contiguous spatial extent over which complementary patches of habitat across a landscape are

exploited during various life stages and for specific ecological processes for all individuals within a population.

Boundaries that demarcate the population neighbourhood are composed of physical features in the landscape that influence the movement of organisms (Cadenasso et al., 2003). For obligate aquatic organisms, movement through dendritic river networks is bidirectional making them highly vulnerable to disruptions in connectivity (Cote et al., 2009; Fagan, 2002). In freshwater ecosystems, fragmented habitat, caused by anthropogenic activities, is a major cause of freshwater extinctions (Strayer & Dudgeon, 2010). Fragmentation of aquatic habitat resulting from dams or culverts limits dispersal rates and the ability of freshwater species to re-establish local populations, which reduces overall species viability (Gido et al., 2015). Over half of the world's large river systems are affected by dams disrupting natural flow regimes and stream connectivity (Nilsson et al., 2005). Species that move across fine (e.g., hundreds of metres between stream reaches) and coarse spatial scales (e.g., thousands of metres between waterbodies) are most susceptible to anthropogenic barriers such as species with diadromous life histories that migrate between freshwater and marine environments to complete their life cycle (McClure et al., 2008; McDowall, 1992).

Pacific salmon and trout (*Oncorhynchus* spp.) are anadromous fishes of significant ecological, cultural, and economic importance, and of conservation concern across most their range (Lichatowich, 2001). In response, public and private groups have been heavily engaged in freshwater habitat restoration to ameliorate salmonid population declines (Bernhardt et al., 2005; Katz et al., 2007). Knowledge of species distributions is critical to the restoration process; however, due to limited resources, time constraints, and broad distributions, conservation managers often do not have the capacity to monitor the entire extent of species distribution. Thus, modelling the distribution of species of concern can provide a useful tool for researchers and conservation managers to compensate for data gaps.

Finer scale (e.g., reach-scale) habitat attributes and site-specific variables (e.g., substrate size, riparian cover, stream depth, water velocity) are nested within landscape-scale drivers and shape the distribution and abundance of salmonids (Beechie et al., 2008; Roni & Quimby, 2005). The large body of work describing the relationship between the landscape and salmonid distribution is often focused on the reach scale (Chelgren & Dunham, 2015; Porter et al., 2000), is life stage specific (Anlauf-Dunn et al., 2014; Firman et al., 2011; Latterell et al., 2003; Steel et al., 2004), or applies large scale empirical relationships developed outside the area of observation (Bidlack et al., 2014; Burnett et al., 2007; Matter et al., 2018; Shallin Busch et al., 2011). The quantification of landscape attributes associated with species-specific freshwater population neighbourhood boundaries to capture the contiguous spatial template of a population across freshwater life stages is scarce in scientific literature

and management practice. The boundary of the freshwater population neighbourhood for anadromous fishes can be determined by identifying the upper limit of freshwater occurrence where all habitat downstream of the upper limit is used for rearing, spawning, or migration.

In this paper, we identify the landscape attributes that explain the population neighbourhood for three salmonid species in a large coastal catchment in southwestern Washington, U.S.A. We hypothesise that the relationship between specific landscape attributes and the population neighbourhood boundary will differ among salmonid species based on species-specific life histories and physiological abilities (Bjornn & Reiser, 1991; Quinn, 2018). Specifically, we predict that the population neighbourhood for coho salmon (*Oncorhynchus kisutch*) will be associated with the broadest range of values within landscape attributes among all three species because the autumn migration timing of adults is synchronised with seasonal precipitation that facilitates access to habitat, and their juvenile offspring use freshwater habitats extensively. Chum salmon (*Oncorhynchus keta*) will be associated with the most contracted range of values within landscape attributes among all three species due to the weaker swimming abilities of adults and the minimal use of freshwater habitats by juvenile offspring. The anadromous life history of steelhead trout (*Oncorhynchus mykiss*) will be associated with an intermediate range of values within landscape attributes compared to coho salmon and chum salmon; their spring migration timing occurs during a declining hydrograph that limits access to habitat but, similar to coho salmon, juvenile steelhead trout use freshwater habitats for extended periods. Our objectives are to test these predictions by (1) documenting the upper limit of occurrence (ULO) of coho salmon, anadromous steelhead trout, and chum salmon in a representative subset of streams; and (2) quantify the relationship between landscape attributes and the ULO for each focal species. Illumination of

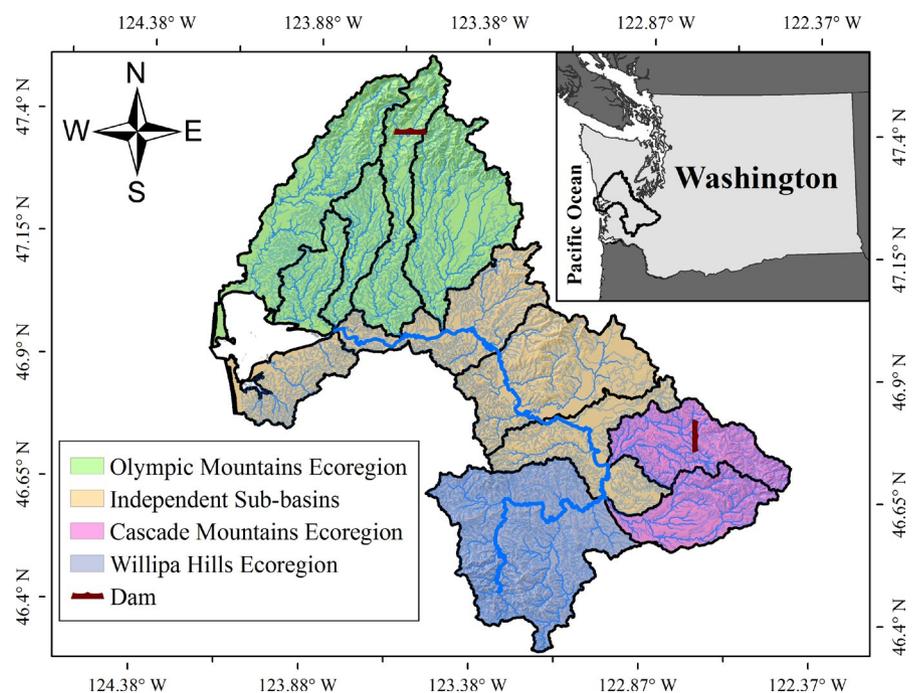
these relationships are the necessary first step towards identifying and prioritising streams for potential conservation or restoration in the basin. After describing the neighbourhood boundary–landscape relationship, researchers can extrapolate across the landscape to predict where species may benefit from habitat reconnection.

2 | METHODS

2.1 | Study area

The Chehalis River basin is a large, coastal catchment draining 6,889 km² in southwestern Washington state with a rain-dominated hydrology (Figure 1). The basin is comprised of multiple sub-basins nested within three bio-climatic ecoregions of unique geomorphological origin (Olympic Mountains, Cascade Mountains, and Willapa Hills). Extending over a stream network of c. 18,500 river kilometres, the main stem of the Chehalis River flows north from its headwaters in the Willapa Hills, abuts the Black Hills and Olympic Mountains, and continues west into Grays Harbor and the Pacific Ocean. The basin supports populations of five anadromous salmonid species—Chinook salmon (*Oncorhynchus tshawytscha*), chum salmon, coho salmon, steelhead trout, and coastal cutthroat trout (*Oncorhynchus clarkii*)—of economic, cultural and ecological importance, as well as having designated critical habitat for bull trout (*Salvelinus confluentus*) which occur as anadromous and resident forms and are listed as *threatened* throughout the coterminous U.S.A. under the U.S. Endangered Species Act (1973). None of the other salmonid populations present in the basin are listed by the U.S. Endangered Species Act. Freshwater habitat in the Chehalis River basin has been heavily impacted by a century of agriculture, forestry, and urbanisation along the associated landscape. Although the main stem river is free

FIGURE 1 Map of the Chehalis River basin, Washington, U.S.A. with the main stem Chehalis River bolded in blue. The bolded outlines demarcate the sub-basins of the Chehalis River used as random effects for modelling. The coloured ecoregions were used for model validation. The two major dams present on tributaries in the basin include the Wynoochee Dam (47.385346, -123.605597) that allows fish passage, and the Skookumchuck Dam (46.782845, -122.718612) that does not allow fish passage. The catchment boundary of the Chehalis River basin is bolded in black in the inset map of Washington State



flowing with no anthropogenic barriers, salmonid migration is impacted by large dams on two major tributaries and over 1,700 culverts that act as fish barriers (D. Barrett, Washington Department of Fish and Wildlife, personal communication).

