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Mapping Habitat Suitability Rangewide for Headwater Stream-Associated Torrent Salamanders

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ABSTRACT

In the moist, coniferous forests of Oregon and Washington, a dense network of headwater streams supports high levels of amphibian species endemism and diversity, including the torrent salamanders (*Rhyacotriton* spp.). The Columbia and Cascade torrent salamanders (*R. kezeri* and *R. cascadae*, respectively) are species of greatest conservation need, but current information is insufficient for an adequate status assessment. We aimed to determine the current distributional extent, occurrence, and abundance of both species across their respective ranges, and to characterize watershed-scale habitat suitability. We conducted rangewide surveys for both species and used a novel, robust model development and refinement process to characterize habitat suitability based on climatic, topographic, forest-structure, hydrological, and water-balance drivers of their distributions. Results supported interspecific differences in rangewide occurrence and abundance patterns, as well as ecological associations that provide insights into potentially divergent patterns of resilience. Topographic, water-balance, and streamflow metrics were top predictors of Columbia torrent occurrences, whereas metrics of seasonal temperature and atmospheric moisture were top predictors of Cascade torrent occurrences. Our findings can inform regional conservation planning efforts to identify likely climate refugia and habitat-connectivity pathways for gene flow and watershed-scale ecological resilience.

1 | Introduction

Biodiversity conservation is one of the foremost challenges of the 21st Century owing to multiple threats, including habitat loss and fragmentation, climate change, invasive species, contaminants, and emerging infectious diseases (IPBES 2019). In particular, the conservation of species in forest ecosystems is of heightened concern because of interactions between high levels of endemism and myriad socioeconomic priorities like commodity production and land conversion. Climate change impacts on forest ecosystems, including those that manifest via megafires, droughts, and extreme weather events (e.g., floods, heat waves), provide emerging evidence that climate change acts as a threat multiplier alongside habitat loss (Vose et al. 2018). Although ecosystem-based forest management approaches have developed over the past three decades to reconcile species conservation with forest land uses (Olson and Van Horne 2017), freshwater species in forests have been considered "weak links" in biodiversity conservation owing to an array of variables and threats (climatic or otherwise) that intersect communities, processes, and functions between water and land (Penaluna et al. 2017).

Aquatic biota in the moist coniferous forests of the U.S. Pacific Northwest (PNW) exemplify a complex interaction between climate change and forest ecosystem management. The PNW is a topographically and ecologically diverse region that spans Oregon and Washington. Heavy seasonal rainfall is a hallmark of PNW climate. The sharp topographic relief and

Summary

- Torrent salamander distributions reflect a dependence on cold, headwater streams within moist coniferous forests that buffer from environmental variability, among other species-specific associations.

parallel alignment of the Coast and Cascade Ranges interact with storm systems to create dual rain-shadow effects resulting in heterogeneous local microclimates and numerous, discrete watersheds with dense streamflow paths that permeate throughout coniferous forests. Smaller streams in headwater sub-basins are spatially or seasonally discontinuous and act as small capillaries that contribute multiple downstream resources (e.g., cold water, nutrients, downed wood, substrate structural components). Within these moist coniferous forests, seeps and headwater streams characterized by high-gradient, rocky reaches can comprise over 70%–80% of the overall drainage area in a large watershed (Gomi et al. 2002) and contribute approximately 55% of the discharge exported from regional river systems (Brinkerhoff et al. 2024). Headwater basins of the Coast and Cascade Ranges are home to a diversity of freshwater-dependent species adapted to cold-water conditions (Thurman et al. 2022). In particular, headwaters support high levels of amphibian species endemism and diversity, which can be important taxonomic barometers of ecosystem health and function (Welsh and Hodgson 1997; Welsh and Ollivier 1998). The amphibian assemblage associated with headwaters of the PNW includes 52 species occurring within or along headwater channels and adjacent riparian forests, most of which are considered rare and of conservation concern (Thurman et al. 2022). Headwater stream-associated amphibians are a major component of stream and riparian forest biomass and play a central role in forest food webs and energy flow because of their unique life histories (Peterman et al. 2008; Best and Welsh Jr. 2014). Stream-breeding species, in particular, exhibit ontogenetic shifts in aquatic and terrestrial habitat use and reciprocally transport nutrients between streams and adjacent riparian forest habitats (e.g., Baxter et al. 2005; Olson et al. 2007; Sánchez-Hernández 2020).

Torrent salamanders (*Rhyacotriton* spp.) comprise a unique clade of four endemic, headwater stream-breeding species, including the Cascade (*R. cascadae*), Columbia (*R. kezeri*), Olympic (*R. olympicus*), and Southern (*R. variegatus*) torrent salamanders (Good and Wake 1992). Despite the establishment of ecosystem-based management approaches to address forest biodiversity conservation in the PNW (e.g., patchwork of streamside protection zones; Olson et al. 2007) and ecology-based forestry objectives to restore ecological integrity and resilience (Reeves et al. 2018; Gaines et al. 2022), all four species are considered to be of high conservation concern (Thurman et al. 2022). Recently, the Columbia and Cascade torrent salamanders were petitioned for listing under the Endangered Species Act (U.S. Fish and Wildlife Service 2015) and are undergoing status review. Both species have a dearth of basic ecological information, but are thought to be highly vulnerable to environmental changes, including forest management practices and climate change (Howell and Maggiulli 2011; Olson and Burton 2019; Thurman et al. 2022).

Torrent salamanders are adapted to cold-water habitats and have among the lowest thermal and desiccation tolerances of any amphibian genus (Ray 1958; Brattstrom 1963; Bury 2008). For example, Cascade torrent salamanders are typically absent from streams that exceed 14°C for extended periods (Pollett et al. 2010). Both Columbia and Cascade torrent salamanders appear to be patchily distributed throughout their ranges and are encountered in fewer sites relative to other co-occurring amphibian species (Corn and Bruce Bury 1989). The distribution of the Cascade torrent salamander extends across portions of the west slopes of the Cascade Range in northern Oregon and southern Washington (Howell and Maggiulli 2011). Columbia torrent salamanders primarily occur in mature, coniferous forests of the Coast Range of northwest Oregon and southwest Washington (Good and Wake 1992) but have been observed in younger stands managed for timber production. Both species are associated with small, often spatially intermittent, high-gradient, cool- or cold-water streams, including seeps and waterfalls, stream edges beneath rocks, moss, or wood, and in the splash zone (Jones et al. 2005; Olson and Weaver 2007; Olson and Burton 2014). During heavy rains, individuals may stray from the stream and can be found under leaf litter, branches, and small logs in upland forests (Howell and Maggiulli 2011).

The main suspected threats to Columbia and Cascade torrent salamanders include factors that degrade habitat quality, particularly those that result in increased water temperatures and sedimentation (Thomas et al. 1993; Lannoo 2005). Other natural and anthropogenic events that destabilize the geomorphology or hydrology of streams (e.g., debris flows that scour bedrock, high peak flows from rain-on-snow events) have also been considered problematic to torrent salamanders (Crisafulli et al. 2005). Several studies have examined impacts of forest management and timber-harvest practices (and associated roads) on stream-associated salamanders, owing to the legacy of widespread, unregulated historical logging in headwater forest drainages, paired with a subsequent intensification of management practices in the PNW (Kroll et al. 2010; Emel et al. 2019). In general, diverse studies have reported: (1) higher torrent abundances in streams of old-growth forests (Corn and Bury 1991; Welsh and Lind 1991); (2) lower torrent abundances in intensively managed forests (i.e., clearcut stands) and younger forest age-classes (e.g., Steele et al. 2003; Kroll et al. 2008), particularly in unbuffered streams (e.g., Pollett et al. 2010) or streams with narrower buffers (e.g., <70 m: Olson and Burton 2014 and <140 m: Olson and Ares 2022); (3) positive associations with north-facing streams and older riparian-forest age-classes of approximately 45 years or more (Steele et al. 2003; Russell et al. 2004, 2005; Kroll et al. 2008); and (4) increased gene flow via overland dispersal of the Columbia and Southern torrent salamanders between watersheds with landscape-scale attributes of forest cover and fewer roads (Emel et al. 2019). Intensive forest management practices increase the risk of elevated in-stream temperatures and sedimentation, potentially altered streamflows, and reduced moisture conditions in riparian forests (Leonard et al. 1993; Thomas et al. 1993; Anderson et al. 2007; Groom et al. 2011; Olson and Burton 2019).

