



# Dietary niche partitioning between Coastal Giant Salamanders (*Dicamptodon tenebrosus*) and Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*)

Ivan Arismendi · Najma Ain · William Gerth · Gwendolynn Bury · Lauren Zatkos

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**Abstract** Understanding the mechanisms that enable species coexistence is essential for explaining community structure and biodiversity. We tested the hypothesis that dietary niche partitioning facilitates coexistence between two dominant stream predators in western North America: Coastal Giant Salamanders (*Dicamptodon tenebrosus*) and Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*). These aquatic predators are important regulators of community dynamics and ecosystem processes in stream networks. We analyzed stomach contents from 81 salamanders and 96 trout collected via electrofishing in a 6-km section of Lookout Creek, Oregon, during low flow conditions in summer. We predicted that

salamanders, primarily nocturnal benthic feeders, and trout, visual consumers of both terrestrial and aquatic prey, would exhibit distinct diets reducing direct diet overlap. We identified 4,897 prey items, classifying them into aquatic (50) and terrestrial (77) sources across 127 categories. Salamanders primarily preyed on aquatic invertebrates (Trichoptera, Ephemeroptera, and Plecoptera), while trout consumed a mix of terrestrial and aquatic invertebrates (Diptera, Trichoptera, and Plecoptera). Partial dietary overlap confirmed niche differentiation as a likely mechanism facilitating the coexistence of trout and salamanders. These findings highlight the role of dietary partitioning in structuring predator communities and inform predictions of how environmental changes may impact stream ecosystems.

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I. Arismendi (✉) · W. Gerth · G. Bury  
Department of Fisheries, Wildlife, and Conservation  
Sciences, Oregon State University, Nash Hall 104,  
Corvallis, OR 97331, USA  
e-mail: [Ivan.Arismendi@oregonstate.edu](mailto:Ivan.Arismendi@oregonstate.edu)

N. Ain  
Bioresources Research Program, Oregon State University,  
430 Strand Agriculture Hall, Corvallis, OR 97331, USA

L. Zatkos  
Wolf Water Resources, 1001 SE Water Avenue, Suite 180,  
Portland, OR 97214, USA

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## Introduction

Understanding the mechanisms that facilitate species coexistence is fundamental to explaining patterns of population dynamics and maintaining species diversity (Holt, 2017; Huston, 1994; Mittelbach & McGill, 2019). In stream ecosystems, research has centered on the competitive exclusion principle (Hardin, 1960) as the primary factor driving the coexistence

of salamanders and fishes (Cecala et al., 2020; Resettarits, 1995; Sepulveda & Lowe, 2011). This principle posits that fully overlapping competitors cannot coexist, thereby competitive asymmetries might arise owing to distinct traits such as morphologies, body sizes, or life histories (Keddy, 1989). Fish and amphibians frequently co-occur in freshwater ecosystems, where their overlapping ecological niches provide an ideal system for studying the mechanisms and outcomes of interspecific competition and coexistence. Several empirical studies have documented asymmetries as a key factor underlying the coexistence of amphibians and fishes (Cudmore & Bury, 2014; Lowe et al., 2018; Parker, 1993; Resettarits, 1995; Sepulveda et al., 2012; Sih et al., 1992). In addition, other studies (Cecala et al., 2020; Sepulveda & Lowe, 2011) have identified temporal variability and behavioral adaptations as alternative mechanisms promoting species coexistence. For example, *Dicamptodon* larvae exhibit shifts in local dispersal (Sepulveda & Lowe, 2011) and increased refuge use in response to trout chemical cues (Rundio & Olson, 2003). Similar forms of behavioral avoidance have been reported in other amphibians exposed to fish predators (Cecala et al., 2020; Kats et al., 1988). Collectively, these studies highlight that beyond competitive asymmetries and behavioral avoidance, additional mechanisms—such as niche partitioning—may also play a critical role in shaping patterns of coexistence between salamanders and fishes.

Modern ecological theory highlights the importance of multiple mechanisms, including resource partitioning, in promoting species coexistence (Holt, 2017; Mittelbach & McGill, 2019). Dietary niche partitioning, as an evolutionary or behavioral response to avoid competitive exclusion, can mitigate interspecific competition and facilitate the coexistence of ecologically similar consumers within a community (Schoener, 1974; Wiens et al., 2010). This mechanism has been proposed to explain the sympatry of multiple salamander species (Cudmore & Bury, 2014; Steele & Brammer, 2006; Vignoli et al., 2016) as well as resource differentiation among fish assemblages (Ross, 1986). However, relatively few studies in headwater streams have directly assessed dietary overlap between salamanders and fishes. Sepulveda et al. (2012) found no evidence of dietary partitioning between Idaho Giant Salamanders [*Dicamptodon aterrimus* (Cope, 1868)] and resident salmonids. In

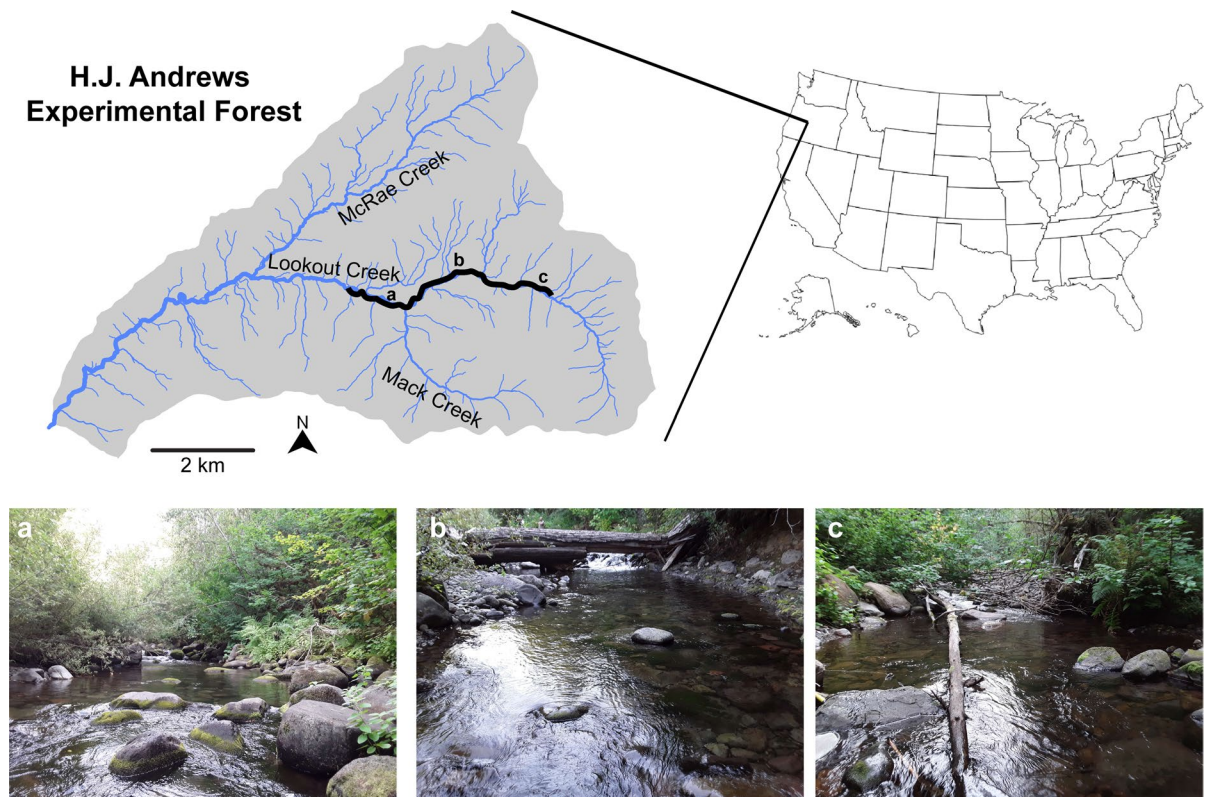
contrast, studies by Falke et al. (2020) and Roon et al. (2022) documented seasonal and size-based dietary divergence between Coastal Giant Salamanders [*D. tenebrosus* (Baird & Girard, 1852)] and co-occurring fish species in Oregon and California. These findings emphasize the need for additional research across broader ecological contexts, including larger stream systems, to better evaluate the role of dietary niche partitioning in facilitating the coexistence of salamanders and fishes.