2.2 | Stream survey site selection

The approach for selecting survey reaches for field data collection followed a multi-step process. Individual routes for each stream segment in the Chehalis basin ($n = 19,783$) were generated in ArcGIS (ESRI, Redlands, U.S.A.) from National Hydrology Dataset (NHD) High Resolution (1:24,000) segments (USGS, 2013), defined as a length of stream from its upstream origin to its merger with a downstream unique stream segment, and given a unique identification code (LLID). The entire set of stream segments were subjected to a series of filters in order to select a subset for field data collection (Figure S1). First, LLID stream segments were filtered for known or presumed fish use as described by the Statewide Washington Integrated Fish Distribution database (Washington Department of Fish & Wildlife, 2018), Water Resource Inventory Area stream catalogue (Phinney & Bucknell, 1975), and stream surveyor observations (C. Holt, Washington Department of Fish and Wildlife, personal communication). Next, LLID stream segments representing the terminal extent of each species' distribution—i.e., uppermost independent stream segment within a stream network, hereafter *terminal streams* (Figure S2)—were extracted from the entire database of LLID stream segments using ArcGIS geoprocessing tools and a Python script to obtain the candidate streams for field data collection. There was previously documented fish occurrence in 92% of the candidate terminal streams for coho salmon, and 85% of the candidate terminal streams for steelhead trout.

For coho salmon and steelhead trout, we implemented unstratified, equal probability Generalized Random Tessellation Stratified (GRTS) sampling in R (R Core Team, 2018) using the package 'sp-survey' (Kincaid et al., 2016) to select a subset of terminal streams that were a random, spatially balanced representation of all terminal streams (Stevens & Olsen, 2004). The GRTS draw was binned into four panels of 30 candidate streams plus an oversample draw of replacement streams to survey. We anticipated that a portion of terminal streams from the original panels could not be surveyed due to failing the selection criteria described below, and therefore the size of the oversample draw was based on a total survey stream sample size of 120 for each focal species and an estimated rejection rate of terminal streams in the original panels.

Prior to initiating field data collection, candidate streams from the statistical draw were removed if they did not meet criteria for logistical suitability, fish passability, and habitat quality. Logistical suitability included obtaining landowner permission and suitable access points to the survey sites. Fish passability included terminal streams above anthropogenic barriers that met the fish passage criteria established by the Washington Department of Fish and Wildlife (2009). Habitat quality was based on three metrics assessed during

field scouting surveys: existing riparian buffer, natural edge habitat, and substrate composition (Table S1). For each candidate stream that did not meet these criteria for habitat quality, we selected a replacement candidate from the oversample draw with comparable landscape attribute values and repeated the screening process on this replacement until a total of 120 streams were selected for field data collection.

Chum salmon data were obtained from a concomitant study occurring within the catchment (see Edwards & Zimmerman, 2018), in which data were collected from all terminal streams within three sub-basins that represented the area in the basin where the majority of chum salmon spawning activity occurs. Prior to including chum salmon field data in the analysis, each surveyed stream was subjected to the same screening process for anthropogenic barriers and habitat quality as the coho salmon and steelhead trout candidate streams.

2.3 | Field documentation of the upper limit of occurrence

Data on fish occurrence were collected over two field seasons from autumn 2017 to spring 2019. The majority of the coho salmon occurrence surveys were conducted between April and mid-May, with a few additional surveys conducted into July to complete the spatial coverage. This timeframe was selected to initiate sampling after an estimated 95% of coho fry have emerged, but before juvenile coho salmon redistribute to summer rearing habitat (Hartman et al., 1982; Winkowski et al., 2018). Steelhead trout occurrence surveys were conducted from May through mid-June. This timeframe was selected to be after peak spawning and during the time that steelhead trout redds, gravel nests where eggs are buried, were still readily distinguishable from the surrounding substrate (C. Holt, *personal communication*). Chum data were collected during November and early December to correspond with peak spawning activity within the survey frame (Edwards & Zimmerman, 2018).

Techniques to determine occurrence varied among species. Coho salmon occurrence was determined based on detection of coho fry during single-pass backpack electrofishing surveys of sampled streams. For habitat where backpack electrofishing was not an effective sampling technique (e.g., wetlands, beaver complexes), we deployed 44.5 × 24.1-cm 3.2-mm mesh baited minnow traps to determine coho occurrence. Steelhead trout occurrence was determined by visual observation of redds, test digs, adult live fish, or adult carcasses. Chum salmon occurrence was determined by visual observations of live adult fish or post-spawned naturally dead adult carcasses. Spatially continuous sampling was conducted in an upstream direction of each selected survey stream until the upper limit of occurrence was determined based on one of four criteria termination criteria defined in Table S2. The locations of ULOs identified in the field were geo-referenced and converted to a GIS shapefile for subsequent analysis.

The type of terminus (lateral, mid-channel, tributary junction; Figures S3–S5, respectively) and any natural barriers associated with each ULO location were documented. Terminus type described whether the ULO occurred mid-channel or was associated with any stream branching (i.e., lateral, tributary junction). Natural barriers encountered were classified as either permanent or transient barriers. Permanent barriers were geologically-formed physical obstructions present in the stream channel (e.g., cascade, falls) and transient barriers were natural obstructions likely to vary within and among years (e.g., beaver dam, log jam). Information on barriers was important to understand the prevalence of localised effects, not necessarily related to landscape features, that influenced the ULO for each species. Each documented ULO was classified as being associated with a natural barrier if the ULO was ≤ 200 m downstream from a complete natural barrier.

2.4 | Landscape attributes associated with ULOs

To address our second objective, we developed statistical models to analyse the location of the upper limit of occurrence for each focal species as a function of landscape attributes derived from remote sensing data. We selected drainage area (km^2), elevation (m), slope (%), mean annual precipitation (cm/year), geology type, and wetland presence as fixed effect covariates based on previous analysis and our own observations of the basin (Fransen et al., 2006). Sub-basin was based on U.S. Geological Survey Hydrological Unit Codes at the level 10-scale (USGS, 2018; Seaber et al., 1987) and was included as a random effect to account for some of the spatial autocorrelation across the study area (Table 1). Using ArcMap 10.6.1 (ESRI, Redlands, U.S.A.), landscape attributes were synthesised using a 10-m digital elevation model (DEM) to generate a flow accumulation and flow direction raster. Landscape attributes were assigned to c. 200 m reaches that were segmented from the National Hydrology Dataset High Resolution hydrology stream vector projected on NAD_1983_HARN_StatePlane_Washington_South_FIPS_4602_Feet coordinate system. A point was generated at the midpoint for each stream reach. The total contributing upstream drainage area for each midpoint, hereafter *drainage area*, was extracted from a flow accumulation raster. The elevation (m) for each midpoint was extracted from the 10-m DEM. Percent slope was calculated for each stream reach by extracting the elevation of the start and end point for each reach and dividing the difference in elevation of the total longitudinal length of each stream reach. Mean annual precipitation (cm/year), hereafter *precipitation*, was generated using the PRISM 30 raster (PRISM Climate Group, 2013) and down-sampled to match the 10-m DEM. Using the drainage area calculated for each midpoint, the mean precipitation was calculated from each pixel within the contributing drainage area for each point. Geology type for each stream reach was generated from a 1:100,000 WA DNR lithology raster. Each stream reach was associated with the dominant (>50%) overlapping geology type. Current wetland presence was generated from the USFWS National Wetlands Inventory dataset (USFWS, 2014).

The wetland type for each pixel was summarised as either present or absent with present indicating that wetlands covered greater than 50% of the stream reach area.