Torrent salamanders are considered sentinels of forest integrity and have been described as critical biological indicators

of cool, moist forests and cold-water refugia (Welsh and Hodgson 1997; McIntyre et al. 2012). Growing concern over potential population declines in both the Columbia and Cascade torrent salamanders and their associations with declining, old-growth forested habitat in the PNW (Corn and Bruce Bury 1989; Welsh and Lind 1996; Strittholt et al. 2006) prompted the current study. We aimed to determine the current distributional extent and prevalence of Columbia and Cascade torrent salamanders across their respective ranges and to use a novel, robust approach to characterize watershed-scale habitat suitability. We conducted rangewide assessments for both species based on a priori modeled habitat associations developed from general habitat metrics associated with historical occurrences, then used contemporary survey results and other site-level data to address more specific climatic, topographic, forest-structure, hydrological, and water-balance drivers of species' distributions. Our approach focuses on broad spatial scales, filling a critical information gap to help inform landscape-scale conservation prioritization, such as through the identification of biophysical and climatic refugia.

2 | Methods

2.1 | Site Selection

We compiled existing information on habitat associations for both species to develop site selection criteria for field surveys. We used ecological niche factor analysis (Hirzel et al. 2002) of broad-based habitat associations (Appendix S1: Table S1) to inform sampling locations by binning model output into three bins corresponding to high-, moderate-, and low-association habitat using R package *adehabitatHS* (Calenge and Basille 2023). We generated random points for selecting sampling sites within the three bins by intersecting points with first- and second-order headwater stream channels (Gomi et al. 2002) and constraining our site selection to streams within 200 m of a road owing to field logistics and site-accessibility constraints. We sampled 50 sites within the range of the Columbia torrent salamander (32 high-association, 15 moderate-association, and 3 low-association habitat sites) (Appendix S1: Figure S1). We sampled 48 sites within the range of the Cascade torrent salamander (37 high-association, 9 moderate-association, and 2 low-association habitat sites). We skewed site selection toward high-association habitat to optimize the potential for encounters and improve our ability to further refine habitat-suitability estimates.

2.2 | Field Surveys and Observational Data

We sampled all 98 sites across both species ranges from April to August 2019, with the bulk of sampling occurring in springtime to coincide with the peak surface-active season. To accommodate sampling across two mountain ranges (Coast Range and Cascade Range) and two U.S. states (Oregon and Washington), we arrayed the timing and location of surveys in a stratified random design to minimize seasonal biases in observations. At each site, we hand-sampled for salamanders using a time-constrained visual-search method; two surveyors walked upstream along different search paths on opposite sides of the stream channel for a total of 1 h. We used a time-constrained approach to accommodate habitat heterogeneity and discontinuity in the stream channel, which allowed surveyors to efficiently search in-stream, along the stream bank and side-channel habitats, and throughout nearby seeps. We collected data on the occurrence and counts (no. animals per person-hour per site) of all amphibian species encountered.

We also collated existing occurrence and count data for torrent salamanders provided by state and federal resource-agency collaborators to supplement our 2019 field survey data. Compiled observational data such as these are prone to errors of observational certainty and geographic sampling biases. To maximize observational certainty, we used only observations documented by a biologist, researcher, or taxonomic expert. Even though the majority of these observations came from targeted inventory or survey efforts, sampling bias was still an issue as data were highly clustered at fine scales in portions of the region. We performed spatial filtering (subsampling) of the historical records to help reduce spatial autocorrelation due to uneven sampling efforts. We randomly subsampled the observations to include only one observation per 1 km grid cell, which accounted for the coarsest spatial resolution of the environmental variables. We also excluded museum records and only retained records pre-1990 if data were from reputable sources and from areas on the landscape that have not had more-contemporary surveys but are expected to still contain torrent salamanders. This included 51 observations of Cascade torrent salamanders from 1977 to 1989 and seven observations of Columbia torrent salamanders from 1968 to 1985. These filtering procedures resulted in a total of 537 observations of Cascade torrent salamanders and 426 observations of Columbia torrent salamanders across their respective ranges.

2.3 | Climatic and Environmental Data

To determine the factors driving watershed-scale habitat suitability for torrent salamanders, we leveraged a large body of spatially comprehensive data on 58 variables representing an a priori model set of topographic, riparian forested habitat, hydrological, water-balance, and climatic conditions (Appendix S2: Table S1). Each variable group is described below, with details on deriving or extracting predictors for use in the variable selection process. All analyses were conducted in QGIS version 3.28.15-Firenze, SAGA GIS version 9.3.1, Python version 3.9, and R version 4.4.1.

2.3.1 | Topographic Variables

We obtained digital elevation model (DEM) datasets at 1/3 arc-second (10-m) resolution from the USGS 3D Elevation Program (U.S. Geological Survey 2023). DEM rasters were reprojected and mosaicked. From the DEM raster, we derived slope (percent) and aspect (degrees) layers. We calculated the topographic wetness index (TWI), which is commonly used to quantify topographic control on hydrological processes (Moore et al. 1991; also known as the Compound Topographic Index [CTI]). Low TWI values represent small catchments and steep slopes; high TWI values represent large catchments and gentle slopes. The equation for TWI is:

$$\ln\left(\frac{a}{tanB}\right) \quad (1)$$

where a represents the catchment area per pixel (10 m × 10 m) and B refers to the slope (in radians). We used SAGA fill sinks tool (Wang and Liu 2006) to identify and fill surface depressions in the DEM, and used SAGA flow accumulation tool to determine the accumulated weight of all cells flowing into each downslope cell (i.e., upslope contributing area or catchment area) using the filled DEM.

2.3.2 | Riparian Habitat Variables

We assessed forest-structure and component variables that characterize riparian forest age, community type, and density. However, our design was not specifically aimed to determine associations with old-growth forest conditions; this was a broader characterization of forest condition at sampled sites. We used two datasets for characterizing riparian habitat: National Land Cover Dataset (Dewitz 2019) and modeled forest-vegetation data from the Landscape Ecology, Modeling, Mapping, and Analysis Team (Landscape Ecology Modeling, Mapping, and Analysis (LEMMA) Team 2020). Dewitz (2019) provide estimates of percent tree canopy, generated primarily from multi-spectral Landsat imagery. The LEMMA Team used gradient nearest-neighbor imputation methods to characterize forest-vegetation structure and components based on 30-m Landsat imagery, Forest Inventory and Analysis data, and other geospatial data products.

We used the Riparian Climate Corridor Index from Krosby et al. (2018) that provided an integrated assessment of how well specific riparian forest areas may serve as corridors to facilitate species movements under climate change. Riparian forest areas are also important for PNW forest-dependent amphibians as they provide cool, moist microclimates (Anderson et al. 2007; Olson and Kluber 2014). High values of the riparian index, which integrates five attributes, are generally found in mountainous areas and characterize riparian areas that are most expected to support climate adaptation because they: (1) span large temperature gradients; (2) have high canopy cover; (3) have low levels of solar exposure; (4) are relatively wide; and/or (5) have minimal human alteration. Corridors were defined as the potential riparian area that runs longitudinally along a stream from the outlet up through the hydrologic network of a watershed, ending at the stream initiation point. The indices were provided for sixth- through first-level HUCs, corresponding to index values of progressively longer downstream potential riparian corridors from the headwaters to the outlet. We used only the sixth-level HUC (HUC12) index attributed to points at the headwaters of each watershed since torrent salamanders are headwater stream-associated species and downstream corridors are likely less relevant to their movement. We performed a nearest-neighbor join function to attribute those index values to nearby torrent salamander sampling locations and scaled the index from 0 to 1.

