Treading Water: Conservation of Headwater-Stream Associated Amphibians in Northwestern North America☆

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Glossary

Benthic Referring to the flora and fauna found on the bottom, or in the bottom sediments, of a waterbody.

Climate change refugia Areas that remain relatively buffered from contemporary climate change over time and enable persistence of valued physical, ecological, and socio-cultural resources.

Desiccation The act or process of drying, or the state of being or becoming dried up (i.e., removal or loss of moisture). Amphibians are prone to desiccation because their skin is permeable for supporting osmoregulation and, therefore, they require environmental moisture.

Environmental DNA (eDNA) Organismal DNA that can be found in the environment. Environmental DNA originates from cellular material shed by organisms (via skin, excrement, etc.) into aquatic or terrestrial environments that can be sampled and monitored using molecular methods.

Facultative Optional or discretionary in response to circumstances.

Headwall seep A seep located at the toe of a cliff or other steep topographical feature.

Headwater The beginning of the initial source of water; the farthest place in a river or stream from its estuary or downstream confluence with another river.

Life history The pattern of survival and reproduction in organisms, along with the traits that directly affect survival and the timing or amount of reproduction.

Metamorphosis A biological process by which an organism physically develops, involving a conspicuous and relatively abrupt change in body structure through cell growth and differentiation.

Microclimate A local set of atmospheric conditions that often differ from those in the surrounding areas.

Neoteny The delaying or slowing of the physiological (or somatic) development of an organism that results in the retention of juvenile traits in adults.

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Obligate Restricted to a particular characteristic by necessity.

Pathogen Any disease-producing agent, such as a virus, bacterium, or other microorganism.

Riparian The interface between land and a river or stream.

Seep A moist or wet place where water, usually groundwater, reaches the earth's surface; connects to the stream channel network via overland flow, and is characterized by loose substrate and/or fractured bedrock with perennial water at or near the surface throughout the year.

Surface water The most recognizable part of the water cycle that we can see; located on top of the Earth's surface, such as rivers, streams, and wetlands.

Watershed A watershed is an area of land that drains all the surface water to a common outlet such as the mouth of a bay, or any point along a stream channel. Watersheds can be as small as a footprint or large enough to encompass all the land that drains water into rivers. The word "watershed" is sometimes used interchangeably with drainage basin or catchment.

Water balance An accounting of the inputs, outputs, and storage changes of water in a system (the major input of water is from precipitation and output is evapotranspiration).

Abstract

Headwater streams of the Pacific Northwest of North America are home to 52 amphibian species, spanning a diversity of taxa and life histories. Headwater stream-associated amphibians occur both within coldwater-stream channels and throughout adjacent riparian habitat, reflective of the important role of old-growth forests in providing cool, moist microclimates for these sensitive species. Forests of the Pacific Northwest have undergone substantial change over the last century, due to a legacy of resource extraction and ever-evolving forest management practices, as well as climate change. These and other stressors have challenged the adaptive capacity of headwater stream-associated amphibians, as more than half of these species are considered to be of conservation concern at the state, provincial, or federal level in the U.S. and Canada. Here, we overview the primary threats to the persistence of this unique and imperiled taxonomic group and emphasize the urgent need for more research and conservation action to mitigate future decline.

Introduction

The Pacific Northwest (PNW) of North America is an ecologically diverse region spanning multiple U.S. states and the Canadian province of British Columbia. This region receives heavy seasonal rainfall and includes the world's largest temperate coniferous rainforest. Expansive mountain ranges create a rain-shadow effect, leading to more arid climates in the interior plateaus, and sharp topographic relief across the landscape. This topography results in a diversity of local microclimates and numerous, discrete *watersheds* with dense stream networks extending from mountain ridgelines to the Pacific Ocean. Smaller streams in *headwater* sub-basins dominate stream lengths within watersheds, including seasonally discontinuous streams which are small capillaries that contribute multiple downstream resources (e.g., cold water, nutrients, downed wood, and substrate structural components).