Each documented ULO was projected and joined with the appropriate 200-m stream reach independently for each species. All 200-m stream reaches upstream of the ULO were classified as outside the population neighbourhood (given the binomial response = 0) and an equal number of reaches downstream of the ULO were classified as inside the population neighbourhood (categorised as '1', see model development section). In order to determine the number of stream reaches inside the population neighbourhood for analysis, we calculated the total number of stream reaches outside the population neighbourhood, divided this number by the total number of ULOs, and used this calculation to select the number of 200-m stream reaches downstream from each ULO to be included in the analysis (Figure 2).

2.5 | Model development

For each focal species, we fit the data with a generalised linear model with a binomial distribution and logit link using the 'lme4' package in R (Bates et al., 2014). We selected the binomial distribution due to the binary response variable (within [1], or outside [0] the population neighbourhood) and because the analysis provided a probabilistic prediction of a stream reach being within the population neighbourhood. Drainage area was log transformed and each continuous covariate was z-score standardised to a mean of 0 and standard deviation of 1. We identified the appropriate model structure and examined collinearity among covariates, as described below. Before fitting the logistic regression model, we examined collinearity among the 10 covariates. One-way ANOVA tests were used to examine associations between categorical geology type and continuous covariates (Table S3). Point biserial correlation coefficients, a form of the Spearman correlation test, were calculated to examine correlations between wetland presence and the continuous covariates (Table S3). Cramer's V test was used to examine correlation between geology type and wetland presence (Table S4). Spearman correlation coefficients were calculated to test for correlation among the continuous covariates. For pairs of covariates with correlation coefficients >0.6 , one variable was dropped from the analyses. As a result, we removed wetted width and bankfull width prior to fitting the model given the strong correlation between these variables and drainage area (Table S5). For the chum salmon dataset only, there was a strong correlation between elevation and precipitation ($\rho = 0.69$) and between drainage area and slope ($\rho = -0.62$, Table S5). The elevation–precipitation and drainage area–slope correlations were not observed for the coho salmon and steelhead trout data because of the broader geographic scale of the catchment included in the analyses for these two species than that included in the chum salmon analysis. Elevation was retained in the chum salmon analysis (and precipitation removed) as elevation is a surrogate for multiple physical

TABLE 1 Fixed and random effect variables included in the global logistic regression mixed-effects models to predict coho salmon, steelhead trout, and chum salmon population neighbourhood boundaries in the Chehalis River basin, Washington

Variable	Type	Catchment processes/habitat condition	Expected biological response	Data source	References
Drainage area (km ²)	Fixed	Indicator of position in catchment and ecosystem processes; surrogate for stream size (related to flow accumulation).	Population neighbourhoods are positively related to drainage area.	10-m DEM	Vannote et al. (1980), Porter et al. (2000), Dauwalter and Rahel (2008)
Elevation (m)	Fixed	Surrogate for stream temperature and stream order (i.e. at higher elevations streams are more likely to be smaller and cooler); physical exertion required of fish to access stream reach.	Population neighbourhoods are negatively related to elevation.	10-m DEM	Dauwalter and Rahel (2008)
Stream channel slope (%)	Fixed	Energy transport (transportation and deposition of substrate); flow velocity positively related to stream slope.	Population neighbourhoods are negatively related stream slope; increasing stream slope limits accessibility and decreases habitat suitability.	10-m DEM	Bjornn and Reiser (1991), Dauwalter and Rahel (2008), Wenger et al. (2011)
Geology type	Fixed	Effects the quality and availability of substrate for spawning and influence of hyporheic flow.	The probability of stream reaches being within the population neighbourhood will vary depending on the geology type. Population neighbourhoods are positively related to alluvium, glacial and basalt geology as they are associated with good spawning gravel and hyporheic flows. Population neighbourhoods are negatively related to and sandstone geology as they are associated poor spawning gravel and hyporheic flow.	WA DNR	Montgomery et al. (1996), Gomi et al. (2005)
Wetland presence	Fixed	Provides good rearing habitat for juvenile salmonids but limited spawning habitat due to substrate being fine dominant. Influences storage and transport of organic matter, nutrients, heat energy, and chemical contaminants. Can be associated with groundwater upwelling and springs.	Population neighbourhoods are negatively related to wetland presence.	USFWS	Leibowitz et al. (2018)
Mean annual precipitation (cm/year)	Fixed	Influence flow regime, stream velocity, substrate deposition and scouring. Related to the accessibility of streams based on timing and magnitude of flow.	Population neighbourhoods are positively related to mean annual precipitation.	PRISM 30	Wenger et al. (2010)
Sub-basin	Random			USGS	Seaber et al. (1987)

Abbreviations: DEM, Digital Elevation Model; PRISM 30, PRISM Climate Group 30-year normal.

processes and had a greater effect size than precipitation in the preliminary analysis. Similarly, drainage area was retained (and slope removed) in the chum salmon analysis. The correlation coefficients among all other covariates were <0.6 and were retained as

predictor variables in the global model for each species (Table S5). Results of the correlation analysis did not change when ULO data associated with complete natural barriers were removed from the analysis.

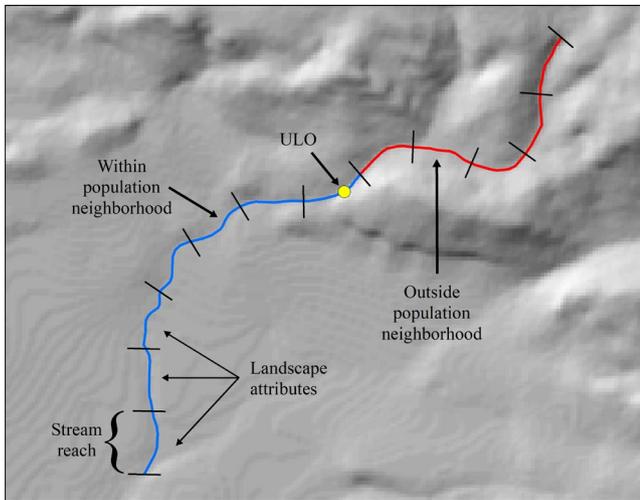


FIGURE 2 Conceptual diagram of a representative stream segment for modelling. The yellow dot represents the observed upper level of occurrence (ULO) that was projected onto the stream network. The black bars along the stream represent the reach breaks. The red stream reaches upstream of the ULO were distinguished as outside the population neighbourhood (binary response [0]), and the stream reaches downstream of the ULO were distinguished as with the population neighbourhood (binary response [1]). Landscape attributes were synthesised for each stream reach along the stream network

Multiple metrics were used to determine the best model structure including theoretical r^2 values, small sample size-corrected Akaike information criterion (AICc), and analysis of deviance using the *MuMIn* (Barton, 2009) and *stats* packages (R Core Team, 2018). We also confirmed greater support for a mixed effects model structure than the fixed effects model for coho salmon ($\chi^2 = 63.8, p < 0.001$), steelhead trout ($\chi^2 = 276.8, p < 0.001$), and chum salmon ($\chi^2 = 115.1, p < 0.001$), reflecting additional spatial influences on fish distribution that were not captured by the selected landscape variables.

We first examined a global model with the logistic function form:

$$P = e^u / (1 + e^u),$$

where, P = the probability of a stream reach being within the population neighbourhood, e = the natural logarithm of 1, and u = the linear model:

$$u = \alpha + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \text{Geo}_j + \text{Wet}_w + \alpha_k,$$

where α is the model intercept, β_n is the regression coefficient for standardised continuous landscape covariates X (drainage area, precipitation, elevation, and slope), Geo_j is the coefficient for geology type j , Wet_w is the coefficient for the binary category of wetland presence w , and α_k is the normally distributed random intercept coefficient for sub-basin k .

Natural barriers (e.g., waterfalls, cascades) can impede salmonid migration and influence distribution at the fine scale. In order to understand the effect of natural barrier on the ULOs in addition to large scale landscape attributes, we compared the model

performance and theoretical r^2 (Nakagawa et al., 2017) of the global model fit with the data set from all the streams surveyed for each species and with the data set that excluded streams where the ULO was associated with natural barriers. When the inclusion of streams with ULOs associated with natural barriers reduced the model performance, the truncated data set was used for the analysis (e.g., coho salmon) otherwise the full data set for each species was retained for analysis (e.g., chum salmon and steelhead trout, Table 2). In addition to the global model, we examined 12 reduced models for coho salmon and steelhead trout, and seven reduced models for chum salmon. Reduced models ranged in complexity from two to nine parameters (Table S7). We used the AICc to select the best possible model. Models with a ΔAICc value of < 4 were considered to have equivalent support and the most parsimonious model was selected for subsequent analyses.