In this study, we use stomach contents analysis to evaluate the dietary composition and overlap of resident Coastal Cutthroat Trout [*Oncorhynchus clarkii clarkii* (Richardson, 1836)] and Coastal Giant Salamanders within a large (fifth order) river during the seasonal low flow. The Coastal Cutthroat Trout is a visual consumer of food sources from both terrestrial and aquatic origins (Trotter, 1989; Wilzbach & Hall, 1985). In contrast, the foraging behavior of the Coastal Giant Salamanders in streams is primarily nocturnal, relying on benthic prey items (Cudmore & Bury, 2014; Parker, 1994). Given these distinct feeding behaviors, we hypothesize dietary niche partitioning will occur between these two opportunistic generalist consumers. Our research offers valuable insights into the ecological interactions between the largest aquatic predators in the headwaters of the Pacific Northwest of North America (Hawkins et al., 1983; Murphy & Hall, 1981). The findings from our study will enhance our understanding of the role these tertiary consumers play in regulating community dynamics and ecosystem processes within stream networks.

## Methods

### Study site

The Lookout Creek Basin (6400-ha) is part of the H.J. Andrews Experimental Forest in the Willamette National Forest (Fig. 1) and is protected for research purposes (Swanson et al., 1982). The basin is surrounded by a mixture of old-growth (up to 700 years old) and second-growth riparian forest consisting of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], Western Hemlock (*Tsuga heterophylla* Sargent), Western Red Cedar (*Thuja plicata* Donn ex D. Don), Red Alder (*Alnus rubra* Bongard), Bigleaf Maple



**Fig. 1** Map of H.J. Andrews Experimental Forest and Lookout Creek, Oregon USA including photos (a–c) that illustrate pool habitats where we sampled Coastal Giant Salamanders

and Coastal Cutthroat Trout within a 6-km section of the mainstem of Lookout Creek. Streams are shown only for drainage areas  $> 1 \text{ km}^2$

(*Acer macrophyllum* Pursh), Black Cottonwood (*Populus trichocarpa* Torr. & A.Gray ex Hook.), and Sitka Willow (*Salix sitchensis* Sanson ex. Bong.). The climate of this region is Mediterranean with wet and mild winters, and dry and warm summers. Mean monthly atmospheric temperatures range between  $0.6^\circ\text{C}$  in January and  $17.8^\circ\text{C}$  in July, whereas annual precipitation across elevations (410–1630 MASL) ranges between 2300 and 3550 mm with most of the precipitation (80%) occurring between November and April.

#### Aquatic vertebrates

Coastal Giant Salamanders and Coastal Cutthroat Trout are top vertebrate predators that co-occur in headwater streams of the Pacific Northwest, playing important roles in stream food webs (Hawkins et al., 1983). Coastal Giant Salamanders are endemic to coastal regions from southern British Columbia to

California (Good, 1989; Nussbaum, 1976) and exhibit complex life histories, including aquatic pedomorphic and metamorphosed terrestrial forms. Although their average lifespan is unknown, individuals may live up to 25 years (Duellman & Trueb, 1994) and reach sexual maturity at 85–115 mm snout-to-vent length (Nussbaum, 1976). They can display facultative pedomorphosis, with food availability influencing rates of metamorphosis (Coriell, 2003), suggesting that competitive dynamics may have cascading effects on broader ecosystem processes. Their home ranges are highly localized, typically  $< 30 \text{ m}$  for both larvae and adults (Chelgren & Adams, 2017; Sagar et al., 2007; Johnston & Frid, 2002). In contrast, Coastal Cutthroat Trout are distributed from Alaska to California (Behnke, 1992; Penaluna et al., 2016), typically live 4–5 years in their stream-resident form (up to 7–8 years in some cases), reach sexual maturity around age two, and maintain home ranges generally restricted to within 200 m of their birthplace (Trotter,

1989). Intraguild predation, particularly between Pacific Giant Salamanders larvae and salmonids, is well-documented. Large salamander larvae have been reported preying on both small trout (Antonelli et al., 1972; Parker, 1993, 1994) and other salamander larvae (Parker, 1994), while small salamander larvae can also be consumed by large trout (Parker, 1992).

#### Animal capture and handling

We sampled Coastal Cutthroat Trout and Coastal Giant Salamanders from a 6-km section of the mainstem of Lookout Creek (Fig. 1). We captured these consumers using a single-pass electrofishing procedure with a Smith-Root LR-24 backpack electroshocker without block nets (Arismendi et al., 2021; Bateman et al., 2005; Hankin & Reeves, 1988). We sampled animals inhabiting pool habitats (mean depth =  $0.66 \pm 0.22$  SD cm) during the end of the seasonal low flow period (i.e., Aug 26–29, 2019). This approach facilitated the sampling of consumers across a diverse range of habitat conditions in a condensed timeframe minimizing the potential impact of episodic food pulses on their diets.

Size-structured populations of trout and salamander can promote ontogenetic shifts in their ecological interactions (Ebenman & Persson, 1988; Werner & Gilliam, 1984). Therefore, we aimed to examine diets of relatively large body sizes to detect the potential occurrence of intraguild predation. An initial assessment of the size structure and abundance of consumers in our study system (Arismendi et al., 2021) suggested trout between 80 and 200 mm (total length, FL) and salamanders between 50 and 300 mm (total length) as target sizes for our diet analysis.

Captured trout were anesthetized using 2.5-mL buffered tricaine methanesulfonate (MS-222) solution from stock solution of 20 g/L diluted using stream water. A duplicated dose for stream salamanders was mixed in a separate bucket. We kept sampled consumers in the anesthetic solution until major locomotion ceased (i.e., until fish rolled onto their sides and salamander did not squirm when being held). Consumers were weighed to the nearest gram and measured to the nearest millimeter (i.e., fork length and total length for trout; snout-vent length and total length for stream salamanders). We performed a gastric lavage procedure (Foster, 1977) to collect stomach contents of consumers. Specifically, we inserted a non-stretchable

straw attached to a 250-mL plastic wash bottle into the esophagus and flushed each stomach with filtered stream water. We filtered stomach contents using a coffee filter and then preserved contents in 90% ethanol before transportation to the lab. After completing the gastric lavage procedure, we placed consumers in an aerated bucket of fresh stream water and released them back to the stream with adequate in-stream cover after full recovery (generally within 15 min of collection).