Within these moist-coniferous forests, *seeps* and headwater streams with high-gradient, rocky reaches are home to a diversity of aquatic-dependent species adapted to coldwater conditions, including amphibians. The PNW assemblage of headwater-stream associated amphibians (hereafter "HSA amphibians") are taxonomically and functionally diverse. There are 52 amphibian species occurring within or along headwater streams and adjacent *riparian* forests, about 60% of which are considered rare and of conservation concern (**Table 1**). In particular, the stream-obligated Rhyacotritonidae and Dicamptodontidae salamanders and Ascaphidae frogs, are ancient lineages represented by 10 endemic species. Additionally, the 20 regionally unique species within the lungless salamander family Plethodontidae have strong ties to cool, moist microhabitats in these forests. Animals with headwater-stream associations may be found in-stream, in isolated or hydrologically connected seeps (peripheral areas of groundwater upwelling), along stream banks, in cool, moist riparian forests under moss pads and downed wood, and in microrefugia within rocky slopes. HSA amphibians comprise a major component of stream and riparian forest biomass, often exceeding fish in numbers and total biomass. HSA amphibians also play a central role in forest food webs due to their unique *life histories*. For instance, *metamorphosis* is a key developmental process in amphibians that coincides with abrupt changes in body structure that often accompany a shift from aquatic to terrestrial habitat, but patterns of metamorphosis vary across species. Further, within-species differences in life history are known across latitudinal and elevational gradients. Some species have terrestrial life stages, while others like *Dicamptodon* species, can retain larval traits (a phenomenon called *neoteny*) and grow to become significant aquatic predators. Stream-breeding species, in particular, transport aquatic-derived nutrients sequestered during aquatic phases of their life cycle into uplands as they transition into the terrestrial phase, and in turn, take terrestrial-derived nutrients back to streams when they return to breed.

For decades, scientists have been raising concern over the rapid, global decline in amphibian populations. Recent estimates suggest that more than 3000 amphibian species (nearly half of known species) are at risk of extinction (González-del-Pliego et al., 2019). Globally, habitat loss and degradation, disease, invasive species, among other direct and indirect stressors, have contributed to population declines. In the PNW, these threats have greatly impacted HSA amphibians, particularly habitat alteration

Table 1 Conservation status, habitats, and primary threats of headwater stream-associated amphibian species of the Pacific Northwest of North America.

	Species	*Conservation status*	*IUCN Red List category (Date of last assessment) * Indicates need for update*	*Habitat associations*	*Primary threats*
Stream Obligates	Southern torrent salamander (*Rhyacotriton variegatus*)	Sensitive (OR), Species of Special Concern (CA)	Least Concern (2004*)	Cold, headwater streams in moist, mature to late-seral forests or in proximate riparian forests in cold springs, seeps, and spray zones	1, 2
	Columbia torrent salamander (*Rhyacotriton kezeri*)	Petitioned for listing by US ESA, Sensitive (OR), Monitored (WA)	Near Threatened (2004*)	Range of low-flow, coldwater streams, including seeps, springs, and backwater (off-channel) habitat; most common in high-gradient, rocky streams	1, 2
	Cascade torrent salamander (*Rhyacotriton cascadae*)	Petitioned for listing by US ESA, Sensitive (OR), Candidate (WA)	Near Threatened (2004*)	High-gradient, cold, rock-dominated streams and seeps, and spray zones	1, 2
	Olympic torrent salamander (*Rhyacotriton olympicus*)	Monitored (WA)	Vulnerable (2004*)	High-gradient, cold, rock-dominated streams and seeps, waterfalls, and spray zones	1, 2
	Coastal giant salamander (*Dicamptodon tenebrosus*)	Under consideration for Threatened status by CAN SARA, Special Concern (BC)	Least Concern (2015)	Variety of lotic waters, from headwaters to rivers, but have been observed in mountain lakes; terrestrial forms utilize near-stream refugia under rocks and logs	1
	Cope's giant salamander (*Dicamptodon copei*)	Sensitive (OR), Monitored (WA)	Least Concern (2004*)	Small, rocky streams; especially abundant in pools within streams, under large rocks	1
	Idaho giant salamander (*Dicamptodon aterrimus*)	Vulnerable (ID)	Least Concern (2014)	Cold, fast-moving streams and sometimes mountain lakes or ponds; terrestrial forms utilize near-stream refugia (burrows) under rocks and logs	1, 3
	California giant salamander (*Dicamptodon ensatus*)	Species of Special Concern (CA)	Near Threatened (2004*)	Permanent or semi-permanent streams in dark, wet, coniferous forests; terrestrial forms utilize near-stream refugia (burrows) under rocks and logs	1, 3, 4
	Red-bellied newt (*Taricha rivularis*)	Species of Special Concern (CA)	Least Concern (2014)	Cold streams with moderate to fast currents and rocky substrates	1
	Coastal tailed frog (*Ascaphus truei*)	Special Concern (CAN SARA), Least Risk (BC) Sensitive (OR), Monitored (WA)	Least Concern (2015)	Cold, rocky, fast-flowing mountain streams; adults can be found along stream banks and in near-stream riparian zones	1, 3, 5
	Rocky Mountain tailed frog (*Ascaphus montanus*)	Sensitive (OR), Candidate (WA), Threatened (CAN SARA) Special Concern (BC)	Least Concern (2015)	Cold, swift, permanently flowing mountain streams; largely restricted to headwaters or areas of cold water and coarse substrate	1, 3
	Foothill yellow-legged frog (*Rana boylii*)	Sensitive Critical (OR), Threatened & Endangered (CA; listing status varies by clade)	Near Threatened (2004*)	Streams large enough to develop bar and backwater habitat; require coarse substrate with interstitial spaces for refugia	1, 6, 7, 8