2.6 | Model analysis

Cross validation was used to evaluate model performance of each candidate model based on the area under receiver operating characteristic curve (AUC) score and percent correct classification rate. AUC measured the model's ability to discriminate between the binary responses. AUC scores of > 0.7 were considered good and scores > 0.9 were considered excellent (Wenger & Olden, 2012). Percent correct classification was the proportion of stream reaches correctly assigned within and outside the population neighbourhood. Stream reach assignment was determined using an index cut-point probability of ≥ 0.50 for stream reaches to be considered within the population neighbourhood, which is a common cut-point used in the literature (Elith & Leathwick, 2009). Percent correct classification was calculated by fitting the model to 70% of the stream reaches after 30% of the streams reaches, stratified to maintain the same proportion of 1:0s present in the full dataset, were randomly withheld as a test data set. This process was repeated 200 times with replacement to determine the model's ability to correctly identify the ULO location.

Model performance of the best model for each species was further evaluated using the error distance between the observed ULO and the predicted ULO. The error distance was calculated by randomly removing 20% of the stream profiles (terminal streams) as test data, fitting the best model with the remaining data, and then predicting the probability that individual stream reaches along each stream profile in the test data set were within the population neighbourhood. The predicted ULO location for each stream profile in the test data set was the last consecutive upstream reach with a predictive value greater than the cut-point probability of 0.5. Negative error distances indicated that the model underpredicted the ULO and positive error distance indicated that the model overpredicted the ULO. This process was repeated 500 times with replacement to calculate the distribution of error distances.

Spatial transferability of the best model for each species was evaluated based on transferability among the four ecoregions

Species	Dataset	PCC ^a	AUC ^b	r ²
Coho	Full (n = 2,272)	0.74 ± 0.01	0.84 ± 0.01	0.71
	Truncated (n = 1,715)	0.78 ± 0.01	0.87 ± 0.01	0.73
Steelhead	Full (n = 4,569)	0.86 ± 0.01	0.93 ± 0.01	0.87
	Truncated (n = 4,334)	0.86 ± 0.01	0.92 ± 0.01	0.86
Chum	Full (n = 2,772)	0.89 ± 0.01	0.96 ± 0.01	0.91
	Truncated (n = 2,448)	0.89 ± 0.01	0.96 ± 0.01	0.92

^aPCC is the mean(±SD) percent correct classification from the 200 cross validation iterations.

^bAUC is the mean(±SD) area under the receiver operating curve from the 200 cross validation iterations; r² are theoretical values (Nakagawa et al., 2017).

identified within the Chehalis River basin. Each ecoregion comprised of stream drainages that had the same mountain range as the source of origin (Figure 1). Drainages that were not sourced from a major mountain range were grouped within an *independent* ecoregion. For coho salmon and steelhead trout, we used a 4-fold transferability assessment (Wenger & Olden, 2012) where stream reaches were non-randomly assigned to four groups based on common ecoregion. For these models, one ecoregion was randomly removed as a test data set and a mean AUC score was obtained for 200 iterations with replacement. For chum salmon, we used a 2-fold transferability assessment where streams were non-randomly assigned to two groups divided longitudinally across the study area. For these models, one ecoregion was non-randomly removed as a test data set to guarantee model convergence and an AUC score was obtained. For all species, only the fixed effects of the models were used to make the predictions for the cross validation since the random effects were spatially discrete.

We examined the effect size of each landscape attribute to determine the magnitude and direction of influence on the population neighbourhood for each species. For continuous variables, larger effect sizes with larger parameter coefficient values represented stronger effects. The effect was considered significant when the 95% confidence intervals of the parameter coefficient did not overlap zero. We visualised the trend between each landscape attribute and the probability of a stream reach being within the population neighbourhood independently by fitting the model holding all other variables constant. Continuous variables (e.g., drainage area, elevation) were held constant at a global mean (i.e., mean of all streams reaches independent of species) and common categorical variables among species were held constant at the global median. The use of global values calculated from the entire dataset of stream reaches allowed for direct comparison among species.

2.7 | Methodological considerations

Prior to transitioning to the results, we would like the reader to be aware of five methodological considerations explicit in our approach. First, we assume that the spawning distribution was representative of the upper limit of occurrence for each focal species, that there was no significant upstream migration of juvenile salmonids following emergence, and that, for coho salmon, fry distribution was

TABLE 2 Model performance results comparing global regression models fit with a dataset from all the streams surveyed (full) and with a dataset (truncated) that excluded streams where the upper limit of occurrence was associated with natural barriers for coho salmon, steelhead trout, and chum salmon in the Chehalis River basin, Washington. *N* is the number of stream reaches included in each dataset

a suitable proxy for adult distribution. Second, the results are based on contemporary abundances of anadromous salmon and steelhead trout and acknowledge that historical distributions during times of differing adult spawning abundances and habitat connectivity and quality might very well have been different. Third, our approach attempts to control for obvious anthropogenic impacts on habitat quality and migration; however, much of the basin has been altered by human activity and more subtle effects of these impacts on species population neighbourhoods are unknown. Fourth, this study only considers the population neighbourhood for the anadromous life history of steelhead trout. Last, the study design did not allow for the incorporation of inter-annual variation in population size or environmental conditions (e.g. stream flow) that are likely to influence the location of the upper limit of occurrence. These considerations will be addressed in greater detail in the discussion section.

3 | RESULTS

3.1 | Documenting the upper limit of occurrence

We conducted 669 km of on-the-ground surveys for fish occurrence and documented the ULO in 115 coho salmon streams, 97 steelhead trout streams, and 57 chum salmon terminal streams (Figure 3). Natural barriers influenced a portion of the ULO locations but were not the primary driver. Just 16.5% of the ULOs were associated with barriers (12.1% permanent, 4.4% transient) for coho salmon; 5.1% of the ULOs were associated with barriers (4.1% permanent, 1.0% transient) for steelhead trout; 15.8% of the ULOs were associated with barriers (14.0% permanent, 1.8% transient) for chum salmon (Table 3). The stream channel terminus type differed among species. Mid channels were the most frequent for coho salmon (60.8%) and chum salmon (50.9%), whereas lateral channel junctions were most frequent for steelhead trout (40.2%; Table 3).

3.2 | Landscape attributes associated with coho salmon ULOs

The most important landscape attributes for defining coho salmon population neighbourhood boundaries included drainage area,

precipitation, elevation, wetlands, and geology (Table 4). Drainage area had the largest effect size followed by elevation and precipitation, respectively (Figure 4, Table S8). Drainage area and precipitation were positively related to the probability of a stream reach being within the population neighbourhood, while elevation was negatively related to the probability of a stream reach being within the population neighbourhood. The inclusion of streams with ULOs associated with natural barriers reduced model performance, thus the truncated data set was used for further analysis (Table 2). The cross-validated model correctly predicted 78% ($\pm 2\%$) of the stream reaches as within or outside the population neighbourhood and demonstrated good discrimination (AUC: 0.87 ± 0.01 ; Table 4). The median error distance between predicted and observed ULO locations was 82.9 m ($n = 9,000$, 25% quantile: -415 m; 75% quantile: 954 m; Figure S6) and the landscape attributes demonstrated good spatial transferability when predicting between ecoregions (AUC: 0.81 ± 0.03).

The probability of a landscape attribute being included within the coho salmon population neighbourhood increased in stream reaches with greater drainage area and precipitation and decreased in reaches with higher elevation and the presence of wetlands (Figure 5). Stream reaches with a drainage area of 50 km² had a 0.96 probability of being within the population neighbourhood for coho salmon, and this probability declined to 0.79 at 8.0 km² and 0.49 at 2.0 km² (Figure 5a). Stream reaches with precipitation of 275 cm/year had a 0.81 probability of being within the population neighbourhood and this probability declined to 0.69 at 220 cm/year and 0.61 at 190 cm/year (Figure 5b). Stream reaches with an elevation of 75 m had a 0.92 probability of being within the population neighbourhood and this probability declined to 0.87 at 130 m and 0.68 at 240 m (Figure 5e). A stream reach with a sandstone geology had about 1.3 times greater probability of being within the population neighbourhood than streams reaches with basalt geology (0.9 and 0.69, respectively). Glacial and alluvium geology types had a similar influence on the stream reaches probability (0.80 and 0.81, respectively), intermediate to sandstone and basalt (Figure 5c). The presence of wetlands reduced the probability of a stream reach being within the population neighbourhood by 0.14; however, there was large variance in the prediction intervals (Figure 5f).