#### Dietary contents and data analyses

In the laboratory, we identified prey items to the finest taxonomic resolution possible using available taxonomic keys (Merritt et al., 2019). In most cases, we were able to identify prey items at the family level. All prey items were counted and grouped in multiple categories and separated by terrestrial or aquatic origin. Adults of Ephemeroptera, Plecoptera, Trichoptera and Diptera with aquatic larvae and pupae were classified as of terrestrial origin. To evaluate how adequately we described prey richness (i.e., number of prey categories), we used sample-based species accumulation curves (Gotelli & Colwell, 2001). We considered each flushed stomach as the sampling unit assuming they represented a random sample of the consumer's diet. Prey richness was adequately measured when the species accumulation curve reached an asymptote (Cortés, 1997). We used the random bootstrapping method (9999 permutations) implemented in the 'vegan' package in R (Oksanen et al., 2001) and adopted the end point prediction as the best estimate of this asymptote. We performed a Mann–Whitney rank test with the Yates continuity correction to compare median consumer sizes (i.e., total length and mass), accounting for the possibility that ontogenetic niche shifts associated with body size could influence dietary comparisons. We visualized diets of consumers at both a population and individual level. At the population level, we used alluvial and bipartite plots based on the frequency of occurrence (%F) as the proportion of stomachs with a respective prey category (Hyslop, 1980). Alluvial and bipartite plots were built using the 'ggalluvial' (Brunson & Read, 2017) and 'bipartite' (Dormann et al., 2007) packages implemented in R. For the alluvial plot, we used log-transformed %F of prey categories grouped by order, whereas for the bipartite consumer–prey network



plot, we used prey categories grouped by family ( $%F > 3$ ). At the individual level, we used a non-metric multidimensional scaling (nMDS) ordination technique implemented in PRIMER-7 (Plymouth Marine Laboratory, PML). For this analysis, we used the numerical frequency ( $%N$ ) as the counts in each prey category divided by the total number of prey items (Hyslop, 1980). We used a square root transformation for prey counts to down-weight the importance of the highly abundant categories (Clarke & Warwick, 2001) and calculated the respective resemblance matrix of distances using the Bray–Curtis similarity index (Clarke, 1993; Marshall & Elliott, 1997). The nMDS technique places each diet category in a multivariate space in the most parsimonious arrangement (relative to each other) and uses iterative optimization (999 random starts) to minimize stress during the dimensional reduction (Clarke & Gorley, 2006). The resulting stress of final 2D plot can be evaluated with  $\text{stress} < 0.05$  indicating an excellent ordination,  $0.2 < \text{stress} < 0.1$  representing a good/acceptable ordination, and  $\text{stress} \geq 0.2$  a poor ordination (Clarke, 1993).

We used multiple analytical approaches to ensure a robust assessment of dietary partitioning, capturing both fine-scale individual variation and broader population-level patterns. This integrative framework enables complementary metrics to highlight distinct aspects of the trophic ecology of trout and salamanders. We evaluated dietary partitioning between salamanders and trout by comparing several indices of niche overlap implemented in the package ‘spaa’ in R (Zhang, 2010) using  $%F$  and the bootstrap option ( $n = 99,999$ ). These indices included Pianka (Pianka, 1973), Schoener (Schoener, 1968), Petraitis (Petraitis, 1979), Morisita (Morisita, 1959), and Levins (Levins, 1974). Indices ranged from 0 to 1, where 0 indicated no overlap and 1 denoted complete overlap. In addition, we used a permutational multivariate analysis of variance (PERMANOVA) implemented in PRIMER-7 (Plymouth Marine Laboratory, PML) to test the hypothesis of diet overlap between salamander and trout based on the Bray–Curtis similarity index of  $%N$  (Clarke, 1993; Marshall & Elliott, 1997). We used similarity of percentages analyses SIMPER (Clarke, 1993) implemented in PRIMER-7 to describe which prey categories contributed most to the level of diet overlap observed between consumers. Lastly, we evaluated similarities of individual

diets using an analysis of similarities (ANOSIM) and estimated the significance of the R test statistic associated with ANOSIM using 99,999 permutations (Clarke, 1993). The R statistic ranges between  $-1$  and  $1$ , where  $-1$  indicated more similarity of diets between consumers than within consumers,  $0$  indicated no difference in diets between consumers, and  $1$  indicated less similarity in diets between consumers than within consumers. We tested differences in diet composition by species and body size (small = total length < median length; large = total length > median length).

## Results

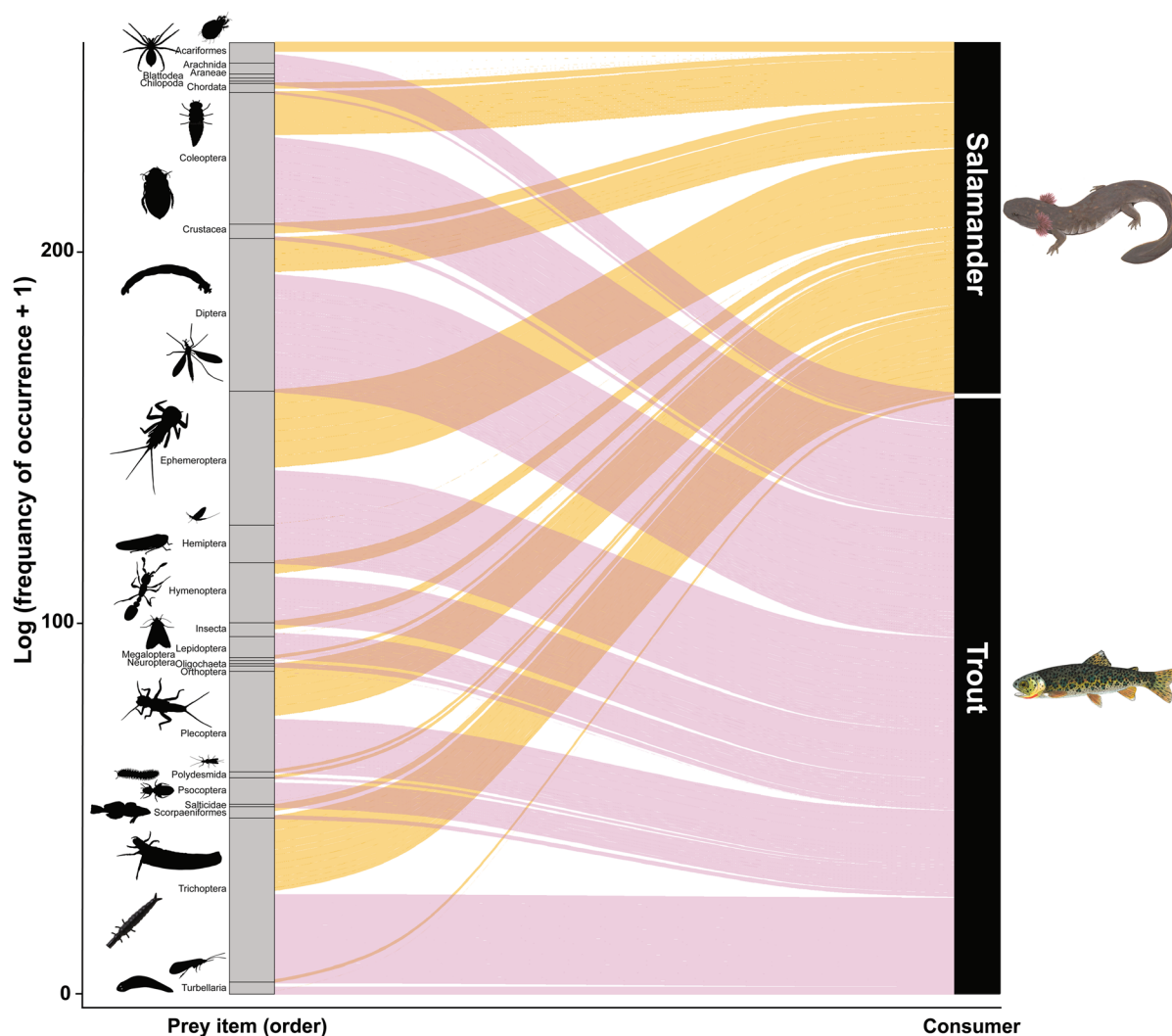
We collected stomach contents from 81 Coastal Giant Salamanders and 96 Coastal Cutthroat Trout. The range of size and mass of these consumers were relatively similar (Fig. S1). Yet, there were more large salamanders so that the median total length of salamanders (199 mm; interquartile range = 160–222 mm) was significantly (Mann–Whitney  $U = 2184.5$ ;  $P < 0.001$ ) larger than trout (152 mm, interquartile range = 143–174 mm). Similarly, the median mass of salamanders (54.3 g; interquartile range = 26.2–72.3 g) was statistically significantly different (Mann–Whitney  $U = 3379$ ;  $P = 0.003$ ) compared to the median mass of trout (33.2 g; interquartile range = 25.4–50.9 g). However, there were no differences in the composition of diets between small and large body size groups for either salamanders (R statistic =  $-0.071$ ; pseudo- $P = 0.863$ ) or trout (R statistic =  $0.024$ ; Pseudo- $P = 0.258$ ). Thus, our further analyses focused only on the comparison of diets between consumers without consideration of their body size.