(Continued)

Table 1 Conservation status, habitats, and primary threats of headwater stream-associated amphibian species of the Pacific Northwest of North America.—cont'd

	Species	*Conservation status*	*IUCN Red List category (Date of last assessment) * Indicates need for update*	*Habitat associations*	*Primary threats*
Facultative Stream Breeders	Northwestern salamander (*Ambystoma gracile*)	Not at Risk (CAN SARA), Least Risk (BC)	Least Concern (2015)	Cool, moist, complex forests; breed primarily in lentic environments (ponds and wetlands) and occasionally slow-moving streams	1, 3, 4, 8, 9
	Long-toed salamander (*Ambystoma macrodactylum*)	Not at Risk (CAN SARA), Least Risk (BC)	Least Concern (2015)	Wide variety, from forests to sub-alpine meadows; primarily utilize temporary or permanent ponds for breeding but can be found in quiet water at the edges of lakes or streams	4, 8
	Rough-skinned newt (*Taricha granulosa*)	Least Risk (BC)	Least Concern (2015)	Forested habitats in rolling and mountainous terrain; adults breed in ponds and wetlands or slower stretches of streams	No major threats known
	California newt (*Taricha torosa*)		Least Concern (2008*)	Coniferous forests and oak woodlands; breed in ponds and slower stretches of streams	3, 7, 5, 8
	Northern red-legged frog (*Rana aurora*)	Sensitive (OR), Species of Special Concern (CA), Under consideration for Special Concern by CAN SARA, Special Concern (BC)	Least Concern (2015)	Forests with diverse understories; require shallow ponds, slow-moving streams with marshy edges, or permanent wetlands for breeding	3, 4, 6, 8, 10
	California red-legged frog (*Rana draytonii*)	Threatened (US ESA), Species of Special Concern (CA)	Vulnerable (2008*)	Breed in seasonal or permanent ponds and marshes, or in the quiet, pond-like parts of streams (less commonly in lakes or other large bodies of water)	2, 3, 4, 5, 6, 8, 10
	Northern leopard frog (*Lithobates pipiens*)	Endangered (WA), Imperiled (ID), Endangered (CAN SARA; Rocky Mountain population), Species of Special Concern (CA), At risk of extinction (BC)	Least Concern (2004*)	Breed in shallow permanent or semi-permanent ponds, slow-moving streams with shallow, marshy edges, or extensive marshes	1, 2, 3, 4, 5, 8, 10
	Oregon spotted frog (*Rana pretiosa*)	Threatened (US ESA), Endangered (CAN SARA), Sensitive Critical (OR) Endangered (WA), Species of Special Concern (CA), At risk of extinction (BC)	Vulnerable (2004*)	Highly aquatic; Relatively large wetland complexes (typically unshaded, shallow, with emergent vegetation); occasionally breed in slow-moving streams	6, 8, 10
	Columbia spotted frog (*Rana luteiventris*)	Sensitive Critical (OR), Candidate (WA), Imperiled (ID; Great Basin population), Not at Risk (CAN SARA), Least Risk (BC)	Least Concern (2015)	Highly aquatic; Relatively exposed, shallow waters of sedge fens, riverine over-bank pools, beaver ponds, and small lakes; occasionally quiet, pond-like parts of streams	1, 3, 6, 8, 10, 11
	Cascades frog (*Rana cascadae*)	Petitioned for listing by US ESA, Sensitive (OR), Monitored (WA), Candidate (CA)	Near Threatened (2004*)	Highly aquatic; Shallow water of ephemeral ponds, deep areas or pothole pools within flooded mountain meadows, lake shores, off-channel pools of streams	2, 8, 9