2.3.3 | Hydrological and Water-Balance Variables

We obtained estimates of streamflow permanence from PROSPER (Sando and Hockman-Wert 2019; Jaeger et al. 2019), a raster-based empirical model that provided probabilistic predictions of stream channels having year-round surface flow for any unregulated and minimally impaired stream channel. The model provides annual predictions for 2004–2016 at 30-m resolution. We also obtained historical streamflow metrics for the western U.S. from Wenger et al. (2010), including annual and seasonal discharge values. Streamflow metrics were based on daily simulations of variable infiltration capacity (VIC) hydrologic-model outputs used to calculate a set of summary flow metrics that describe key attributes of the flow regime for each stream segment in the 1:100,000-scale National Hydrography Dataset for the period 1977–2006.

We obtained multiple water-balance metrics from several sources. First, we obtained precipitation and maximum vapor-pressure deficit (VPD) data from PRISM (Parameter-elevation Relationships on Independent Slopes Model) version AN81 at 800-m spatial resolution, available as continuous rasters of daily values (Daly et al. 2008). We derived metrics for winter and summer conditions for the seasons spanning 01 November–31 March and 01 June–31 August, respectively. We additionally included the growing season (01 April–15 October) for precipitation. Second, we obtained spatially gridded, monthly water-balance model data from Tercek et al. (2018) at 1-km resolution for actual evapotranspiration (AET), moisture deficit, and soil-water storage, available via a THREDDS server (Appendix S2: Table S1). The water-balance values were then calculated as either sums (AET and moisture deficit) or means (soil-water storage) for the winter (01 November–31 March) and summer (01 June–31 August) months. Lastly, we obtained daily snow-water equivalent (SWE) and water vapor-pressure data from DAYMET (Thornton et al. 2020) at 1-km resolution, available as NetCDF rasters. We stacked and subset SWE rasters by winter season (01 November–31 March) and conducted cell-by-cell calculations of the cumulative sum of SWE (i.e., total accumulation) for the winter season.

For each water-balance variable, we summarized prevailing conditions as preceding 5-year means and standard deviations. The 5-year means and standard deviations were calculated as the means and standard deviations of annual or seasonal means (or totals) across the 5 years prior to our surveys (inclusive of survey year). These 5-year means and standard deviations were chosen to avoid potential biases arising from anomalous conditions within a single year or season.

2.3.4 | Climatic Variables

We characterized ambient air temperatures for different seasons using 30-m resolution PRISM climate data (Daly et al. 2008). Methods for extracting temperature data followed the same procedure as for precipitation and VPD (see section on hydrological and water-balance variables). We additionally derived heat-stress values based on hypothesized thermal optima. Brattstrom (1963) determined *Rhyacotriton* (species unknown) had a low critical thermal maximum (CT_{max}) of 28.3°C. Bury (2008) determined adult *R. variegatus* reached CT_{max} at 27.9°C (±1.1°C; larvae ranged 26.7°C ± 0.7°C). We used this information on CT_{max} for *Rhyacotriton* to derive a heat-stress variable that reflects exceedances in temperature tolerance, defined as the total number of days exceeding the

predetermined threshold temperature (T_{Max}) of 27.9°C in the summer season. Note that *R. variegatus* occurs south of both our focal species and, therefore, CTM for *R. variegatus* may slightly differ. Heat stress was measured as the total number of days throughout the summer season when $T_{Max} \geq 27.9$°C (and summarized as 5-year mean and standard deviation). We also obtained modeled mean August stream temperatures, averaged for 1993–2011, from NorWeST (Isaak et al. 2017) at 1-km intervals along stream channels. Most headwater streams surveyed in this study are not included in the NorWeST dataset; therefore, temperature values of nearest neighbor streams were used as proxies.

Spatial data manipulation and calculations of climate variables in R were conducted using packages *tidyverse* 2.0.0 (Wickham et al. 2019), *dplyr* 1.1.4 (Wickham et al. 2023), *gtools* 3.9.5 (Warnes et al. 2023), *purrr* 1.0.2 (Wickham and Henry 2023), *raster* 3.6-26 (Hijmans 2023), (Pebesma 2018; Pebesma and Bivand 2023) and *terra* 1.7-78 (Hijmans 2024).

2.4 | Variable Selection

To reduce the number of variables used in analyses, we calculated all pairwise Pearson's product moment correlation coefficients (r) and used a predetermined threshold of $r \leq -0.7$ or ≥ 0.7 to identify pairs of variables that were too highly correlated for both to be included in the model. The variable within a correlated pair that had more ecological relevance was retained. Variables that had multiple high intercorrelations with other variables of ecological meaning were removed.

2.5 | Statistical Modeling

We used boosted-regression trees (BRTs) to identify predictors of torrent salamander occurrence and to inform habitat suitability. BRTs construct many individual regression trees that recursively partition the response variable(s) given a candidate set of predictor variables, and then use a stochastic machine-learning technique (boosting) to ensemble individual regression trees (De'ath 2007; Elith et al. 2008). A gradient boosting machine-learning algorithm was used because it allows for the simultaneous consideration of nonlinearities, different scales of measurement, and interactions. For the construction of occurrence (presence/absence) models, we used a binomial distribution, with a learning rate of 0.001, bag fraction of 0.5, and a tree complexity of 3, to allow for two- and three-way interactions to be considered.

We followed a BRT model simplification procedure described in Elith et al. (2008) that used 10-fold cross-validation (CV) to assess changes in predictive deviance relative to the full model when a predictor is removed; akin to a backward selection process in linear regression. The procedure then used average CV error to determine the optimal predictors for removal. We conducted 10 runs per species and calculated the number of runs (out of 10) that each predictor was identified for removal and removed predictors that were identified in at least 50% of model simplification runs.

We evaluated BRT model performance using three statistics: (1) the CV estimate of predictive deviance (a measure of how well the models predicted the subsets of withheld data; Buston and Elith 2011); (2) the percentage of deviance in the response variable explained by the model; and (3) the mean area under the curve of the receiver-operator characteristic (ROC-AUC). Predictive deviance is a common loss function in boosted-regression analysis used to measure the performance of the model, wherein the goal is to minimize predictive deviance and improve model accuracy through an iterative process until the model reaches an optimal level of performance. ROC-AUC values range from zero to one, wherein an ROC-AUC value of 0.5 represents model performance no better than chance, and values increasing toward 1 indicate improved model ability to discriminate presence from absence observations. We report the relative influence of predictor variables, which is a measure based on the number of times a variable is selected for splitting, weighted by the squared improvement to the model as a result of each recursive split, and averaged over all trees. The relative influence (or contribution) of each variable is scaled so that the sum adds to 100, with higher numbers indicating stronger influence on the response. Following Elith et al. (2008), we examined the magnitude of pairwise interaction effects by quantifying the residual variance of a linear model fitted to determine the influence of the variable interaction on overall model variance. A residual variance of zero indicates no interaction, with increasing residual variance signaling greater interaction strength. BRT analyses were conducted in R using packages *gbm* 2.2.2 (Ridgeway and GBM Developers 2024) and *dismo* 1.3-14 (Hijmans et al. 2023).