3.3 | Landscape attributes associated with steelhead trout ULOs

The most important landscape attributes for defining steelhead trout population neighbourhood boundaries included drainage area, elevation, slope, wetlands, and geology (Table 4). Drainage area had the largest effect, followed by elevation and slope, respectively (Figure 4, Table S8). Drainage area was positively related to the probability of a stream reach being within the population neighbourhood, while elevation and slope were negatively related to the probability of a stream reach being within the population neighbourhood. The inclusion of streams with ULOs associated with natural barriers did

not reduce model performance, so the full data set was used for further analysis (Table 2). The cross-validated model correctly predicted 87% ($\pm 1\%$) of the stream reaches as within or outside the population neighbourhood and demonstrated excellent discrimination (AUC: 0.94 ± 0.01 ; Table 4). The median error distance between the observed and predicted ULO locations was 0 m ($n = 9,500$, 25% quantile: -200 m; 75% quantile 1,488 m; Figure S6), and the landscape attributes demonstrated excellent spatial transferability between ecoregions (AUC: 0.90 ± 0.02).

The probability of landscape attributes being included within the steelhead trout population neighbourhood was higher for stream reaches with greater drainage area, and lower for reaches with greater precipitation, slope, and elevation (Figure 5). Stream reaches with a drainage area of 50 km² had a 0.86 probability of being within the population neighbourhood and this probability declined to 0.19 at 8 km² and 0.02 at 2 km² (Figure 5a). Stream reaches with a slope of 0.0% had a 0.32 probability of being within the population neighbourhood and this probability declined to 0.26 at 4.0% slope and 0.17 at 10.0% slope (Figure 5d). Stream reaches with an elevation of 75 m had a 0.42 probability of being within the population neighbourhood and this probability declined to 0.29 at 130 m and 0.11 at 240 m (Figure 5e). There was a minimal difference in magnitude of effect of geology type on the probability of a stream reach being within the population neighbourhood (Figure 5c). The greatest difference occurred between stream reaches with basalt geology (0.31) and glacial geology (0.20). However, there was large variation in the predictions and the median for each geology type fell within the 95% prediction interval of every geology type. The presence of wetlands increased the probability of a stream reach being within the population neighbourhood for steelhead by 0.16 (Figure 5f).

3.4 | Landscape attributes associated with chum salmon ULOs

The most important landscape attributes for defining chum salmon population neighbourhood boundaries included drainage area, elevation, and geology (Table 4). Elevation had the largest effect followed by drainage area (Figure 4, Table S8). Drainage area was positively related to the probability of a stream reach being within the population neighbourhood, while elevation was negatively related to the probability of a stream reach being within the population neighbourhood. The inclusion of streams with ULOs associated with natural barriers did not reduce model performance, so the full data set was used for further analysis (Table 2). The cross-validated model correctly predicted 89% ($\pm 1\%$) of the stream reaches as within or outside the population neighbourhood and demonstrated excellent discrimination (AUC: 0.96 ± 0.01 ; Table 4). The median error distance between the observed and predicted ULO locations was 0 m ($n = 5,500$, 25% quantile: -376 m; 75% quantile: 663 m; Figure S6), and the landscape attributes demonstrated excellent spatial transferability (AUC: 0.95 ± 0.00).

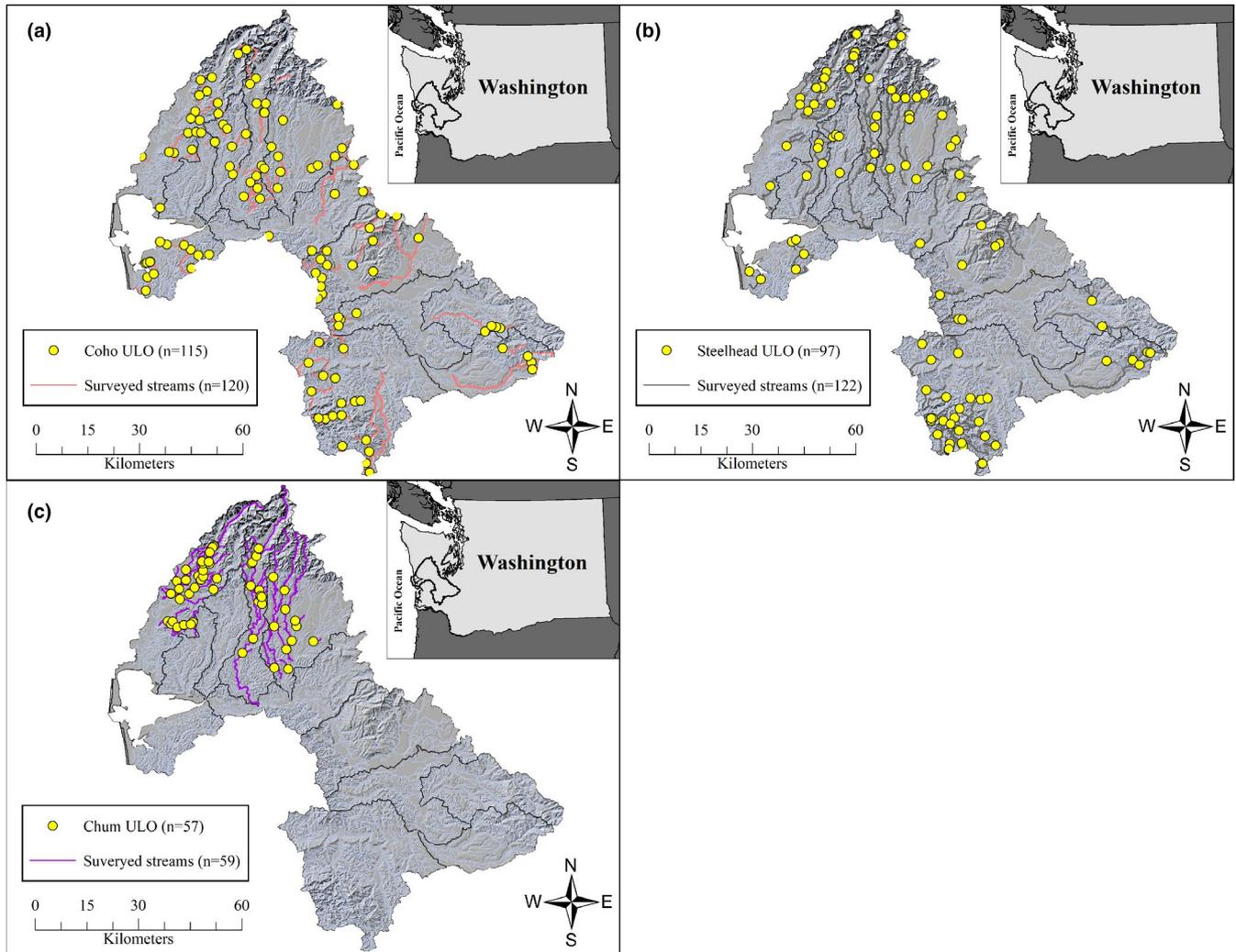


FIGURE 3 Field documented upper limit of occurrence (ULO) locations (yellow dots) for coho salmon (a), steelhead trout (b), and chum salmon (c) in the Chehalis River basin, Washington, U.S.A., collected between 2017–2019

Species	ULO type	Barrier Type		
		No Barrier	Permanent	Transient
Coho	Lateral	6.1 (7)	0.0 (0)	0.0 (0)
	Mid Channel	49.6 (57)	7.8 (9)	3.5 (4)
	Tributary Junction	27.8 (31)	4.3 (5)	0.9 (1)
Steelhead	Lateral	40.2 (39)	0.0 (0)	0.0 (0)
	Mid Channel	23.7 (23)	3.1 (3)	1.0 (1)
	Tributary Junction	30.9 (30)	1.0 (1)	0.0 (0)
Chum	Lateral	43.9 (25)	0.0 (0)	0.0 (0)
	Mid Channel	38.6 (22)	12.3 (7)	0.0 (0)
	Tributary Junction	1.8 (1)	1.8 (1)	1.8 (1)