	Wood frog (*Rana sylvatica*)	Least Risk (BC)	Least Concern (2015*)	Predominately forest dwellers; utilize ephemeral, fish-free ponds and marshes, lakes, and backwaters of streams for breeding	1, 4
	{Invasive} American bullfrog (*Rana catesbeiana*)		Least Concern (2015)	Highly aquatic; utilize most any permanent, warm water including slow-moving streams and backwaters	No threats known
	{Invasive} Green frog (*Rana clamitans*)		Least Concern (2015)	Highly aquatic; utilize most any permanent, warm water including slow-moving streams and backwaters	No threats known
	Western toad (*Anaxyrus boreas*)	Sensitive (OR), Candidate (WA), Imperiled (ID), Least Risk (BC)	Least Concern (2020)	Breed in slow portions of streams, springs, ponds, lakes, reservoirs, or stock ponds; non-breeding stages occur in diverse habitat from forests to grasslands.	1, 3, 4, 5, 8, 10, 12
	Woodhouse's toad (*Anaxyrus woodhousii*)	Candidate (WA), Imperiled (ID)	Least Concern (2004*)	Terrestrial habitats include grassland and shrub-steppe; utilize a variety of permanent and temporal waterbodies for breeding, including rain-filled pools, slow-flowing springs, ponds, sloughs, and irrigation ditches	No threats known
	Great Basin spadefoot (*Spea intermontana*)	Special Concern (BC)	Least Concern (2015)	Terrestrial habitats include shrub-steppe, grassland, and open Ponderosa pine forest; utilize a variety of permanent and temporary waterbodies for breeding, including rain-filled pools, springs, sloughs, irrigation ditches, still-water edges of streams, and ponds	3
	Pacific tree frog (*Hyliolus regilla*)	Least Risk (BC)	Least Concern (2004*)	Breed in nearly any freshwater habitat that are primarily fishless, including the slower stretches of streams	No threats known
	Boreal chorus frog (*Pseudacris maculata*)	Least Risk (BC)	Least Concern (2015)	Breed in nearly any freshwater habitat that are primarily fishless, including the slower stretches of streams	4, 10
Obligate Riparian Breeders	Dunn's salamander (*Plethodon dunni*)	Candidate (WA)	Least Concern (2014)	Associated with rocks along banks of small streams in cool, moist areas	No threats known
	Van Dyke's salamander (*Plethodon vandykei*)	Candidate (WA)	Least Concern (2014)	Associated with rocky, steep-walled stream valleys, often between slabs of wood or bark on large logs near streams; Often found in exfoliating rock or gravel, splash zones, or adjacent chutes and cascades of waterfalls; Has been found within blast zone of Mount Saint Helens in seeps without forest	1, 2
	Coeur d'Alene salamander (*Plethodon idahoensis*)	Special Concern (CAN SARA), Least Risk (BC)	Least Concern (2015)	Associated with steep streams and in waterfall spray zones and seepages; Can be found in deep underground refugia such as talus or rock crevices	1, 2, 3, 5, 6, 7, 8

(Continued)

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Facultative Riparian Breeders	Ensatina (*Ensatina eschscholtzii*)	Least Risk (BC)	Least Concern (2015)	Broadly distributed among coniferous and deciduous forests; Require moist microhabitats and can be found under rocks and logs, in talus, leaf litter, and bark piles	1, 10
	Shasta salamander (*Hydromantes shastae*)	Threatened (CA)	Vulnerable (2004)	Habitat specialist; associated with limestone and volcanic rock outcrops, meta-sedimentary rock talus, and areas with scattered surface rock; Occur in caves and rock crevices	6, 11, 12
	Samwel Shasta salamander (*Hydromantes samweli*)	Threatened (CA)	New species not yet assessed; part of the Shasta salamander complex of species with similar ecology	Habitat specialist; associated with limestone and volcanic rock outcrops, meta-sedimentary rock talus, and areas with scattered surface rock; Occur in caves and rock crevices	6, 11, 12
	Wintu Shasta salamander (*Hydromantes wintu*)	Threatened (CA)	New species not yet assessed; part of the Shasta salamander complex of species with similar ecology	Habitat specialist; associated with limestone and volcanic rock outcrops, meta-sedimentary rock talus, and areas with scattered surface rock; Occur in caves and rock crevices	6, 11, 12
	Scott Bar salamander (*Plethodon asupak*)	Threatened (CA)	Vulnerable (2006*)	Associated with rocks along banks of small streams in cool, moist areas; May also be found in talus, under woody debris, moss, or other cover at edges of streams	1
	Del Norte salamander (*Plethodon elongatus*)	Sensitive (OR)	Near Threatened (2004*)	Strongly associated with talus and rocky substrates in mature or late-seral Redwood and Douglas Fir forests, except in marine-influenced coastal areas, where they utilize talus	1
	Larch Mountain salamander (*Plethodon larselli*)	Sensitive Critical (OR), Sensitive (WA)	Near Threatened (2004*)	Old-growth forests, young, naturally regenerated forest with residual late-successional features, shrub-dominated communities, scree and talus, and lava-tube entrances	1, 3, 11
	Siskiyou Mountains salamander (*Plethodon stormi*)	Sensitive Critical (OR), Threatened (CA)	Endangered (2004*)	Talus or forested rocky habitat obligate in mature and late-seral forest	1
	Western red-backed salamander (*Plethodon vehiculum*)	Not at Risk (CAN SARA), Least Risk (BC)	Least Concern (2015)	Found in all forest ages; Utilize microhabitats within and under decaying wood, rocks, and vegetations or within talus crevices	No threats known
	Clouded salamander (*Aneides ferreus*)	Sensitive (OR)	Near Threatened (2004*)	Large, decaying logs and stumps, rock outcrops and road cuts	1
	Black salamander (*Aneides flavipunctatus*)		Near Threatened (2004*)	Downed wood, bark or rocks (including talus slopes); Restricted to rocky ravines, stream-riparian areas, and seeps in more interior and southern locations	1
	[Shasta] Black salamander (*Aneides iecanus*)	Not yet assessed	New species not yet assessed; part of the Black salamander complex of species with similar ecology	Downed wood, bark or rocks (including talus slopes); Restricted to rocky ravines, stream-riparian areas, and seeps in more interior and southern locations	6