2.6 | Habitat Suitability

Using rasters for each of the variables selected from the BRT models, we first resampled rasters to a common resolution (30 m) using bilinear interpolation, as needed, and masked all rasters to stream reaches. The fitted BRT models were used to predict habitat suitability (i.e., probability of occurrence based on highest performing environmental predictors; Table 1) using the *predict* function in the R *terra* package (Hijmans 2024). Occurrence probability, or the likelihood the species is present at a given location, puts the focus on habitat characteristics influencing species presence rather than species detection, which assumes the species is present. For predictions of habitat suitability across the landscape, we added HUC12 watersheds without torrent salamander observations to fill in gaps in the distributions of both species (i.e., watersheds that serve as important connections on the landscape between watersheds with torrent salamander observations). See Appendix S2: Figure S1 for an overview of these gap-watersheds. The resulting output provides stream reach-level habitat-suitability rasters. Although the species distribution models were built on presence/absence data collected via this study and collated from historical records, species counts were also made at sites surveyed in 2019. We used these count data to examine the relationship between species' counts and predicted habitat suitability. We summarized the predicted habitat suitability at sites for which counts were measured by creating a 100-m buffer around sampling sites and calculating the median habitat-suitability score within each buffer. Buffers of 100 m were created to capture variability in habitat suitability at a spatial scale relevant to torrent salamander movement. We

TABLE 1 | Final suite of variables included in boosted-regression trees for Cascade torrent (*Rhyacotriton cascadae*) and Columbia torrent (*R. kezeri*) salamanders, their associated variable groups, and descriptions.

Group	Variable	Description	Cascade torrent salamander	Columbia torrent salamander
Topographic	**Aspect**	Compass direction (in degrees) of a topographic slope	X	X
	Slope	Measure of steepness (i.e., degree of inclination)	X	X
	Topographic Wetness Index (TWI)	An index of the effect of local topography on runoff flow direction and accumulation	X	
Riparian habitat	**Canopy cover**	Sum of percent canopy cover of live trees	X	X
	Riparian Climate Corridor Index (RCCI)	An index of how well riparian forest areas may serve as corridors to facilitate species movements under climate change	X	X
	Stand height	Mean height of all dominant and codominant trees (in m)	X	
	Number of trees per hectare (TPH)	Density of live trees (i.e., number of trees per hectare) ≥ 2.5 cm DBH	X	X
	Volume of trees per hectare (VPH)	Volume of live trees ≥ 2.5 cm DBH (in m^3/ha)		X
Water balance and hydrology	25-year flood	Annual maximum series of flows (i.e., the highest flow each year) for the historical period (1977–2006) which occurs every 25 years on average		X
	Actual evapotranspiration (AET; mean)	Preceding 5-year mean of total daily AET (in mm) during peak summer	X	
	Actual evapotranspiration (AET; SD)	Variation (std. deviation) in preceding 5-year mean of total daily AET (in mm) during peak summer		X
	Base flow index	Historical mean (1977–2006) ratio of the lowest 7-day flow of summer (May 1–September 30) to the average annual flow	X	X
	Growing-season precipitation (mean)	Preceding 5-year mean of total daily precipitation (in mm) during the growing season		X
	Mean August flow	Historical mean (1977–2006) of daily August cumulative discharge values	X	
	Snow-water equivalent (SWE; mean)	Preceding 5-year mean of the cumulative sum of daily snow-water equivalent (in kg/m^2) during winter		X
	Soil-water storage (mean)	Preceding 5-year mean of mean daily soil-water storage (in mm) during peak summer		X
	Streamflow permanence (PROSPER; mean)	12-year mean probability of streamflow permanence	X	X

(Continues)

TABLE 1 | (Continued)

Group	Variable	Description	Cascade torrent salamander	Columbia torrent salamander
	Streamflow permanence (PROSPER; SD)	Variation (std. deviation) in 12-year mean probability of streamflow permanence	X	X
	Summer maximum vapor-pressure deficit (SD)	Variation (std. deviation) in preceding 5-year mean daily maximum vapor-pressure deficit (VPD; in hPa) during peak summer	X	
	Summer water vapor pressure (mean)	Preceding 5-year mean of mean daily water vapor pressure (in Pa) during peak summer	X	X
	Summer water vapor pressure (SD)	Variation (std. deviation) in preceding 5-year mean of mean daily water vapor pressure (in Pa) during peak summer	X	
	Winter maximum vapor-pressure deficit (mean)	Preceding 5-year mean daily maximum VPD (in hPa) during winter	X	
	Winter maximum vapor-pressure deficit (SD)	Variation (std. deviation) in preceding 5-year mean daily maximum VPD (in hPa) during winter	X	X
	Winter precipitation (SD)	Variation (std. deviation) in preceding 5-year mean of total daily precipitation (in mm) during winter	X	
	Winter water vapor pressure (mean)	Preceding 5-year mean of mean daily water vapor pressure (in Pa) during winter	X	
Temperature	August stream temperature	19-year historical average August stream temperatures (1993–2011)		X
	Heat stress (SD)	Variation (std. deviation) in preceding 5-year mean heat stress (total number of days throughout the peak summer season when $T_{Max} \geq 27.9°C$)	X	X
	Summer maximum temperature (SD)	Variation (std. deviation) in Preceding 5-year mean of mean daily maximum temperature (in °C) during peak summer		X
	Summer mean temperature (mean)	Preceding 5-year mean daily temperature (in °C) during peak summer		X
	Summer mean temperature (SD)	Variation (std. deviation) in preceding 5-year mean daily temperature (in °C) during peak summer	X	
	Summer temperature range (mean)	Preceding 5-year mean daily temperature range (difference between T_{Min} and T_{Max}; in °C) during peak summer	X	
	Winter mean temperature (mean)	Preceding 5-year mean daily temperature (in °C) during winter		X
	Winter mean temperature (SD)	Variation (std. deviation) in preceding 5-year mean daily temperature (in °C) during winter	X	X
	Winter temperature range (mean)	Preceding 5-year mean daily temperature range (difference between T_{Min} and T_{Max}; in °C) during winter		X
	Winter temperature range (SD)	Variation (std. deviation) in preceding 5-year mean daily temperature range (difference between T_{Min} and T_{Max}; in °C) during winter	X	

Note: The abbreviation, "SD," refers to standard deviation. Variables selected for inclusion in final BRT models for both species are bolded.

chose to report the median score because it better represents the central tendency for skewed distributions of data (i.e., skewed toward lower count values).

3 | Results

Columbia torrent salamanders were found at 36 of 50 sites surveyed in 2019 (mean counts = 11.90 ± 17.22 SD individuals/person-hour at a surveyed site), whereas Cascade torrent salamanders were found at only 16 of 48 sites (mean counts = 3.48 ± 6.78 SD). Average historical, site-level counts of Columbia torrent salamanders were 10.17 (±14.10 SD) individuals/person-hour, and Cascade torrent salamanders were 4.98 (±13.34 SD) individuals/person-hour. The final BRT models were fitted with 10-fold cross-validation using 2350 trees for the Cascade torrent salamander model and 950 trees for the Columbia torrent salamander model. Predictive performance was estimated from the subset of data excluded from model fitting. The cross-validation estimate of mean predictive deviance (i.e., prediction error) in the Cascade torrent salamander model was 0.48 (±0.03), with 43% of the deviance in the response explained by the model. The final model had an ROC-AUC score of 0.71 (±0.06). The cross-validation estimate of mean predictive deviance in the Columbia torrent salamander model was 0.267 (±0.07), with 40% of the deviance in the response explained by the model. The final model had an ROC-AUC score of 0.72 (±0.07).