TABLE 3 Upper limit of occurrence (ULO) boundary types for terminal streams in the Chehalis River basin, Washington surveyed for coho salmon ($n = 115$), steelhead trout ($n = 97$), and chum salmon ($n = 57$), and the percentage (count) of streams where the field documented ULO is associated with a permanent or transient complete natural barrier

The probability of a landscape attribute being included within chum salmon population neighbourhood increased in stream reaches with greater drainage area and decreased in reaches with greater elevation (Figure 4). Stream reaches with a drainage area of

50 km² had a 0.26 probability of being within the population neighbourhood and this probability declined to 0.02 at 8 km² and 0.0 at 2 km². Stream reach with an elevation of 75 m had a 0.39 probability of being within the population neighbourhood and this probability

TABLE 4 Model selection metrics (mean \pm SD) for predicting the population neighbourhood for coho salmon, steelhead trout, and chum salmon in the Chehalis River basin, Washington

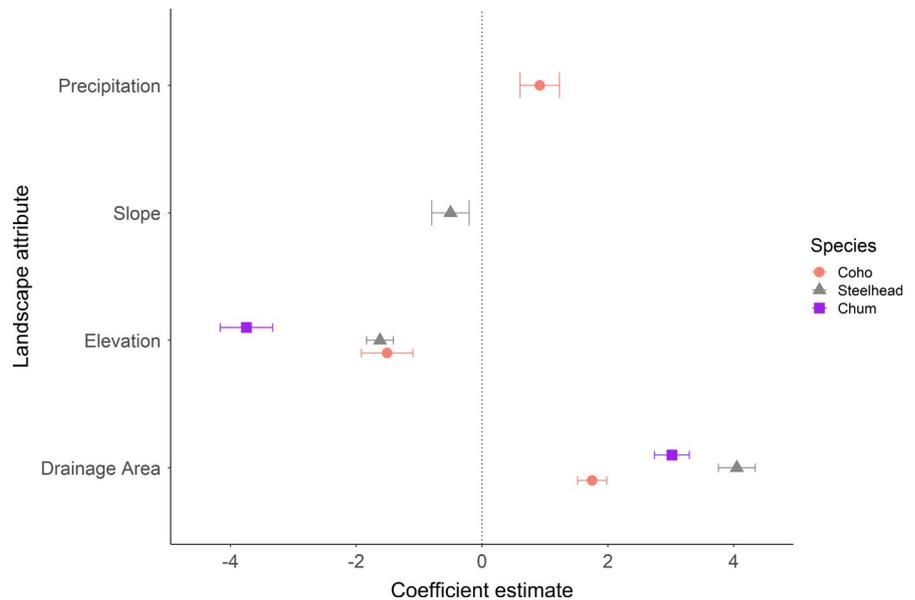
Species	Model	Landscape attributes	K^a	PCC ^b	AUC ^c	Δ AICc	w_i
Coho	A	Global	10	0.78 \pm 0.02	0.87 \pm 0.01	0	0.65
	B	A + P+E + W+G	9	0.78 \pm 0.02	0.87 \pm 0.01	1.34	0.33
Steelhead	A	Global	10	0.86 \pm 0.01	0.92 \pm 0.01	0	0.51
	C	A + E+S + W+G	9	0.87 \pm 0.01	0.94 \pm 0.01	0.09	0.49
Chum	B	A + E+G	7	0.89 \pm 0.01	0.96 \pm 0.01	0	0.71
	A	Global	8	0.89 \pm 0.01	0.96 \pm 0.01	1.8	0.29

Note: The global coho salmon and steelhead trout model includes the landscape attributes drainage area (A), precipitation (P), elevation (E), slope (S), wetland presence (W) and geology type (G) as fixed effect parameters. The global chum model includes (A), elevation (E), wetland presence (W) and geology type (G) as fixed effect parameters. Bolded model letter identifies the best model. Model results are ranked by small sample size-corrected Akaike information criterion (AICc) and Akaike weights (w_i). Only candidate models with $w_i > 0.05$ are shown. The complete list of candidate models and model selection metrics are provided in Table S7.

^a K is the number of estimated parameters.

^b PCC is the mean (\pm SD) percent correct classification from the 200 cross validation iterations.

^c AUC is the mean (\pm SD) area under the receiver operating curve from the 200 cross validation iterations.

FIGURE 4 The effect size of continuous predictor variables for the best model for each species fit with data collected across the Chehalis River basin, Washington, U.S.A. The point values and error bars represent the mean and 95% confidence intervals for the effect size

declined to 0.08 at 130 m and 0.0 at 240 m. With respect to chum salmon population neighbourhoods, the variability among geology types was minimal, and the median for each geology type fell within the 95% prediction interval of every geology type (Figure 5c). The absolute probabilities associated with each geology type were low due to how we set up the analysis to compare the covariate influences among species. While describing the influence of a specific covariate, such as geology, we held other covariates in the model at the global mean rather than species-specific means. The global mean drainage area and elevation across all species occurred where the relative likelihood of chum salmon occurring was already low.

4 | DISCUSSION

In this paper, we identified the landscape attributes that define population neighbourhoods of three culturally and ecologically important

anadromous fish species in a large, coastal catchment in southwestern Washington, U.S.A. We successfully documented ULO locations for coho salmon ($n = 115$), steelhead trout ($n = 97$), and chum salmon ($n = 57$) in a subset of streams and related landscape attributes to the probability of a stream reach being within or outside the population neighbourhood. As predicted, the suite of landscape attributes associated with these ULO locations varied among species; however, drainage area, elevation, and geology were important predictors for all species. The magnitude of the relationship between these common landscape attributes and the probability of stream reaches being within or outside the population neighbourhood varied among the three species, reflecting species-specific habitat requirements and life histories. While there is synergy between these multiple landscape attributes, they were not statistically correlated, and each attribute independently contributed to the unique population neighbourhood boundary for each species. Identifying species-specific landscape attribute values that shape population neighbourhoods is