From all stomach contents analyzed, we identified 4,897 items and classified them into aquatic ( $n = 50$ ) and terrestrial ( $n = 77$ ) sources totaling 127 prey categories (Figs. S2–3). Only 19 stomachs were empty or fully digested, including 17 salamanders and two trout. Sample-based prey richness accumulation curves showed that our sampling size was roughly adequate to describe the diets of these aquatic vertebrate consumers (Fig. S4).

The alluvial plot representing the overall diet of salamanders and trout at the order level showed that salamanders primarily preyed on aquatic invertebrates

(i.e., Trichoptera, Ephemeroptera, and Plecoptera), whereas trout preyed on a mixture of terrestrial and aquatic invertebrates including Diptera, Trichoptera and Plecoptera (Fig. 2). Similarly, bipartite predator–prey networks illustrating the diet of each stomach at the family level confirmed that salamanders preyed infrequently on terrestrial resources contrasting to trout that preyed on resources of both terrestrial and aquatic origin (Fig. 3). For salamanders, mayflies in the families Baetidae, Ameletidae, and Heptageniidae were consumed more often, %F of 72, 46 and 45%, respectively. Other common prey items were in

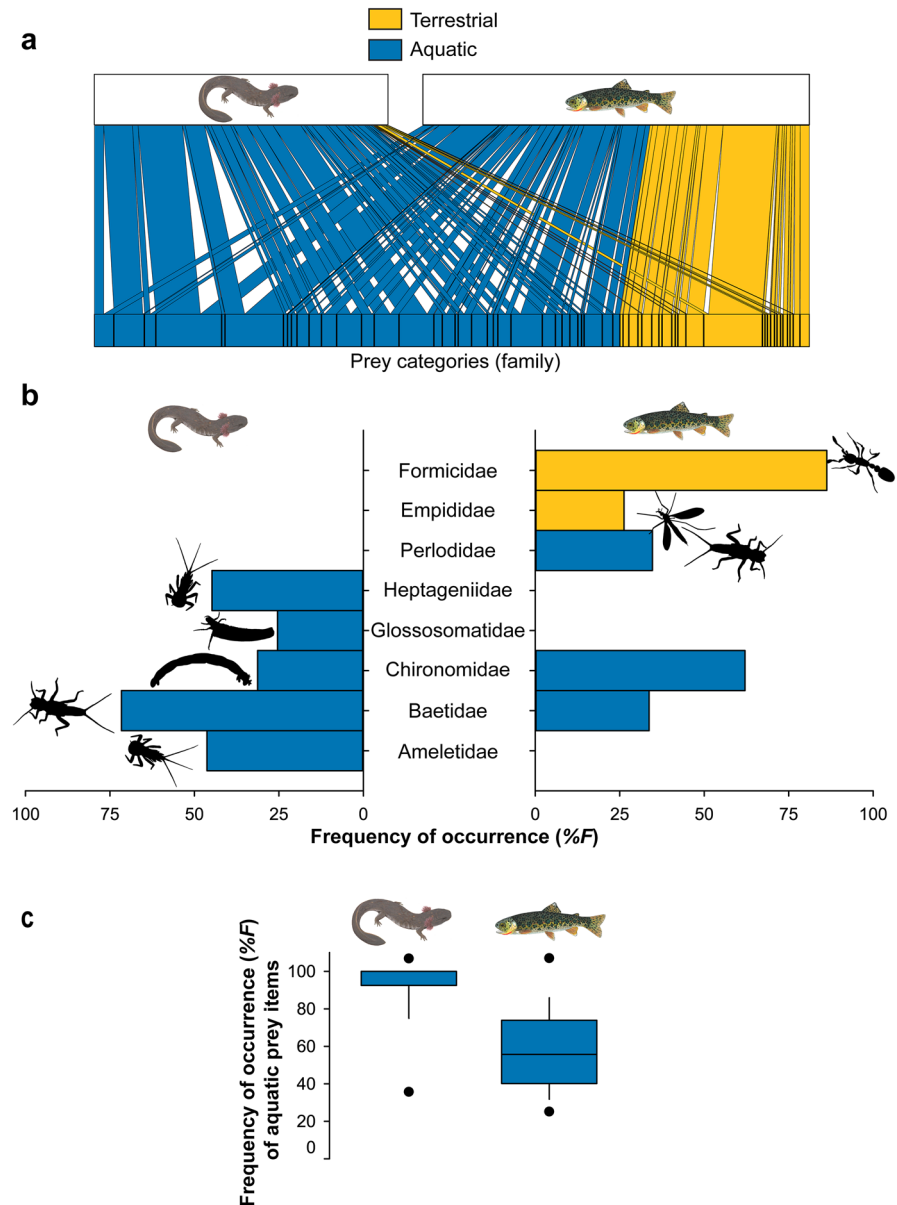
the families Chironomidae (31%) and Glossosomatidae (25%). All these families were of aquatic origin. For trout, the most common prey items were the terrestrial Formicidae, and the aquatic families Chironomidae and Perlodidae, %F of 86, 62 and 35%, respectively. Other common prey families included aquatic Baetidae (34%) and terrestrial Empididae (26%). There was evidence of piscivory (Cottidae—sculpins) in both salamanders and trout, but this prey category occurred infrequently (<6%; Fig. S2). Moreover, we did not find evidence of intraguild predation between trout and salamanders.