3.1 | Cascade Torrent Salamander

Seasonal temperature and water-balance metrics were key predictors of Cascade torrent salamander habitat suitability, comprising most of the variable influence on predicted occurrence (24.03% and 45.94%, respectively, of the total relative influence) (Figure 1a). Topographic, hydrological, and riparian forest conditions accounted for 12.18%, 11.04%, and 6.81% of the variable influence, respectively. Five of the top eight most important predictors of habitat suitability were seasonal atmospheric moisture conditions. Atmospheric moisture metrics (a subcategory of the water-balance metrics) accounted for 40.28% of the total relative influence across all covariates. The relationship between most of these metrics and predicted occurrence forms a bell-shaped curve. Therefore, highest habitat suitability is associated with moderate or intermediate levels of these factors (Appendix S3: Figure S1). For instance, variation in summer maximum vapor-pressure deficit, a measure of variability in evaporative water loss, had the highest relative influence of any variable, with predicted occurrence peaking at low to moderate levels of variability in this metric. Similarly, Cascade torrent salamanders appear to be most highly associated with low to moderate levels of several other water-balance factors, including variability in winter precipitation, variability in winter maximum vapor-pressure deficit, winter water vapor pressure, and actual evapotranspiration. Together, these variables indicate habitat suitability declines with increasing extremes in water-balance conditions. However, a positive linear relationship was evident with summer water vapor pressure (i.e., humidity), which had substantial influence on predicted habitat suitability for this species (Appendix S3: Figure S1). Summer air temperature range, a measure of the difference in daily minimum and maximum temperatures, had the strongest relative influence of any temperature-related variable. The probability of occurrence for Cascade torrent salamanders was highest in areas with low-to-moderate temperature differences in the summer. Examination of residual variances used to indicate significant interactions among covariates from the fitted model revealed 29 variable pairs as having non-zero residuals (Appendix S3: Table S1), with 21 of the pairwise interactions including the top five most influential variables (summer maximum vapor-pressure deficit, summer temperature range, winter water vapor pressure, Topographic Wetness Index, and summer water vapor pressure). However, residual variances were close to zero and, therefore, only marginally significant.

Habitat-suitability values for Cascade torrent salamanders ranged from 0.06 to 0.99 at the stream-reach level and are summarized at the HUC12 watershed level (Figure 2), with an example of the finest resolution of habitat-suitability data (30-m) provided for the Little Nisqually watershed (Figure 3). The relationship between median habitat-suitability values and Cascade torrent salamander counts from field surveys was log-linear ($F_{1,46} = 32.62$, $p < 0.001$), wherein the number of individuals observed increases logarithmically with increasing habitat-suitability values (Appendix S3: Figure S3a). A steep increase in counts occurs above suitability values of 0.8.

3.2 | Columbia Torrent Salamander

The top eight most influential predictors of Columbia torrent salamander habitat-suitability were an almost equal representation of the different categories of covariates. Slope was the top predictor of habitat suitability (19.65% relative influence; Figure 1b). Probability of occurrence increases with increasing slope, a typical feature of headwater stream systems (Appendix S3: Figure S2). Water-balance metrics comprised the majority of the total variable influence on predicted occurrence (28.9%), most notably mean summer water vapor pressure and variation in actual evapotranspiration. Temperature variables were the most represented of all the categories across the model set, but comprised the second lowest percentage of variable influence (17.84%). Riparian habitat and hydrological metrics accounted for 11.95% and 21.67% of the total variable influence, respectively. Climatic and water-balance conditions in the summer were highly influential, with higher habitat suitability associated with increasing water vapor pressure and low to moderate variability in actual evapotranspiration in the summer. Probability of occurrence, and thereby habitat suitability, declined with increasing mean temperature in the summer. With respect to stream hydrology, probability of occurrence was greater with lower base flows and low to moderate variability in streamflow permanence. Higher percent canopy cover, associated with a moderate volume of trees per hectare, was also indicative of higher suitability habitat. Examination of residual variances used to indicate significant interactions among covariates from the fitted model revealed 26 variable pairs as having non-zero residuals (Appendix S3: Table S1), with 23 of the pairwise interactions including the top five most influential variables (slope, mean summer water vapor pressure, Base Flow Index, variation in actual evapotranspiration, and variation in

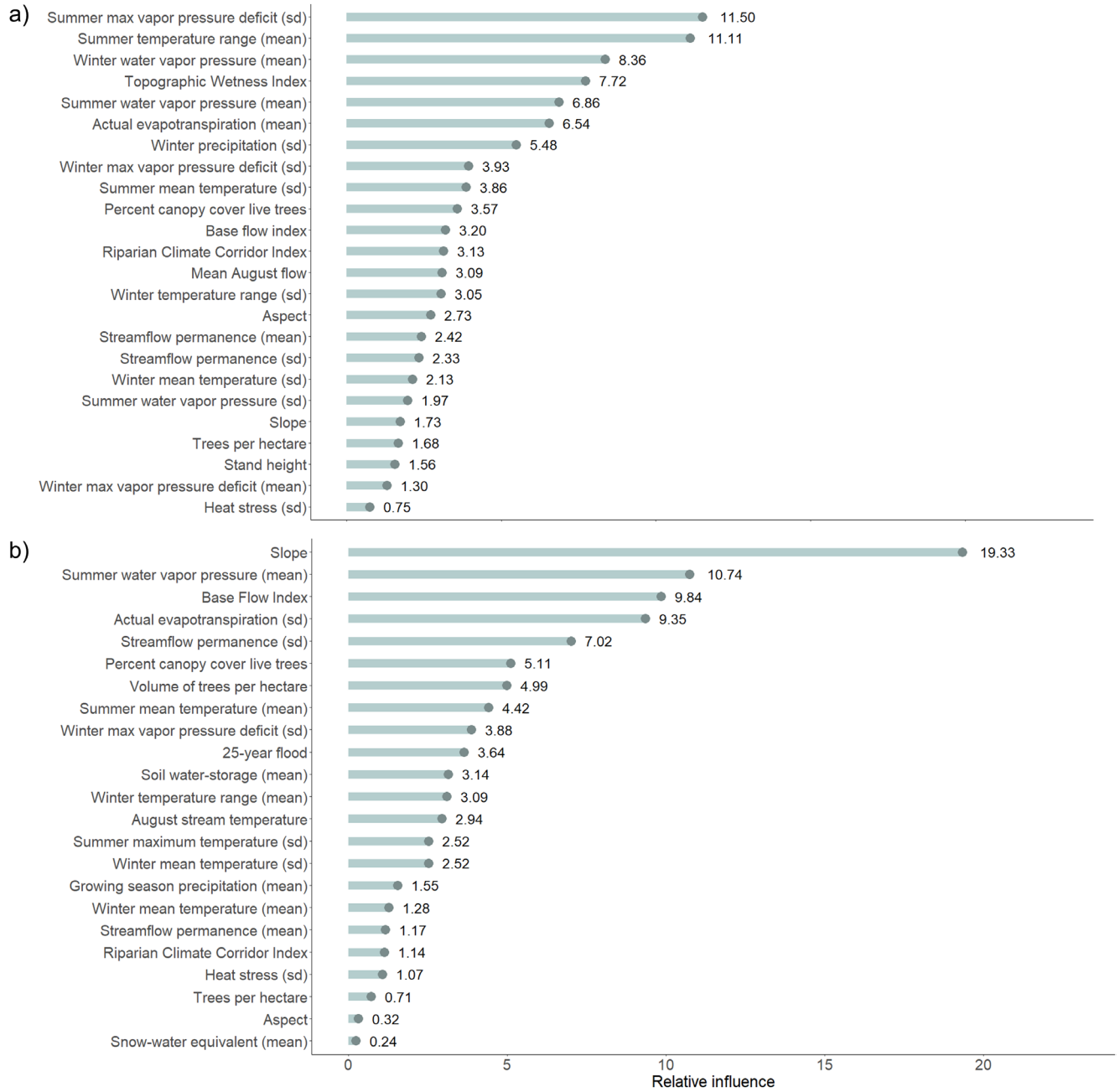

FIGURE 1 | Predictor variables, ordered by relative influence (%), identified from a boosted-regression tree model developed with cross-validation (after model simplification procedure) and used in spatial prediction of habitat suitability for the (a) Cascade torrent salamander and (b) Columbia torrent salamander.

streamflow permanence). However, residual variances were close to zero and, therefore, only marginally significant.

Habitat-suitability values for Columbia torrent salamanders ranged from 0.13 to 0.99 at the stream-reach level and were summarized at the HUC12 watershed level (Figure 4). The relationship between median habitat-suitability values and Columbia torrent salamander counts from field surveys exhibited a log-linear relationship ($F_{1,48} = 36.29$, $p < 0.001$), wherein the number of individuals observed increases gradually (and logarithmically) with increasing habitat-suitability values beginning around 0.6 (Appendix S3: Figure S3a). The main difference between this modeled relationship and that of Cascade torrent salamanders is the greater steepness in the relationship gradient and frequency of zeros (presumed absences) seen in the latter.