[Klamath] Black salamander (*Aneides klamathensis*)	Not yet assessed	New species not yet assessed; part of the Black salamander complex of species with similar ecology	Downed wood, bark or rocks (including talus slopes); Restricted to rocky ravines, stream-riparian areas, and seeps in more interior and southern locations	
Arboreal salamander (*Aneides lugubris*)		Least Concern (2008*)	Coastal oak woodlands and forests; Utilizes surface cover and trees	1, 4, 10
[Niger] Black salamander *Aneides niger*			Downed wood, bark or rocks (including talus slopes); Restricted to rocky ravines, stream-riparian areas, and seeps in more interior and southern locations	2
Wandering salamander (*Aneides vagrans*)	Special Concern (CAN SARA), Special Concern (BC)	Near Threatened (2015)	Typically found in cavities within decaying logs and stumps or under loose bark in old- and second-growth forests	1, 4, 10
California slender salamander (*Batrachoseps attenuatus*)		Least Concern (2004*)	In wooded areas or in ecotones at the edges of forest and grassland	No threats known
Oregon slender salamander (*Batrachoseps wrighti*)	Sensitive (OR)	Vulnerable (2004*)	Associated with moist, microhabitat and large, downed wood typically in old-growth forests	1
Western tiger salamander (*Ambystoma mavortium*)	Monitored (WA)	Least Concern (2015)	Uses variety of habitat, needs substrate for burrowing and nearby water bodies for breeding. Can be found in forest, shrubland, grassland, wetlands, desert, and agricultural areas.	1, 6, 8, 10

Status includes state, provincial, and federal categories of species of conservation concern in Canada and the U.S. and IUCN Red List rankings. Abbreviations are: U.S. Endangered Species Act of 1973 (US ESA), Oregon (OR), Washington (WA), Idaho (ID), California (CA), Canada Species at Risk Act of 2002 (CAN SARA), British Columbia (BC). Primary threats codes: 1. Logging and wood harvesting; 2. Climate change (including drought); 3. Roads; 4. Residential and commercial development; 5. Urban, agricultural, or forestry wastewater and effluent; 6. Dams and water management or use; 7. Wildfire or fire suppression; 8. Invasive species; 9. Pollution; 10. Agriculture or ranching practices; 11. Mining or quarrying; 12. Recreation.

Habitat information primarily from Jones L, Leonard W, and Olson D (2005) *Amphibians of the Pacific Northwest*. Seattle, WA, USA: Seattle Audubon Society, 227 pp.

from broad-scale forest management practices and the myriad effects of ongoing climate change on species habitat and physiology (Olson, 2009). Emerging concerns that warrant further investigation and are expected to significantly threaten the persistence of HSA amphibians include the potential synergistic interactions between climate change, increasing frequency and severity of wildfires, and diseases caused by novel *pathogens* like *Batrachochytrium salamandrivorans* (*Bsal*).

Conservation challenges

Forest management practices

Natural resources of the iconic cathedral forests of the PNW have long been a public commons, used initially by Native American Tribes and now by a global society (Olson and Van Horne, 2017). Since the 1800s, wood production and salmonid fisheries have been regional socioeconomic boons, sustaining local communities throughout the region. Historically, resource extraction was prioritized as primary forests of Douglas-Fir, Western Hemlock, and California Redwood trees were extensive and fish stocks of Coho, Sockeye, and Chinook Salmon and Steelhead and Cutthroat Trout were abundant. However, new regulations for timber and fish sustainability emerged as those industries developed and eventually laws were passed to ensure water quality and the protection of rare species, such as the U.S. Clean Water Act of 1972 and U.S. Endangered Species Act of 1973, respectively. The lens on natural-resource sustainability took on renewed focus with the 1994 implementation of the Northwest Forest Plan, as species associated with late-successional and old-growth (LSOG) forests (e.g., Northern Spotted Owl) were diminishing and heralded changes in forest protections. Among these LSOG species of concern are 18 amphibians, including numerous HSA species.