**Fig. 2** Overall composition of prey items in sampled stomachs of salamander and trout organized alphabetically by order. Lines represent log-transformed frequency of occurrence (%F)

of prey categories across all sampled stomachs. Detailed information about diets at the family level can be found in the Supplement (Figs. S2–3)

**Fig. 3** **A** Bipartite predator–prey networks for salamander and trout. Lower bars represent the origin (terrestrial or aquatic) and frequency of occurrence ( $\%F > 3$  percent) of prey categories at the family level whereas upper bars represent individual stomachs sampled for each consumer. Linkage width indicates frequency of each trophic interaction. **B** Frequency of occurrence ( $\%F$ ) and origin (terrestrial or aquatic) of top-five major prey categories for salamander and trout diets at the family level. **C** Boxplots of frequency of occurrence ( $\%F$ ) of aquatic prey categories from sampled stomachs of salamander and trout. Dots represent 5th and 95th percentiles, whereas boxes include median, and interquartile range. Detailed information of diets at the family level can be found in the Supplement (Figs. S2–3)



There was only partial dietary overlap between salamanders and trout based on multiple indices of

niche similarity (Table 1). In addition, there was less similarity in diets between salamanders and trout than

**Table 1** Indices of niche similarity to assess dietary overlap between salamanders and trout in Lookout Creek, Oregon. Values were estimated based on a bootstrap option in the package ‘spaa’ in R (Zhang, 2010)

Index of similarity	Observed	Average <sub>b</sub>	SD <sub>b</sub>	Lower CI <sub>b</sub> 95%	Upper CI <sub>b</sub> 95%
Pianka	0.499	0.519	0.102	0.320	0.790
Schoener	0.404	0.410	0.053	0.305	0.514
Petraitis	0.425	0.448	0.084	0.300	0.626
Morisita	0.489	0.500	0.096	0.310	0.681
Levins	0.608	0.656	0.188	0.343	1.070

within these consumers (ANOSIM; R statistic=0.56; pseudo- $P < 0.001$ ). Diets of salamanders and trout were statistically significantly different (Fig. 3; PERMANOVA; pseudo- $F = 35.39$ ;  $df = 1$ ; pseudo- $P < 0.001$ ), revealing dietary partitioning between them. The SIMPER analysis showed relatively high dissimilarity (89.25%) of diets between salamanders and trout. There were 39 families that contributed 90% to this prey dissimilarity (Table S1) with 11 families contributing the most (63%), including terrestrial Formicidae (16%), aquatic Ameletidae (10%), aquatic Chironomidae (7%), aquatic Baetidae (6%), aquatic Heptageniidae (5%), aquatic Perlodidae (4%), aquatic Glossosomatidae (4%), aquatic Crustacea (3%), aquatic Ephemerellidae (3%), aquatic Leptophlebiidae (3%), and terrestrial Empididae (2%) (Fig. 4).

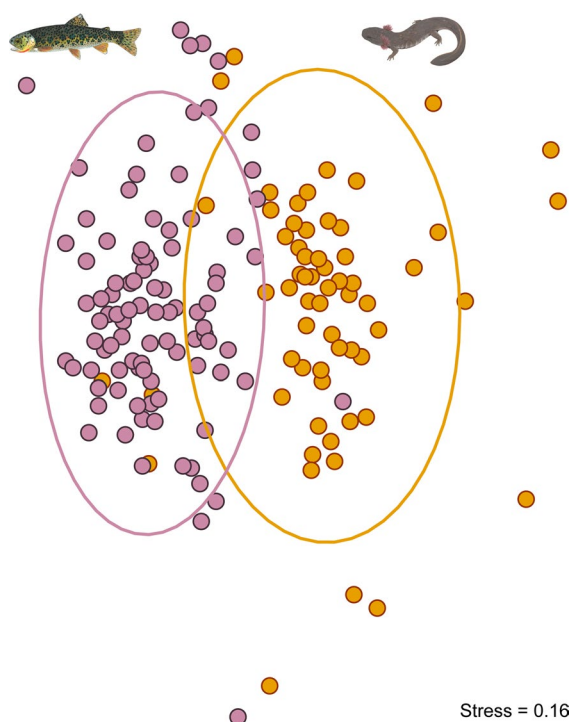
In addition, the SIMPER analysis showed an average similarity of diets within individual salamanders of 24.34%. There were seven families preyed upon that contributed 90% to this level of similarity

including Ameletidae (48%), Baetidae (15%), Heptageniidae (14%), Chironomidae (5%), Glossosomatidae (4%), Crustacea (3%), and Leptophlebiidae (3%). All these families were of aquatic origin. For trout, the SIMPER analysis showed 30.04% average similarity of diets within individuals. Six prey families from a mixture of terrestrial and aquatic origin contributed 90% to this similarity including terrestrial Formicidae (65%), aquatic Chironomidae (14%), aquatic Perlodidae (5%), aquatic Ameletidae (3%), terrestrial Empididae (2%), and aquatic Simuliidae (2%).

## Discussion

Our findings are consistent with the hypothesis of dietary partitioning between Coastal Giant Salamanders and Coastal Cutthroat Trout during seasonal low flow. We show disparities in the use of food sources between these two consumers with each species exhibiting distinctive diets with higher intra- than interspecific similarities. Specifically, salamanders rely mainly on aquatic sources whereas trout use food resources from both terrestrial and aquatic origin. This is consistent with the literature for both Coastal Cutthroat Trout (Trotter, 1989; Wilzbach & Hall, 1985) and Coastal Giant Salamander (Bury, 1972; Cudmore & Bury, 2014; Parker, 1994). Our study incorporates a broader spatial extent over a relatively short temporal scale and demonstrates that dietary partitioning may arise as a direct response to competitive interactions, providing an additional mechanism that facilitates the coexistence of salamanders and fishes in stream ecosystems.

The dietary divergence between Coastal Giant Salamanders and Coastal Cutthroat Trout may result from at least four non-mutually exclusive mechanisms. The first mechanism pertains to potential differences in dietary preferences between these two consumers. Unfortunately, a comprehensive evaluation of this mechanism was not possible due to the need for additional information on resource availability and quality. Terrestrial invertebrates, often more energy-dense than their aquatic counterparts (Cummins & Wuycheck, 1971), could influence the higher frequency of terrestrial items in trout diets compared to salamanders. However, our findings reveal a diverse diet composition for both consumers.



**Fig. 4** Nonmetric multidimensional scaling (nMDS) ordination of individual stomach contents of salamanders and trout based on Bray–Curtis dissimilarities of square root transformed of %N including 127 prey categories in Lookout Creek, Oregon. Symbols represent individual stomachs. The ellipses delineate 95% confidence intervals



Furthermore, substantial evidence points out that both Coastal Giant Salamander (Bury, 1972; Cudmore & Bury, 2014; Esselstyn & Wildman, 1997; Parker, 1994) and Coastal Cutthroat Trout (Trotter, 1989; Wilzbach & Hall, 1985) are opportunistic generalist consumers with no clear dietary preferences.

The second mechanism is tied to the spatial variation in food availability. Our sampling procedure encompasses stomach contents of consumers in pool habitats within the mainstem of our study river. These habitats are known to support relatively similar within-stream macroinvertebrate assemblages (Li et al., 2001). In addition, both Coastal Giant Salamanders (Sagar et al., 2007) and Coastal Cutthroat Trout (Trotter, 1989) are stream residents with restricted movement within their habitat ranges (less than 30 m and 200 m, respectively). Consequently, the spatial variation in food sources or consumer movement within our study river are unlikely to greatly influence our findings.