4 | Discussion

This study represents the first comprehensive, rangewide assessment of torrent salamander distributions and watershed-scale habitat associations. Using a robust process of model development and refinement, our results support Columbia torrent salamanders as being generally more widespread throughout their range and having higher local counts than Cascade torrent salamanders. As evidenced by our 2019 field surveys,

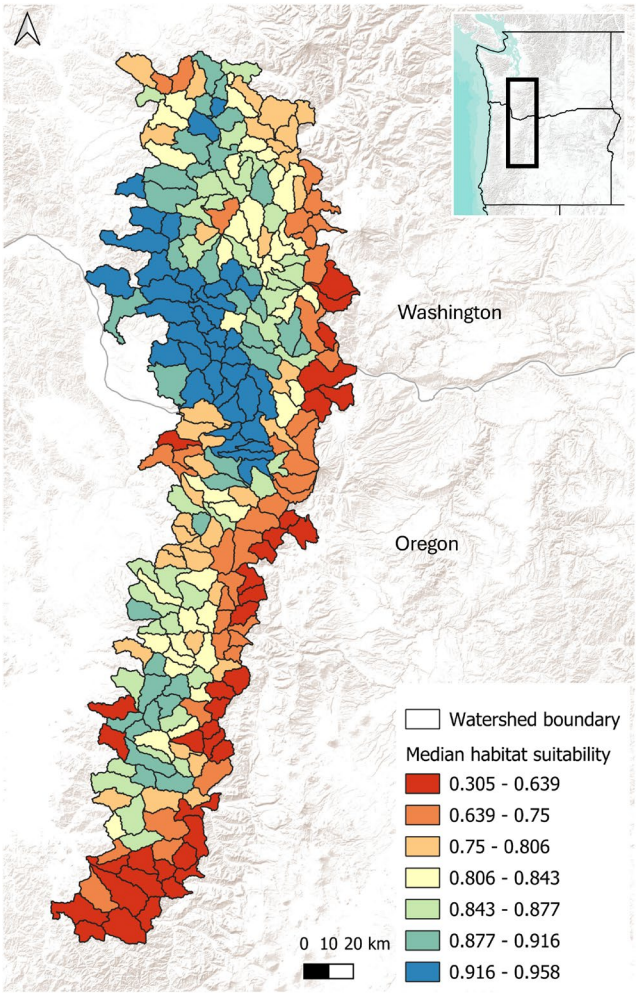

FIGURE 2 | Median habitat-suitability (index scaled from 0 to 1; lowest to highest suitability) at the HUC12 watershed level for the Cascade torrent salamander.

Columbia torrent salamanders were found at the majority (72%) of sites surveyed, whereas Cascade torrent salamanders were found at only 33% of sites surveyed. Fewer observations of Cascade torrent salamanders during our surveys could have been due to less accurate preliminary habitat association models. However, historical datasets reflected similar patterns of occurrence across the distribution of both species. Among historical observations, Cascade torrent salamanders tend to have fewer and more variable counts relative to Columbia torrent salamanders. Collectively, our results suggest that Cascade torrent salamanders may be more sensitive to environmental change or disturbances owing to their more fragmented distribution and variable counts. Our results offer important considerations for the development of effective watershed-scale management plans to address species conservation.

Our analyses of habitat suitability found a significant, positive relationship between species counts and habitat-suitability values for both species. Cascade torrent salamanders exhibit a steeper relationship between observed counts in the field and modeled habitat suitability. This may be due to detectability, high habitat specialization, or population declines in suboptimal areas, but it could also be a consequence of seasonal drought conditions experienced in the Cascade Range during the spring and summer of 2019. Prolonged drought may have resulted in lower detectability, particularly in less-suitable habitats, if animals were seeking refuge. Torrent salamanders are known to migrate vertically through substrates to use subsurface moisture, flows, or groundwater during dry conditions, which can also affect detectability (Howell and Maggiulli 2011). Further investigation into fine-scale habitat requirements and utilization would improve our understanding of potential drivers of population declines and range contraction, if they are occurring as expected. Paired with the results from our habitat-suitability model, our Cascade torrent salamander survey findings support a strong association with—or sensitivity to—key climatological conditions like temperature and moisture measured at macroecological scales.

Seasonal and interannual stability in temperature and moisture conditions, across both summer and winter, was a key determinant of higher habitat-suitability for Cascade torrent salamanders. Two components of atmospheric moisture were considered important to characterizing habitat suitability, including vapor-pressure deficit and water vapor pressure. Water vapor pressure is the pressure at which atmospheric water vapor is in thermodynamic equilibrium with its condensed state. As water vapor pressure increases (approaching dew point), gaseous water condenses to liquid, whereas at lower pressures it evaporates or sublimates. Cascade torrent salamander occupancy was positively associated with habitats retaining higher seasonal water vapor pressure (i.e., humidity) in both summer and winter.

Vapor-pressure deficit (VPD) represents the holding capacity for more water vapor in the air and has a linear relationship to the rate of evapotranspiration and other measures of evaporation. VPD is expected to rise globally due to the combination of increased temperature and, depending on the region, decreased relative humidity (Yuan et al. 2019). High VPD results in increased rates of water loss from moist soils, causing drying and heating of the terrestrial surfaces and contributing to drought events and plant water stress (Dai 2013). The significant relationship between VPD and Cascade torrent habitat suitability was based on variability in maximum VPD, rather than mean conditions, and showed a greater association with less extreme VPD values. Disentangling VPD effects from other climatic forces can be quite challenging (Grossiord et al. 2020), as exemplified by numerous interactions between VPD and other temperature and moisture metrics (Appendix S3: Table S1). For instance, high VPD conditions usually occur concurrently with drought and heat waves (Grossiord et al. 2020). Inclusion of moisture metrics like VPD in habitat-suitability modeling offers a new and noteworthy approach to characterizing species-climate relationships, particularly for desiccation-intolerant species like torrent salamanders and other riparian-associated species. Emerging research in ungulates (Harris et al. 2015), small mammals (Johnston et al. 2019, 2021), and other salamanders (Riddell et al. 2017) reveals the importance of considering moisture—and specifically VPD—when characterizing climatic influences on species distributions. In some instances, moisture retention can buffer species from the effects of temperature extremes (McArthur 1991; Davis et al. 2019) during periods of snow drought or heat waves, at least for a short period.