The changing mindset and practices of forest and fisheries management has had significant implications for streams and stream-associated species. Historically, there had been no regulated streamside retention or riparian buffer zones. In some areas, forested streams were even used as conduits for timber transport—logs were dragged up small channels to roads and splash dams were constructed and then dynamited to sluice logs downstream. As part of forest management, an extensive road network was built in the PNW, and where roads crossed streams, there was little consideration for the aquatic denizens. Fish-bearing streams now have streamside protected areas to retain stream habitat integrity and their inhabitants. However, an extensive resource extraction footprint remains on both stream habitats and their biotic communities from many of these historical practices. Even into the 21st Century, recognition of the protection-worthy ecological values of headwater streams has varied across jurisdictions, with streams on some private lands and ephemeral (fishless) portions of headwater basins still frequently lacking protection (e.g., Olson et al., 2007).

The North American model for wildlife management is for science to inform management and policy actions. This model has been applied to HSA amphibians, as a host of landscape-scale studies have been conducted to understand the response of this unique, endemic fauna and their habitat elements to alternative stream-riparian forest management practices. Retrospective studies and novel experiments of streamside-buffer protection along small streams have been implemented, with different studies considering different geographies, stream size constraints, aquatic communities, management treatments, and monitoring time frames. A review of this body of research by Olson and Van Horne (2017), suggests that no-harvest streamside buffers have positive impacts on preserving water temperatures in harvested stands (6 m buffer width) and for protecting sensitive salamander species (>15 m buffer width). However, heterogeneity of conditions supports case-by-case decisions, and an integrated strategy of mixed-width buffers across a watershed or landscape. In addition, it has been recognized that upland foraging and dispersal habitat is critical for species conservation, and extends from the stream up to watershed ridgelines. Forest cover and roads can affect connectivity of amphibian populations across the landscape, adding new habitat considerations for broad conservation planning (Emel et al., 2019; Olson and Burnett, 2009). This initial pulse of headwater stream-buffer research is being followed by a next-generation of studies that will expand upon initial results and explore alternative approaches to headwater management. Simultaneously, a new set of timber harvest rules are emerging, balancing streamside management approaches with the institution of habitat conservation areas.

Climate change

Climate change is projected to increase stream temperatures and alter *water balances* in the PNW. Stream warming will occur as a direct result of increases in air temperature but will also be exacerbated by drought conditions and the resulting increasing intensity and severity of wildfire (Luce et al., 2014). Coldwater stream temperatures are expected to increase by 0.2–0.4 °C for every 1 °C change in air temperature in the PNW (Luce et al., 2014). These changes in the stream environment are expected to have significant effects on stream biota, particularly the most sensitive, cold-adapted species like HSA amphibians. Given that these amphibians are *ectothermic* and coldwater dependent, increasing water temperatures may cause physiological stress or mortality if species thermal tolerances are exceeded. For instance, increases in the severity and duration of summer heat waves will likely impact HSA amphibians with critical thermal maxima below 30 °C, such as tailed frogs, giant salamanders, and torrent salamanders (Bury, 2008). Stream warming may be mitigated by forest management practices that retain riparian buffers and encourage streamside shading. Conversely, canopy cover loss (e.g., due to wildfire [see section below] or defoliating insects) may exacerbate stream temperature increases and their resulting impacts on coldwater-dependent amphibians.

Surface-water flow in headwaters is, by nature, spatially and temporally intermittent but a 4.5–11.5% loss in surface flow in part of the PNW was projected with climate change by 2055–2085 (Olson and Burton, 2019). As HSA amphibians are *desiccation-*

intolerant, reduced surface-water flows may restrict surface activities, resulting in longer subsurface summer seasons with consequent effects on critical functions like foraging, breeding, and dispersal. It may also force animals downstream, which could extend over-ridgeline dispersal distances, thereby disrupting population connectivity. Forced downstream movements would alter aquatic community composition and could also increase predation risk on amphibians by downstream predators; fish are less prevalent in headwater streams due to waterflow discontinuity and ephemerality but pose a significant predation threat to amphibians downstream.

Climate change has also been tied to increased frequency and severity of wildfires. Although fire impacts on HSA amphibians in PNW forests are inconclusive, a few studies have offered insights into their recovery capacity. For example, Hossack and Honeycutt (2017) found that Rocky Mountain tailed frog abundance in burned streams had nearly recovered to pre-fire conditions within two generations. For other PNW species, most of which occur in less fire-adapted regions, several wildfire impacts could emerge. Loss of upland forest from wildfire may change local *microclimates* and elevate in-stream temperature, alter flow regimes, and increase headwater debris flows, enacting direct effects on amphibians by sluicing streams (Burnett and Miller, 2007). Patchy wildfires could also contribute to habitat fragmentation for HSA amphibians, isolating populations unable to disperse across areas with diminished forest cover (Emel et al., 2019). Alternatively, downed-wood dependent species may benefit from the added debris from dead trees that provide overwintering habitat and refuge during the dry season. Wildfires may also increase in-stream sediment loads. To our knowledge, the specific effects of wildfire-caused sedimentation on HSA amphibians are yet to be investigated but may decrease local species abundances similar to observed patterns following road construction. Wildfire-caused sedimentation could be particularly detrimental to the reproductive success of stream-breeding amphibians if it infills submerged crevices used for egg deposition.