The third mechanism involves the temporal variation in food availability. The diet partitioning observed between Coastal Giant Salamanders and Coastal Cutthroat Trout could be influenced by the typical low availability of drift during the seasonal low flow in the region (Wooster et al., 2016). This suggests that competition for these limited, high-energy terrestrial resources (Cummins & Wuycheck, 1971) could promote diet partitioning, as observed in other vertebrates (Porter et al., 2022). We demonstrate a relatively low diet overlap between these two consumers during the seasonal low flow, but the low diet overlap is also consistent in other river systems across seasons (Roon et al., 2022). Hence, temporal variation in food availability likely has little influence on our results.

Unfortunately, assessing competitive exclusion as the fourth mechanism explaining dietary partition between Coastal Giant Salamander and Coastal Cutthroat Trout would necessitate experimental manipulation to exclude consumers. However, we demonstrate a greater intra-specific than interspecific overlap in diets as it has been reported in other river systems where these two consumers are in sympatry (Roon et al., 2022). If intra-specific competition in salamanders (Jaeger, 1980; Nussbaum et al., 1983) and trout (Chapman, 1966; Grossman & Simon, 2020) is stronger than interspecific competition, competitive exclusion might not occur (Chesson, 2000). Indirect

evidence from long-term studies in our study system suggests that interspecific interactions might be of less relevance compared to intra-specific interactions. For instance, conspecific negative density-dependence has been shown to be an important driver of annual growth of Coastal Cutthroat Trout (Arismendi et al., 2024) and body size of both Coastal Giant Salamanders and Coastal Cutthroat Trout (Arismendi et al., 2024; Penaluna et al., 2025). Furthermore, differences in morphology and behavior can contribute to dietary niche partitioning. Coastal Giant Salamanders are primarily benthic and spend much of their time sheltering under cover objects (Cudmore & Bury, 2014; Parker, 1994), making encounters with terrestrial prey on the water surface less probable. In contrast, Coastal Cutthroat Trout are active visual predators that forage in the water column, relying heavily on sight to capture both aquatic and terrestrial prey (Trotter, 1989; Wilzbach & Hall, 1985). These contrasting foraging strategies could reduce direct competition and help facilitate their coexistence in shared stream habitats.

Our study has some limitations including the ability to evaluate potential seasonal variation in diets between consumers (Falke et al., 2020; Roon et al., 2022). However, Roon et al. (2022) documented consistent low diet overlap between Coastal Giant Salamander and Coastal Cutthroat Trout in California across seasons suggesting diet partitioning year-round. In addition, our sampling procedure cannot evaluate dietary differences associated with the ontogeny of these consumers (Ebenman & Persson, 1988; Falke et al., 2020; Werner & Gilliam, 1984). We document no differences in dietary composition of consumers by size, but we cannot extrapolate our findings to animals smaller than 10 mm (total length). Instead, we evaluate potential intraguild predation between salamander and trout (Antonelli et al., 1972; Parker, 1993, 1994) and show that piscivory occurs infrequently for these consumers in our study system. Future studies conducted in other settings and controlled stream mesocosms can complement our findings to elucidate the mechanisms of competitive and facilitative interactions.

We provide a comprehensive baseline of information about the dietary composition of Coastal Giant Salamander and Coastal Cutthroat Trout in a relatively large river system with implications for future studies assessing the impact of natural and

human-related disturbances in stream networks such as droughts and wildfires. These consumers are the largest aquatic predators in the headwaters of the Pacific Northwest of North America (Hawkins et al., 1983; Murphy & Hall, 1981). We demonstrate that dietary partitioning during low flow is consistent with other studies in smaller systems (Falke et al., 2020; Roon et al., 2022) supporting niche partitioning as a mechanism that explains the coexistence of these consumers. Salamanders and trout play an important role regulating community dynamics and ecosystem processes in streams and the better understanding of their coexistence can serve the needs of the conservation of these aquatic systems in a rapidly changing world.

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**Author contributions** NA, IA, and GB designed the study. NA, GB, and IA collected the data. NA, LZ, and BG analyzed and identified the stomach contents. IA performed the data analysis and prepared the figures. IA and NA wrote the first version of this manuscript. All authors contributed with edits and approved the final version of this manuscript.

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**Data availability** All data supporting the findings of this study are included in the Supplementary Information.

## Declarations

**Conflict of interest** Authors declare no conflict of interest.

## References

- Antonelli, A., R. A. Nussbaum & S. D. Smith, 1972. Comparative food habits of four species of stream-dwelling vertebrates (*Dicamptodon ensatus*, *D. copei*, *Cottus tenuis*, *Salmo gairdneri*). Northwest Science 46: 277–289.
- Arismendi, I., G. Bury, L. Zatkos, J. Snyder & D. Lindley, 2021. A method to evaluate body length of live aquatic vertebrates using digital images. Ecology and Evolution 11: 5497–5502. <https://doi.org/10.1002/ece3.7444>.
- Arismendi, I., S. V. Gregory, D. S. Bateman & B. E. Penaluna, 2024. Shrinking sizes of trout and salamanders are unexplained by climate warming alone. Scientific Reports 14: 13614. <https://doi.org/10.1038/s41598-024-64145-x>.
- Arismendi, I., B. E. Penaluna & S. V. Gregory, 2024. Trout Under Drought: A Long-Term Study of Annual Growth and Condition of Stream-Living Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*). In Lobon-Cervia, J., P. Budy & R. Gresswell (eds), Advances in the Ecology of Stream-Dwelling Salmonids, Vol. 44. Springer: 343–369. [https://doi.org/10.1007/978-3-031-44389-3\\_16](https://doi.org/10.1007/978-3-031-44389-3_16).
- Bateman, D. S., R. E. Gresswell & C. E. Torgersen, 2005. Evaluating single-pass catch as a tool for identifying spatial pattern in fish distribution. Journal of Freshwater Ecology 20: 335–345. <https://doi.org/10.1080/02705060.2005.9664974>.
- Behnke, R. J., 1992. Native trout of western North America. American Fisheries Society monograph (USA). no. 6. Bethesda, MD.
- Brunson, J. C. & Q. D. Read, 2017. ggalluvial: alluvial Plots in “ggplot2” (p. 0.12.5). <https://doi.org/10.32614/CRAN.package.ggalluvial>.
- Bury, R. B., 1972. Small mammals and other prey in the diet of the Pacific giant salamander (*Dicamptodon ensatus*). American Midland Naturalist 87: 524. <https://doi.org/10.2307/2423582>.
- Cecala, K. K., E. H. Walker, J. R. Ennen, S. M. Fix & J. M. Davenport, 2020. Seasonal variation in the strength of interference competition among headwater stream predators. Freshwater Biology 65: 1440–1449. <https://doi.org/10.1111/fwb.13511>.
- Chapman, D. W., 1966. Food and space as regulators of salmonid populations in streams. The American Naturalist 100: 345–357.
- Chelgren, N. D. & M. J. Adams, 2017. Inference of timber harvest effects on survival of stream amphibians is complicated by movement. Copeia 105: 712–725.
- Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31: 343–366. <https://doi.org/10.1146/annurev.ecolsys.31.1.343>.
- Clarke, K. R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117–143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>.
- Clarke, K. R. & R. N. Gorley, 2006. Primer V6: user Manual—Tutorial (Plymouth Routines in Multivariate Ecological Research). PRIMER-E Limited, Plymouth. <https://books.google.com/books?id=fsWqmwEACAAJ>.
- Clarke, K. R. & R. M. Warwick, 2001. Change in Marine Communities: an Approach to Statistical Analysis and Interpretation (2nd ed.). Plymouth Marine Laboratory, PRIMER-E Limited. <https://books.google.com/books?id=vYr5QwAACAAJ>.