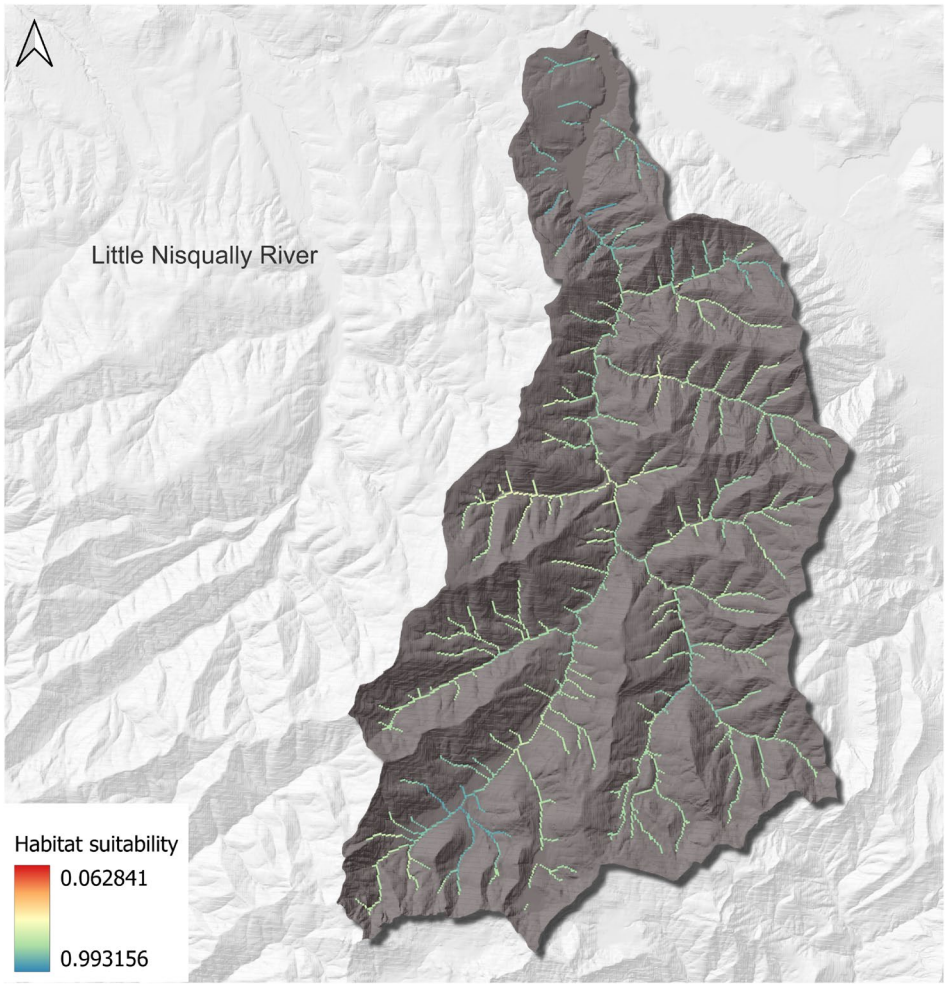

FIGURE 3 | Example of habitat suitability (index scaled from 0 to 1; lowest to highest suitability) at 30-m resolution for stream reaches in the Little Nisqually watershed of Washington.

We aimed to further capture climatic extremes and variability in our variable suite through derivation of a heat-stress variable. Heat stress was measured as the mean number of days that maximum temperature was equal to or exceeded 27.9°C (approximate CT_{max} of *Rhyacotriton* spp.) during the peak summer season. Although heat stress was not a top predictor of either species' habitat suitability, variation in heat stress was included in the final fitted models. For Cascade torrent salamanders, this relationship was further supported by the greater influence of summer temperature range in the fitted model, reflecting an association with narrower temperature ranges and temperature stability during the summer (i.e., year-to-year consistency in temperatures within a narrower range of variability). The significance of various moisture and temperature variability metrics likely reflects the delicate balance of evaporative cooling, condensation (humidity), and precipitation that is historically a predominant feature of the Cascades region.

Habitat suitability for Columbia torrent salamanders was largely reflective of the topographic features (e.g., slope) of headwater streams and their influence on water balance in the system. Streamflow conditions were a stronger determinant of habitat suitability for Columbia torrent salamanders than for Cascade torrent salamanders, with both base flow and streamflow permanence identified as highly influential variables. Probability of occurrence was greater with lower base flows but low to moderate variation in streamflow permanence, demonstrating their association with seasonally intermittent headwater streams. Lower August stream temperatures were also a moderately important feature of Columbia torrent salamander habitat. Headwater stream temperatures were extrapolated from the NorWeST model (Isaak et al. 2017), which does not include data for most headwater stream reaches. Leach et al. (2017) illustrated how headwater stream temperatures were much more variable within and across seasons than higher-order streams (as modeled in NorWeST), even though average temperatures may be congruent. Leach et al. (2017) hypothesized that divergence in headwater vs. higher-order stream temperatures was likely due to the model's dependence on geomorphological factors that influenced surface-water energy exchange, rather than thermal influences of groundwater interactions. Given the marginal importance of lower August stream temperatures (extrapolated from NorWeST) to Columbia torrent salamander habitat, the model may better approximate headwater stream conditions within a lower range of temperatures and, thus, exhibit greater decoupling at higher temperatures.

Riparian forest characteristics showed higher importance as features of landscape-scale (macroecological) habitat suitability for Columbia torrent salamanders than for Cascade torrent

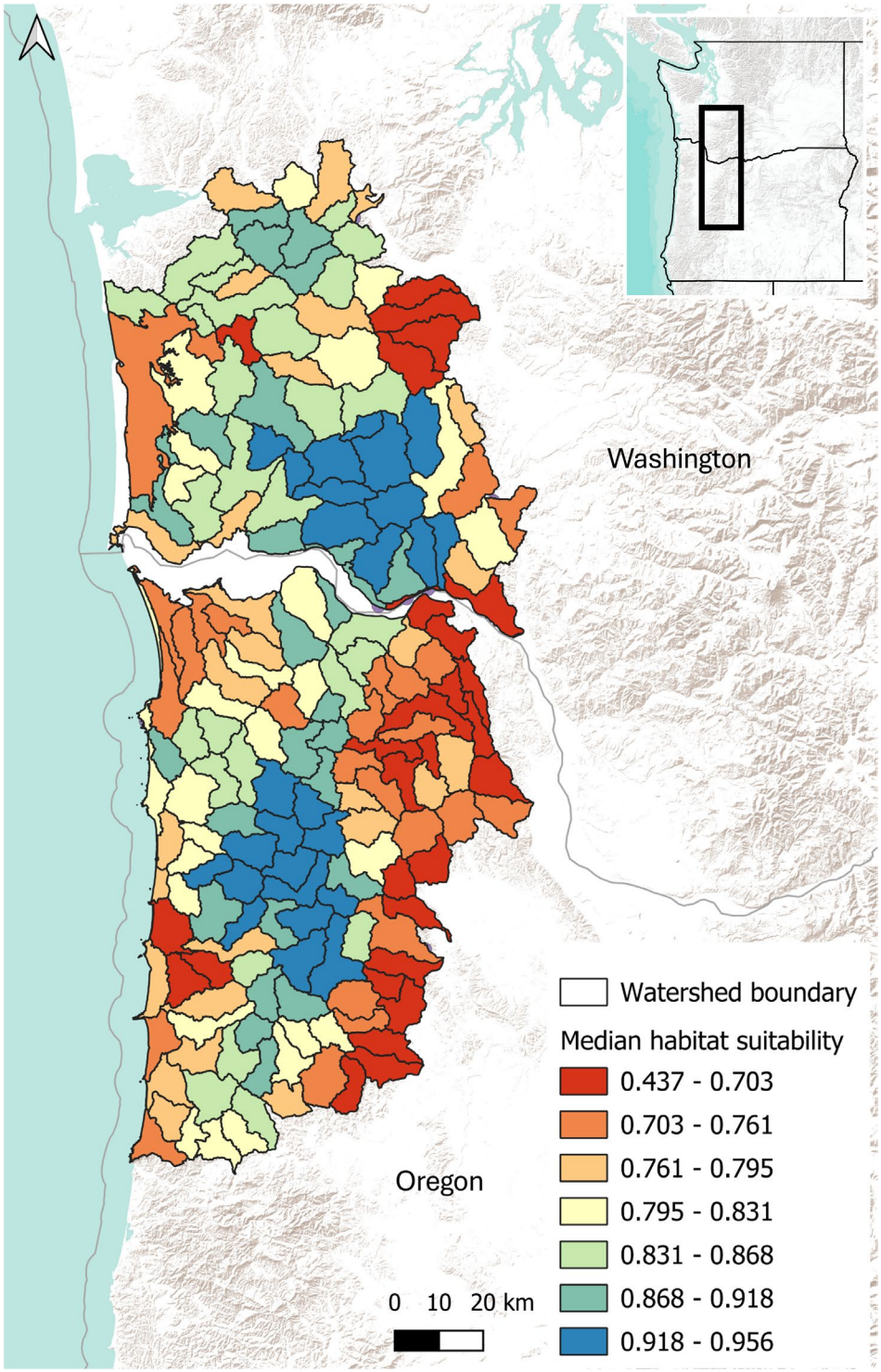

FIGURE 4 | Median habitat suitability (index scaled from 0 to 1; lowest to highest suitability) at the HUC12 watershed level for the Columbia torrent salamander.

salamanders. Percent canopy cover of live trees and volume of trees per hectare were top predictors. We hypothesize that the relatively low influence of these predictors is not indicative of a lack of ecological relevance; instead, finer-scale processes like disturbance, management of riparian forest structure, and groundwater interactions (and their effects on microclimates) are not adequately captured in the types of spatial datasets available for this analysis (e.g., Rykken et al. 2007). We suggest broad-scale habitat-suitability information, such as that provided in this study, be paired with assessments of finer-scale habitat associations (e.g., substrate types, riparian buffer widths, forest stand conditions, microclimates) to inform multi-scale conservation prioritization. Finer-scale assessments will continue to be important for species like torrent salamanders that move locally between aquatic, semi-aquatic, and terrestrial (riparian) habitats throughout the year.