Disease

Emerging Infectious Diseases (EIDs) pose a growing threat to amphibian biodiversity and are recognized as an important driver of global amphibian declines. Of the several disease agents identified thus far, *Batrachochytrium dendrobatidis* (*Bd*), *B. salamandrivorans* (*Bsal*), and *Ranavirus* are of greatest concern. The chytrid fungal pathogens *Bd* and *Bsal* have been implicated as contributing factors to hundreds of population declines and dozens of species extinctions across the globe. Both pathogens infect amphibian skin, an important respiratory structure, and are associated with high mortality rates in susceptible species. *Bd* is widespread in the PNW but its prevalence is relatively low in headwater streams compared to other habitat types (Hossack et al., 2010). Despite strong evidence for *Bd*-driven declines in some facultative stream-breeding HSA amphibians (e.g., Cascades frog; Piovia-Scott et al., 2015), there is not yet clear evidence for such effects on most HSA amphibians in the PNW. However, data are lacking for some species, including cryptic, seep-associated salamanders. While *Bd* tends to have strong effects on frogs and toads, salamanders are more strongly impacted when infected with *Bsal*. Recent surveys have not detected *Bsal* in North America and it appears that this pathogen has not yet become established on the continent. However, the PNW has been identified as a region of high vulnerability to *Bsal* given its high salamander biodiversity, climatic suitability for *Bsal*, and high likelihood of introduction through international trade (Yap et al., 2015). In addition, some HSA salamanders have shown moderate to high susceptibility to disease in *Bsal*-exposure trials (Piovia-Scott, pers. comm.).

Ranaviruses infect a wide range of ectothermic host taxa and have been associated with mass mortality events in some amphibian hosts. Clinical signs include lethargy, skin reddening and necrosis (tissue death), internal bleeding, and mortality. There has been relatively little ranavirus sampling in the PNW, though there have been detections in California and at least two mass mortality events recorded in Idaho. Other pathogens and parasites that may influence HSA amphibians in the PNW include: the water mold *Saprolegnia ferax* that has contributed to mass mortality events in frog embryos in the Oregon Cascade Range; red-leg syndrome, a bacterial infection caused by *Aeromonas hydrophila* that has been associated with some mortality events; the protozoan *Trichodina* that has been found in the endemic HSA amphibians *Dicamptodon copei* and *D. tenebrosus;* and various species of helminths (including nematodes and trematodes) that have been found in *Taricha granulosa*, *D. ensatus*, and multiple *Plethodon* species. Unfortunately, there is limited evidence regarding the magnitude of the threat posed by these microparasites or how they may be exacerbated by climate change and other stressors.

Species profiles

All amphibian species described herein have either *obligate* or *facultative* stream associations, with a quarter being obligate forms with life histories reliant on headwater streams (Olson et al., 2007). We provide vignettes for six species representative of four types of headwater-stream associations, including stream obligates, facultative stream breeders, obligate riparian breeders, and facultative riparian breeders. Of the 52 species included in **Table 1**, two are considered invasive and 32 (~62% of native species) are considered species of conservation concern at the state, provincial, or federal level in the U.S. and/or Canada. For these species of concern, rankings range from sensitive/monitored to endangered, including some candidates for listing at the state and federal level.

Stream obligates

Stream obligate amphibians are dependent on headwater streams for reproduction and larval rearing, and have physiological adaptations to the cold, fast flowing water of headwater streams, such as the short gills of larval torrent salamanders and the suctorial (adhesive) mouths of tailed frog tadpoles. Common habitat features required by members of this group include high-gradient streams and seeps, and permanent water sources due to the multiyear larval life stages of most of these species. This group includes the PNW-endemic torrent salamanders (Rhyacotritonidae). Torrent salamanders are regarded as being sensitive to changes in streamflow and temperature and are highly susceptible to desiccation. Conservation practices for stream obligates will need to emphasize stream buffers to mitigate in-stream warming, as well as protection of over-ridge corridors allowing for movement between streams (Olson and Burton, 2019).