- Coriell, S., 2003. Environmental factors affecting paedomorphosis in the Pacific giant salamander, *Dicamptodon tenebrosus*. Doctoral Dissertation, Humboldt State University, Arcata, California.
- Cortés, E., 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 726–738. <https://doi.org/10.1139/f96-316>.
- Cudmore, W. W. & R. B. Bury, 2014. Resource Partitioning in Two Stream Salamanders, *Dicamptodon tenebrosus* and *Rhyacotriton cascadae*, from the Oregon Cascade Mountains. *The American Midland Naturalist* 172: 191–199. <https://doi.org/10.1674/0003-0031-172.1.191>.
- Cummins, K. W. & J. C. Wuycheck, 1971. Caloric Equivalents for Investigations in Ecological Energetics. *SIL Communications* 1953–1996(18): 1–158. <https://doi.org/10.1080/05384680.1971.11903918>.
- Dormann, C. F., J. Fruend & B. Gruber, 2007. bipartite: visualising Bipartite Networks and Calculating Some (Ecological) Indices (p. 2.20). <https://doi.org/10.32614/CRAN.package.bipartite>.
- Duellman, W. E. & L. Trueb, 1994. *Biology of Amphibians*, JHU Press.
- Ebenman, B. & L. Persson, 1988. *Size-Structured Populations: Ecology and Evolution*, Springer.
- Esselstyn, J. A. & R. C. Wildman, 1997. Observations of *Juga* in the Diet of Larval Pacific Giant Salamanders (*Dicamptodon tenebrosus*). *Northwestern Naturalist* 78: 70. <https://doi.org/10.2307/3536849>.
- Falke, L. P., J. S. Henderson, M. Novak & D. L. Preston, 2020. Temporal shifts in intraspecific and interspecific diet variation among 3 stream predators. *Freshwater Science* 39: 115–125. <https://doi.org/10.1086/707599>.
- Foster, J. R., 1977. Pulsed gastric lavage: an efficient method of removing the stomach contents of live fish. *The Progressive Fish-Culturist* 39: 166–169. [https://doi.org/10.1577/1548-8659\(1977\)39\[166:PGLJ2.0.CO;2](https://doi.org/10.1577/1548-8659(1977)39[166:PGLJ2.0.CO;2).
- Good, D. A., 1989. Hybridization and cryptic species in *Dicamptodon* (Caudata: Dicamptodontidae). *Evolution* 43: 728–744. <https://doi.org/10.1111/j.1558-5646.1989.tb05172.x>.
- Gotelli, N. J. & R. K. Colwell, 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>.
- Grossman, G. D. & T. N. Simon, 2020. Density-dependent effects on salmonid populations: a review. *Ecology of Freshwater Fish* 29: 400–418. <https://doi.org/10.1111/eff.12523>.
- Hankin, D. G. & G. H. Reeves, 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 834–844. <https://doi.org/10.1139/f88-101>.
- Hardin, G., 1960. The Competitive Exclusion Principle: an idea that took a century to be born has implications in ecology, economics, and genetics. *Science* 131: 1292–1297. <https://doi.org/10.1126/science.131.3409.1292>.
- Hawkins, C. P., M. L. Murphy, N. H. Anderson & M. A. Wilzbach, 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the Northwestern United States. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 1173–1185. <https://doi.org/10.1139/f83-134>.
- Holt, R. D., 2017. Species Coexistence. In: *Reference Module in Life Sciences* (p. B9780128096338023529). Elsevier. <https://doi.org/10.1016/B978-0-12-809633-8.02352-9>.
- Huston, M. A., 1994. *Biological Diversity: The Coexistence of Species on Changing Landscapes*, Cambridge University Press.
- Hyslop, E. J., 1980. Stomach contents analysis: a review of methods and their application. *Journal of Fish Biology* 17: 411–429. <https://doi.org/10.1111/j.1095-8649.1980.tb02775.x>.
- Jaeger, R. G., 1980. Density-dependent and density-independent causes of extinction of a salamander population. *Evolution* 34: 617. <https://doi.org/10.2307/2408016>.
- Johnston, B. & L. Frid, 2002. Clearcut logging restricts the movements of terrestrial Pacific giant salamanders (*Dicamptodon tenebrosus* Good). *Canadian Journal of Zoology* 80: 2170–2177. <https://doi.org/10.1139/z02-213>.
- Kats, L. B., J. W. Petranksa & A. Sih, 1988. Antipredator defenses and the persistence of amphibian larvae with fishes. *Ecology* 69: 1865–1870. <https://doi.org/10.2307/1941163>.
- Keddy, P. A., 1989. *Competition*, Springer, Netherlands. <https://doi.org/10.1007/978-94-010-9011-7>.
- Levins, R. A., 1974. *Evolution in Changing Environments: Some Theoretical Explorations*, Princeton University Press.
- Li, J., A. Herlihy, W. Gerth, P. Kaufmann, S. Gregory, S. Urquhart & D. P. Larsen, 2001. Variability in stream macroinvertebrates at multiple spatial scales. *Freshwater Biology* 46: 87–97. <https://doi.org/10.1111/j.1365-2427.2001.00628.x>.
- Lowe, W. H., B. R. Addis, M. R. Smith & J. M. Davenport, 2018. The spatial structure of variation in salamander survival, body condition and morphology in a headwater stream network. *Freshwater Biology* 63: 1287–1299. <https://doi.org/10.1111/fwb.13133>.
- Marshall, S. & M. Elliott, 1997. A comparison of univariate and multivariate numerical and graphical techniques for determining inter- and intraspecific feeding relationships in estuarine fish. *Journal of Fish Biology* 51: 526–545. <https://doi.org/10.1111/j.1095-8649.1997.tb01510.x>.
- Merritt, R. W., K. W. Cummins & M. B. Berg (eds), 2019. *An Introduction to the Aquatic Insects of North America*, 5th ed. Kendall Hunt Publishing Company.
- Mittelbach, G. G. & B. J. McGill, 2019. Species Coexistence and Niche Theory. In: Mittelbach, G. G. & B. J. McGill (eds), *Community Ecology* Oxford University Press: 141–157. <https://doi.org/10.1093/oso/9780198835851.003.0008>.
- Morisita, M., 1959. Measuring of dispersion of individuals and analysis of the distributional patterns. *Memoirs of the Faculty of Science, Kyushu University. Series Biology* 2: 215–235.
- Murphy, M. L. & J. D. Hall, 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. *Canadian Journal of*