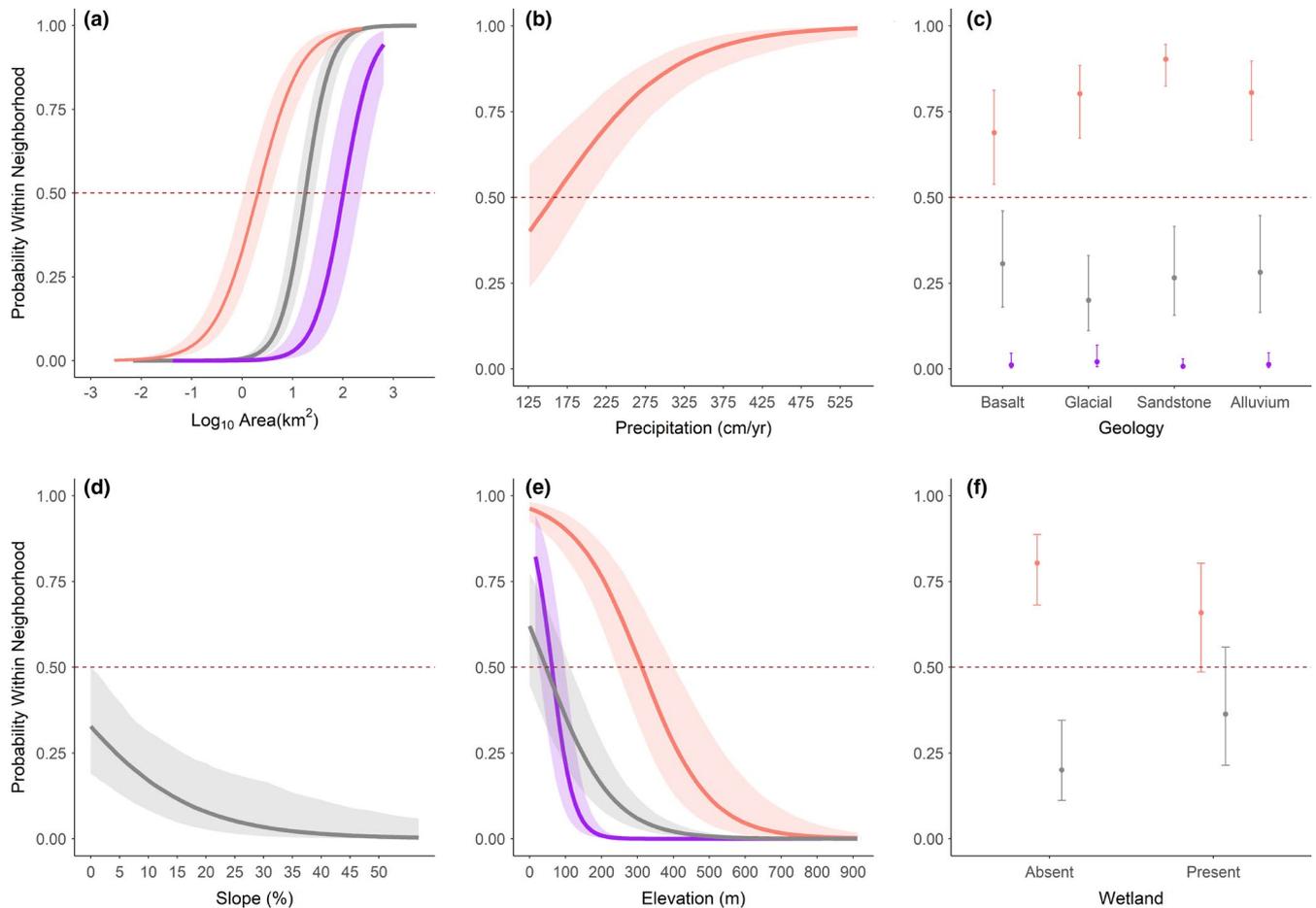


FIGURE 5 Predictive curves for each landscape attribute demonstrating the probability of a stream reach being within the population neighbourhood. Bolded curve lines represent the mean predictive value and the ribbons represent the 95% confidence interval. The curves in pink represent coho salmon; the curves in grey represent steelhead trout; the curves in purple represent chum salmon. Predictive curves for each landscape attribute were fit using the best model with all other model parameters held constant at their mean value. Common continuous predictor variables among models (drainage area, elevation) were held constant at the global mean. Unique predictor variables were held at the species-specific data set mean. Common categorical variables were held constant at the global median (glacial geology type and wetlands absent)

critical to prioritising restoration actions in this catchment because not all actions will have equal benefits for each species of interest.

4.1 | Influence of landscape variables on neighbourhood boundaries

Stream reaches with larger drainage areas are generally lower in stream networks, have greater habitat complexity, and have a shorter migration distance to and from the marine environment. Similar to the findings of Pess et al. (2014), we found that larger drainage areas corresponded with the sympatric occurrence of multiple salmon species. However, different life history and habitat requirements among coho salmon, steelhead trout, and chum salmon probably influenced the minimum drainage areas within the respective population neighbourhood. In general, coho salmon utilise smaller substrate and require less stream area for spawning compared to other anadromous salmonids (Bjornn & Reiser, 1991; Kondolf & Wolman, 1993)

facilitating the exploitation of smaller drainages. In contrast, chum salmon spawning was associated with channel braids, side channels, and sloughs found lower in the stream network of the major sub basins of the Chehalis River, which have broad and unconstrained river valleys and larger drainage areas. Stream branching was associated with 72% of all steelhead trout ULOs, which suggests that locations in the catchment with major transitions in drainage area are important for identifying the population neighbourhood boundary for the anadromous form of this species. Abrupt changes in drainage areas that occur at tributary junctions alter the hydrologic characteristics at these locations that effect bed material size and shape (Knighton, 1982), and water chemistry (Teti, 1984). The tributary junctions represent discontinuities in stream networks (Benda et al., 2004) where higher nutrient concentrations, food resource availability, and greater habitat volume and complexity slightly downstream create *biochemical hotspots* that may be related to shifts in fish assemblage and productivity (Kiffney et al., 2006; Wipfli & Gregovich, 2002).

Different migration phenologies between coho salmon and steelhead trout illuminate the role of precipitation and the range of drainage area values represented within population neighbourhoods. The autumn spawn timing of coho salmon coincides with the seasonal onset of autumn precipitation that increases stream flows and facilitates access to small tributary streams that may be inaccessible to salmonids with migration under lower stream flow conditions (Sandercock, 1991). For example, the late winter and early spring migration period for steelhead trout limits their ability to take advantage of areas that receive greater amounts of annual precipitation occurring during the autumn months. A decreasing hydrograph during the spring spawning period for steelhead may necessitate the exploitation of larger streams that have adequate depths for adult fish, and suitable flows for egg incubation and juvenile rearing. The impact of these asynchronous migration periods on habitat utilisation is supported by our findings that indicate flow-induced accessibility is an important driver of the population neighbourhood for coho salmon but not steelhead trout.

Elevation was negatively related to the probability of a stream reach being within the population neighbourhood for all species, but the maximum elevation associated with the population neighbourhoods varied among species. Elevation has been used to successfully predict the distribution of both cold water (Bozek & Hubert, 1992; Porter et al., 2000) and warm water fishes (Quist et al., 2004), as well as other aquatic organisms (Lenssen & Kroon, 2005). In our study, elevation was probably a correlative landscape attribute that captured a broad array of drivers that directly shape the distribution of a species (Tonkin et al., 2016). For example, the negative relationship between elevation among all species and their population neighbourhood boundary may reflect limits to the physical exertion associated with accessing reaches farther upstream in the stream network. A biological parameter to quantify migration exertion was explored by multiplying the elevation of a reach by its distance to the estuary. However, this parameter was highly correlated with elevation ($\rho > 0.90$) and was not retained for modelling. Elevation could also be a surrogate for climate and stream temperature (Dauwalter & Rahel, 2008; Isaak & Hubert, 2001; Quist et al., 2004), and the observed response may represent an indirect thermal limit to fish distribution.

While we expected slope to be an important predictor for all species, surprisingly this attribute was only relevant to steelhead trout. In addition, the lower slope values associated with the steelhead trout population neighbourhood were counterintuitive when considering the leaping abilities of the species (Powers & Orsborn, 1985) and the typical observation that steelhead trout are able to ascend steep stream reaches with cascades and falls (Bryant et al., 2004; Reiser et al., 2006). Our analysis was designed to contrast slopes within and outside the population neighbourhood rather than detect the localised influence of slope specific to a particular reach. Our results suggest that anadromous steelhead trout may restrict their spawning distribution to areas of the catchment with lower slope that ensure adequate wetted space for spring spawning and rearing in a rain-dominant system (Bjornn & Reiser, 1991). For coho salmon,

slope was not a significant driver of population neighbourhoods compared to other landscape attributes such as drainage area and precipitation. This result probably reflects the specific landscape of the Chehalis River basin which is relatively low gradient throughout. The ULOs of upstream migrating coho salmon in this basin appear to be influenced by other landscape attributes before encountering slopes that limit their migration abilities. Further, reach-scale slopes both within and outside population neighbourhoods were variable and limited the utility of this attribute as a predictor variable. For example, while slope increased in an upstream direction for some terminal streams, other terminal streams were characterised by headwater wetlands and beaver complexes (i.e., low slope reaches) that existed outside the observed population neighbourhood for coho salmon. While we did not identify an association between slope and the population neighbourhood for coho salmon in this study, slope is known to be an important factor in determining habitat suitability of specific reaches within a population neighbourhood (McMillan et al., 2013; Reeves et al., 2011; Sharma & Hilborn, 2001).