Our results elevate the threat that climate change may pose to torrent salamanders and their habitats in the Pacific Northwest. Air temperatures have increased across the region, with an average warming of almost 2°F since 1900 (Chang et al. 2023). Warming is predicted to continue to occur during all seasons, with annual average temperatures projected to increase by 4.7°F–10.0°F by the 2080s (representing the range of the low to high emissions scenarios: SSP1-2.6 and SSP5-8.5). Future changes in headwater stream temperatures are less certain, with estimates of in-stream warming of 0.73°C–1.42°C by mid-century (Isaak et al. 2017) that are expected to be highly sensitive to changes in ambient conditions (Leach and Moore 2019). The response of historically cold streams to climate warming will depend on myriad factors, such as snowpack, groundwater exchange, antecedent conditions, and thermal memory (Leach and Moore 2019), as well as secondary influences such as disturbance, riparian vegetation structure, forest-harvest practices, and other human influences (Arismendi et al. 2012). Interannual variability in precipitation is projected to persist, and observed lower streamflow in summer is expected to decrease even further due to reduced snow storage, increased evapotranspiration, and longer lags between summer precipitation events (Dalton and Fleishman 2021). Warming air temperatures and altered precipitation will affect several hydrological processes, including the amount, timing, and type of precipitation (Luce et al. 2012, 2013). Hydrological responses to climate change, such as changes in streamflow (Hidalgo et al. 2009; Olson and Burton 2019) and stream temperatures (Isaak et al. 2012; Luce et al. 2014), will depend upon the dominant form of precipitation in a particular watershed along with forest cover and groundwater characteristics. In general, earlier and lower spring peak flow, higher winter flow, and lower late-summer flow (Raymondi et al. 2013), along with more frequent extreme hydrological events (Tohver et al. 2014) are expected.

Stream-associated species like torrent salamanders will be challenged to either persist-in-place or shift-in-space (*sensu* Thurman et al. 2020) under these changing conditions. Given the overlap among climate change factors and habitat-suitability characteristics for torrent salamanders, identification of climate change refugia (Michalak et al. 2020; Morelli et al. 2020) to support conservation prioritization is a practical next step. In turn, identification of optimal habitat conditions in connectivity corridors among headwater refugia may promote overland dispersal of terrestrial adults (Olson and Burnett 2009, 2013; Olson and Kluber 2014). In particular, identification of optimum ecohydrological refugia (i.e., aquatic or mesic environments that are relatively buffered from climate change; McLaughlin et al. 2017) will be critical for protecting these vulnerable species from drought and warming. Areas with a higher probability of maintaining surface or groundwater in drought years (Cartwright et al. 2020), or areas slightly or temporarily decoupled from temperature changes in the surrounding landscape (e.g., maintenance of cool, moist "stream effect"; Olson et al. 2007) can act as oases that facilitate species' adaptive capacity and reduce extinction risks. Refugia identification at macro- and micro- habitat scales may be particularly important for Cascade torrent salamanders owing to the concentration of suitable habitat in the north-central portion of their range surrounding the Columbia River (Figure 2) and their low dispersal capacity. Torrent salamanders have limited capacity for long-distance dispersal that is likely further constrained by fragmentation of suitable habitat resulting from interacting disturbances like climate change, forest management, and roads, which can affect population genetic structure and gene flow (Emel et al. 2019). Although areas of higher habitat suitability appear more contiguous across the range of Columbia torrent salamanders, the species is exposed to widespread land management and timber-harvest practices. Hence, simultaneously with refugia identification, the maintenance or restoration of connectivity areas among headwater streams and over ridgelines (Olson and Burnett 2013) may provide the dual benefit of facilitating persistence (or adaptation) in situ as well as access to nearby suitable habitat to support climate tracking across neighboring drainages.

5 | Conclusions

Headwater streams are integral components of forest ecosystems in the Pacific Northwest not only because they contribute to water supply and storage, buffer against extreme flooding events, and maintain sediment transport, but also because they are critical pinch points in the ecological connectivity both to downstream channels and upland forests. Many headwater stream-associated species are in peril, including torrent salamanders, whose strong association with cool, moist microclimates and seasonally discontinuous streams will likely leave them vulnerable to climate change because of drought and habitat loss. Here, we used modern habitat-modeling approaches and metrics to demonstrate the different ecologies of sister species. Our results indicate that Cascade torrent salamanders may be of heightened conservation concern due to their narrow environmental tolerances. Climate-smart conservation planning will be critical to minimize negative effects of watershed-scale climatic changes on these vulnerable species' unique headwater ecosystems, including changes to atmospheric conditions as well as ground-level disturbances affecting overstory conditions and consequently riparian microclimates.

Author Contributions

Lindsey L. Thurman: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, visualization, writing – original draft, writing – review and editing. **Christopher Cousins:** data curation, project administration, resources, writing – review and editing. **Tiffany S. Garcia:** conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, writing – review and editing. **Deanna H. Olson:** conceptualization, funding acquisition, investigation, methodology, project administration, resources, writing – review and editing. **Brooke E. Penaluna:** conceptualization, funding acquisition, investigation, methodology, project administration, resources, writing – review and editing.

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Ethics Statement

Appropriate permits were obtained (WA DNR License No. 60-PC2003; ODF Permit No. 314.37277; ODFW Permit No. 069-19; WDFW Permit No. 19-076; Oregon State University Animal Care and Use Protocol No. 5148; U.S. Forest Service Animal Care and Use Protocol No. 2019-004). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

GIS products will be made publicly available through USGS ScienceBase.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Preliminary habitat association models. **Table S1:** Environmental variables and their units of measurement, resolution, geographic coordinate systems (and projections, if applicable), and data sources. **Figure S1:** Results from ecological-niche factor analysis for the Columbia torrent and Cascade torrent salamanders, indicating a gradation in the degree of association between species' occurrences and modeled habitat conditions. Sampling sites are indicated by black points. **Appendix S2:** Observational data and predictor variable suite. **Figure S1:** Locations of 2019 survey sites and watersheds included in mapping habitat suitability for Columbia torrent salamanders (distribution on left of map) and Cascade torrent salamanders (distribution on right of map). **Table S1:** Predictor variables, units, resolution, geographic coordinate systems (and projections), and data sources. **Appendix S3:** Model performance and results. **Figure S1:** Partial dependence plots for the top eight most influential variables showing the marginal effect of each variable on predicted occurrence of Cascade torrent salamanders. **Figure S2:** Partial dependence plots for the top eight most influential variables showing the marginal effect of each variable on predicted occurrence of Columbia torrent salamanders. **Figure S3:** Habitat-suitability thresholds identified by relationships between counts of individuals taken from surveys in 2019 and median habitat-suitability scores (extracted from within 100 m of each sampling site) for the (a) Cascade torrent salamander and (b) Columbia torrent salamander. **Table S1:** Relative strengths of pairwise interactions calculated as residual variances from boosted-regression tree models.