- Fisheries and Aquatic Sciences 38: 137–145. <https://doi.org/10.1139/f81-018>.
- Nussbaum, R. A., 1976. Geographic variation and systematics of salamanders of the genus *Dicamptodon* Strauch (Ambystomatidae). Miscellaneous Publications of the Museum of Zoology, University of Michigan 149: 1–94.
- Nussbaum, R. A., E. D. Brodie & R. M. Storm, 1983. Amphibians and Reptiles of the Pacific Northwest, University Press of Idaho:
- Oksanen, J., G. L. Simpson, F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, P. Solymos, M. H. H. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard, G. Carvalho, M. Chirico, M. De Caceres, S. Durand & J. Weedon, 2001. vegan: Community Ecology Package (p. 2.6–6.1) . <https://doi.org/10.32614/CRAN.package.vegan>.
- Parker, M. S., 1992. Feeding ecology of larvae of the Pacific giant salamander (*Dicamptodon tenebrosus*) and their role as top predator in a headwater stream benthic community. Dissertation University of California, Davis.
- Parker, M. S., 1993. Predation by Pacific giant salamander larvae on juvenile steelhead trout. *Northwestern Naturalist* 74: 77. <https://doi.org/10.2307/3536601>.
- Parker, M. S., 1994. Feeding ecology of stream-dwelling Pacific giant salamander larvae (*Dicamptodon tenebrosus*). *Copeia* 1994: 705. <https://doi.org/10.2307/1447187>.
- Penaluna, B. E., A. Abadía-Cardoso, J. B. Dunham, F. J. García-Dé León, R. E. Gresswell, A. R. Luna, E. B. Taylor, B. B. Shepard, R. Al-Chokhachy, C. C. Muhlfeld, K. R. Bestgen, K. Rogers, M. A. Escalante, E. R. Keeley, G. M. Temple, J. E. Williams, K. R. Matthews, R. Pierce, R. L. Mayden, R. P. Kovach, J. C. Garza & K. D. Fausch, 2016. Conservation of native Pacific trout diversity in western North America. *Fisheries* 41: 286–300. <https://doi.org/10.1080/03632415.2016.1175888>.
- Penaluna, B.E., S.L. Johnson, A.M.M. Pollock, I. Arismendi & D.R. Warren, 2025. Biotic interactions and stream network position affect body size of aquatic vertebrates across watersheds. *Ecosphere* 16(6):e70299. <https://doi.org/10.1002/ecs2.70299>.
- Petraitis, P. S., 1979. Likelihood measures of niche breadth and overlap. *Ecology* 60: 703–710. <https://doi.org/10.2307/1936607>.
- Pianka, E. R., 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4: 53–74. <https://doi.org/10.1146/annurev.es.04.110173.000413>.
- Porter, C. K., J. Golcher-Benavides & C. W. Benkman, 2022. Seasonal patterns of dietary partitioning in vertebrates. *Ecology Letters* 25: 2463–2475. <https://doi.org/10.1111/ele.14100>.
- Resetarits, W. J., 1995. Competitive asymmetry and coexistence in size-structured populations of brook trout and spring salamanders. *Oikos* 73: 188. <https://doi.org/10.2307/3545907>.
- Roon, D. A., J. B. Dunham, J. R. Bellmore, D. H. Olson & B. C. Harvey, 2022. Influence of riparian thinning on trophic pathways supporting stream food webs in forested watersheds. *Ecosphere* 13: e4219. <https://doi.org/10.1002/ecs2.4219>.
- Ross, S. T., 1986. Resource partitioning in fish assemblages: a review of field studies. *Copeia* 1986: 352. <https://doi.org/10.2307/1444996>.
- Rundio, D. E. & D. H. Olson, 2003. Antipredator Defenses of Larval Pacific Giant Salamanders (*Dicamptodon tenebrosus*) against Cutthroat Trout (*Oncorhynchus clarkii*). *Copeia* 2003: 402–407. [https://doi.org/10.1643/0045-8511\(2003\)003\[0402:ADOLPG\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2003)003[0402:ADOLPG]2.0.CO;2).
- Sagar, J. P., D. H. Olson & R. A. Schmitz, 2007. Survival and Growth of Larval Coastal Giant Salamanders (*Dicamptodon tenebrosus*) in Streams in the Oregon Coast Range. *Copeia* 2007: 123–130. [https://doi.org/10.1643/0045-8511\(2007\)7\[123:SAGOLC\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2007)7[123:SAGOLC]2.0.CO;2).
- Schoener, T. W., 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704–726. <https://doi.org/10.2307/1935534>.
- Schoener, T. W., 1974. Resource Partitioning in Ecological Communities: research on how similar species divide resources helps reveal the natural regulation of species diversity. *Science* 185: 27–39. <https://doi.org/10.1126/science.185.4145.27>.
- Sepulveda, A. J. & W. H. Lowe, 2011. Coexistence in streams: Do source–sink dynamics allow salamanders to persist with fish predators? *Oecologia* 166: 1043–1054. <https://doi.org/10.1007/s00442-011-1935-y>.
- Sepulveda, A. J., W. H. Lowe & P. P. Marra, 2012. Using stable isotopes to test for trophic niche partitioning: a case study with stream salamanders and fish. *Freshwater Biology* 57: 1399–1409. <https://doi.org/10.1111/j.1365-2427.2012.02800.x>.
- Sih, A., L. B. Kats & R. D. Moore, 1992. Effects of predatory sunfish on the density, drift, and refuge use of stream salamander larvae. *Ecology* 73: 1418–1430. <https://doi.org/10.2307/1940687>.
- Steele, C. A. & C. Brammer, 2006. Dietary overlap in Giant Salamanders (*Dicamptodon*): applying null models to resource partitioning. *Western North American Naturalist* 66: 115–120. [https://doi.org/10.3398/1527-0904\(2006\)66\[115:DOIGSD\]2.0.CO;2](https://doi.org/10.3398/1527-0904(2006)66[115:DOIGSD]2.0.CO;2).
- Swanson, F. J., S. V. Gregory, J. R. Sedell & A. G. Campbell, 1982. Land-water interactions: The riparian zone. In R. L. Edmonds (Ed.), *Analysis of coniferous forest ecosystems in the Western United States*. pp. 267–291. Hutchinson Ross Pub. Co, Academic Press.
- Trotter, P. C., 1989. Coastal cutthroat trout: a life history compendium. *Transactions of the American Fisheries Society* 118: 463–473. [https://doi.org/10.1577/1548-8659\(1989\)118%3c0463:CCTALH%3e2.3.CO;2](https://doi.org/10.1577/1548-8659(1989)118%3c0463:CCTALH%3e2.3.CO;2).
- Vignoli, L., A. M. Bissattini & L. Luiselli, 2016. Food partitioning and the evolution of non-randomly structured communities in tailed amphibians: a worldwide systematic review. *Biological Journal of the Linnean Society*. <https://doi.org/10.1111/bij.12906>.
- Werner, E. E. & J. F. Gilliam, 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15: 393–425. <https://doi.org/10.1146/annurev.es.15.110184.002141>.
- Wiens, J. J. D. D., A. P. Ackerly, B. L. Allen, L. B. Anacker, H. V. Buckley, E. I. Cornell, T. J. Damschen, J. Davies, S. P. Grytnes, B. A. Harrison, R. D. Hawkins & C. M. Holt, 2010. Niche conservatism as an emerging principle



- in ecology and conservation biology. *Ecology Letters* 13: 1310–1324. <https://doi.org/10.1111/j.1461-0248.2010.01515.x>.
- Wilzbach, M. A. & J. D. Hall, 1985. Prey availability and foraging behavior of cutthroat trout in an open and forested section of stream. *SIL Proceedings* 1922–2010(22): 2516–2522. <https://doi.org/10.1080/03680770.1983.11897715>.
- Wooster, D., S. W. Miller & S. J. DeBano, 2016. Impact of season-long water abstraction on invertebrate drift composition and concentration. *Hydrobiologia* 772: 15–30. <https://doi.org/10.1007/s10750-015-2611-8>.
- Zhang, J., 2010. spaa: Species Association Analysis (p. 0.2.2) . <https://doi.org/10.32614/CRAN.package.spaa>.

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