Unlike previous models that have demonstrated strong relationships between underlying geology and the abundance and occurrence of salmonids (Firman et al., 2011; Pess et al., 2002; Taylor et al., 2017), geology had weak or variable influence on the population neighbourhood boundaries among species. Underlying geology influences erosion rates, channel forming processes, discharge, and sediment loading, all of which affect substrate suitability for spawning within a stream reach (Firman et al., 2011; Montgomery & Buffington, 1998). We included geology in the analysis because we expected the association between this attribute and spawning gravel to influence salmonid population neighbourhoods. However, our results did not always support spawning gravel as a mechanistic explanation for an association between geology and population neighbourhoods. For example, reaches with sandstone geology, which is prone to erosion and generally has smaller substrate (Gomi et al., 2005; Hicks, 1989), had the strongest positive influence on coho salmon population neighbourhoods. In contrast, alluvial deposits, which are associated with higher quality spawning habitat (Montgomery et al., 1996; Steel et al., 2004), had an intermediate association with population neighbourhoods for each species compared to other geology types. This may be the result of the spatial distribution of geology types across the basin and local adaptation to the geologic history of the Chehalis River basin as a refuge during the last glaciation (Hocutt & Wiley, 1986). The direction and magnitude of the relationships between the underlying geology and population neighbourhoods may be indirectly related to landscape attributes that correlate or overlap with the spatial distribution of geology types.

4.2 | Influence of natural barriers on neighbourhood boundaries

Localised influence of natural barriers had a minimal yet detectable influence on the population neighbourhood boundaries

independent of the overall landscape. The importance of natural barriers to the boundaries for each species was probably determined by species-specific physical capabilities and distribution across the catchment. Population neighbourhoods of coho salmon were the most likely to be restricted by natural barriers. Coho salmon also had population neighbourhoods that included the smallest stream sizes (smallest drainage areas) compared to the other two species. Smaller streams make natural barriers more challenging to navigate due to the lack of sufficient plunge pool depth, and also have a lower transport capacity for large woody debris (MacDonald & Coe, 2007) that may account for the high percentage of transient barriers associated with coho salmon ULOs. In comparison with coho salmon, the population neighbourhood of steelhead trout was less restricted by natural barriers. The larger stream size in the population neighbourhood for steelhead and the greater leaping ability of this species allows for navigation around stream obstructions that may be barriers to other salmonid species (Reiser et al., 2006). Population neighbourhoods of chum salmon included streams lower in the stream network where large natural barriers are less common. Chum salmon were not observed to use smaller tributaries (<10 km²) where natural barriers to upstream migration are more prevalent (Brunner & Montgomery, 2003; MacDonald & Coe, 2007).

4.3 | Model accuracy

The strong predictive accuracy of each model demonstrated the utility of using landscape attributes to describe population neighbourhoods. We found that these coarse-scale attributes were highly effective at describing species-specific differences in boundaries of population neighbourhoods within a catchment. For example, there was good to excellent spatial transferability of predictive models among the different ecoregions in the catchment, specifically for coho salmon and steelhead trout. The coho salmon model had lower predictive accuracy than the other two species, a result that may be influenced by high variability in local conditions of small streams associated with the population neighbourhood for this species. Population neighbourhoods of coho salmon included smaller streams compared to the other two species. Small streams are more likely to experience greater magnitudes of natural disturbance such as landslides that alter the suitability of the local habitat (Bisson et al., 2009). The greater spatial heterogeneity of streams in small drainage areas may contribute to the overprediction of coho salmon ULOs (i.e., c. 80 m median error distance). While the predicted ULO locations for steelhead trout and chum salmon were accurate (0-m median error distance), the distribution of the error between predicted and observed was varied and right-skewed (i.e., the predicted locations were further upstream than the observed locations). For chum salmon, this result could be related to their inability to navigate natural barriers, which our predictive model was not designed to explicitly detect (Reiser et al., 2006). Also, the total lengths of the terminal streams were relatively longer for steelhead trout and

chum salmon compared to coho salmon, which may contribute to the larger error distance absolute values.

4.4 | Caveats

Freshwater habitat degradation and loss has been linked to population declines (Bond et al., 2019; Gayeski et al., 2011), which influence the extent to which salmonids are distributed across the landscape (Isaak & Thurow, 2006). Current salmonid population abundances in the Chehalis River basin are much lower compared to historical abundances. Thus, our occurrence observations may be more representative of core habitat use at low abundances, which would result in an underestimation of the natural population neighbourhood when run sizes were larger. For steelhead trout, natural selection against the anadromous life history above anthropogenic barriers (Apgar et al., 2017; Pearse et al., 2014) may also contribute to a reduction in the abundance of anadromous *O. mykiss* over time (Kendall et al., 2017). However, resident rainbow trout (non-anadromous life history form of *O. mykiss*) are often functionally connected to anadromous steelhead trout populations (Kendall et al., 2015) and we would expect a broader range of landscape attributes associated with *O. mykiss* population neighbourhoods if both the resident and anadromous life history forms were considered in this study. The use of redds as the predominate determinant of steelhead trout ULOs was most representative for female anadromous steelhead trout and may underestimate population neighbourhoods for male anadromous steelhead trout. While we attempted to control for overt anthropogenic impacts on habitat quality, over a century of landscape alteration (e.g., urbanisation, agriculture, forestry) across the basin has probably contributed to shaping the population neighbourhoods of each focal species. This study provides a temporal snapshot, with the exact ULO locations possibly changing among years, and a longer time frame for monitoring would be required to evaluate how interannual variability in abundance and environmental conditions may shape species-specific population neighbourhood boundaries (Cram et al., 2017).

The results of the regression model included an important caveat that the binary points developed for analysis were not independent of each other. The inclusion of sub-basin as a random effect in our model addressed some, but not all, of this lack of independence. However, the lack of independence does not affect the final predictive equation, which was the focus of our work. As a result, the probabilities associated with predicted values should be interpreted as an index for the relative likelihood (sensu Fransen et al., 2006), rather than an absolute probability, of a stream reach being within the population neighbourhood. The two different collection methods used for coho salmon occurrence surveys (electrofishing and minnow trapping) may have introduced sampling bias that influenced the location of the observed ULO. However, minnow traps were only deployed for eight of the 120 coho salmon surveys, and therefore the different sampling methods are unlikely to have substantially altered the final model equation.

Our modelling was conducted using a single species occurrence framework that did not consider additional biological factors that may influence population neighbourhood boundaries. In smaller headwater streams, space and food resources are limited and interspecific competition can shape fish assemblage (Pess et al., 2011; Rosenfeld et al., 2000; Schlosser, 1991). Qualitative observations from our field sampling in headwater streams documented an abrupt shift in the species detected as stream size decreased transitioning from predominantly coho salmon to predominantly resident cutthroat trout. Sympatric resident cutthroat trout compete with smaller juvenile coho salmon for space and food resources (Buehrens et al., 2014; Sabo & Pauley, 1997). If these competitive interactions intensify in smaller headwater streams, cutthroat trout densities in addition to physical landscape attributes could limit the upstream distribution of coho salmon. The integration of both landscape and biotic factors could increase the biological interpretative power of the model.

4.5 | Concluding thoughts

To effectively guide management problems and conservation planning, the ecological investigation must align with the scale of the problem. Restoring habitat connectivity to ameliorate population viability has been a strategy proposed across taxa (Clauzel et al., 2015; Mulligan et al., 2013; Pess et al., 2014; Schultz & Crone, 2005). During stream restoration planning, the accessibility to heterogeneous habitats that support a population across multiple life stages over time is often overlooked and instead the focus is on summarising the amount of habitat for a specific life stage (Flitcroft et al., 2019). Research on species distributions is often focused on either reach-scale occupancy (e.g., Polivka et al., 2015) or broad spatial patterns over vast geographical areas (e.g., Buddendorf et al., 2019) with less attention on population boundaries within a catchment of interest. In addition, past efforts are often limited to a specific life stage for a single species (Anlauf-Dunn et al., 2014; Steel et al., 2004). Our study provides an approach to accurately and consistently define population neighbourhood boundaries. This information is needed to guide conservation and management actions toward the locations where reconnecting habitat will have the greatest impact and to identify the amount of impact associated with actions at a specific location. Ultimately, the ability to quantify landscape attributes that describe population neighbourhood boundaries is the necessary first step for predicting distributions of species over broad spatial extents and illuminates how the biology and life history of a species is captured across the landscape.

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DATA AVAILABILITY STATEMENT

All data and R script used for the statistical analysis in this study is publicly available at the Knowledge Network for Biocomplexity (KNB) repository: <https://doi.org/10.5063/4JOCJX>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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