*Cascade torrent salamander (*Rhyacotriton cascadae*)*

Cascade torrent salamanders (Fig. 1) occur patchily throughout the western slope of the Cascade Range of Oregon and Washington, from sea level to approximately 1200 m. This species is most abundant in the uppermost headwaters, characterized by high-gradient reaches (both permanent and intermittent), waterfalls, and seeps. The species has two distinct life stages, larval and metamorphosed adults, with metamorphosis taking place 2–4 years after hatching. Their strong association with discontinuous streams will likely leave them vulnerable to climate change as a result of drought and habitat shrinkage (Olson and Burton, 2019). Cascade torrent salamanders have also been impacted by timber harvest practices that alter stream temperatures and flow regimes due to changes in riparian forest structure and coverage, as their occupancy is highly linked to stream temperature. As of 2015, this species—along with the Columbia torrent salamander and Cascades frog—is under review for listing by the U.S. Endangered Species Act. Data are actively being collected on range-wide abundances and habitat associations to inform this listing decision (Thurman et al., unpublished data).

*Coastal giant salamander (*Dicamptodon tenebrosus*)*

Coastal giant salamanders (Fig. 2) are widespread in the PNW, occurring in high-gradient streams throughout the Cascade and Coast Ranges from northwestern California to southwestern British Columbia. Similar to Cascade torrent salamanders, they have multi-year larval and metamorphosed life stages; unlike torrents they are known to exhibit neoteny wherein reproductive adults retain gills and other larval characteristics. Neotenic adults are often the largest vertebrates in their streams, far exceeding the body size of other stream amphibians, and can supplant fish as the dominant predator instream. This life history trait, coupled with their multi-year aquatic life stage, makes permanent water sources vital for persistence. Larvae are important predators in their streams. Field studies and experiments have shown that larval *D. tenebrosus* can eat a wide variety and size range of *benthic* organisms. Although they are common throughout much of their range, coastal giant salamanders are granted conservation status in Canada, where they are under consideration for Threatened status by the Canadian Species at Risk Act and a species of special concern in the province of British Columbia.

*Coastal tailed frog (*Ascaphus truei*)*

Both species of tailed frogs are endemic to the Pacific Northwest. This family contains the basal species for all anurans and retains many primitive features lost in other frog species. Like the torrent and giant salamanders, coastal tailed frogs (Fig. 3) are associated with high-gradient streams and have larval and adult life stages. The tadpole (larval) stage, which can last from 1 to 4 years, has a characteristic suctorial mouth which it uses to attach to rocks in fast-flowing streams. The adults also contain unique traits adapted for fast-flowing streams. The 'tail' in their name refers to the copulatory organ that males use for internal fertilization which minimizes sperm loss in turbulent water; tailed frogs are the only North American frog species with this reproductive strategy. Like torrent salamanders, they are sensitive to increased water temperatures and siltation, both of which are a common consequence

Fig. 1 Photo of Cascade torrent salamander (*Rhyacotriton cascadae*). © Christopher Cousins.

Fig. 2 Photo of Coastal giant salamander (*Dicamptodon tenebrosus*). © Lindsey Thurman.

Fig. 3 Photo of Coastal tailed frog (*Ascaphus truei*). © Christopher Cousins.

of timber harvest and wildfires. While not federally listed in the U.S., Oregon lists coastal tailed frogs as a state-sensitive species, Washington lists them as a monitored species, and Canada has designated them as a species of special concern.

Facultative stream breeders

Whereas stream obligate amphibians are completely dependent on headwater streams, facultative stream breeders can utilize other habitats for life-cycle processes, such as reproduction. One of the distinctions between this functional group and stream obligates is that the latter is adapted to fast-flowing, high-gradient streams, while facultative stream breeders can utilize slower moving water. This is reflected in physiological differences, such as the noticeably large external gills of Ambystomatidae salamanders, reflecting the lower oxygen content and slower moving water of their preferred habitat. Facultative stream breeders can be found in a broad diversity of habitat types, including forests, wetlands and ponds, larger streams and rivers, and agricultural areas. This functional group also contains species that need multiple habitats for their life history, often requiring upland habitat for adults as well as permanent water bodies for breeding and larvae (Olson et al., 2007). This creates distinct challenges for conservation, as practitioners must accommodate species use of multiple habitat types and their needs for habitat connectivity that may change over space and time.

*Northern red-legged frog (*Rana aurora*)*

Northern red-legged frogs (Fig. 4) have a widespread distribution, ranging from northwestern California to southwestern British Columbia. This species utilizes diverse aquatic habitats for breeding, including shallow ponds and wetlands and slow-moving streams. *Rana aurora* has been found in or along headwater streams but is considered to be infrequently encountered in these habitats. This could be due to prey availability or other factors, such as opportunistic use of streams as movement corridors, but more research is needed. Within a year, tadpoles metamorphose to adults, which can then live up to 12 years. Unlike most other frog species, adult Northern red-legged frogs vocalize underwater during breeding periods. Activity of this species drops markedly with low temperatures, and adults overwinter in both aquatic and terrestrial habitats. Habitat loss and pollution are key threats across most of its range, particularly in or near urban areas. Northern red-legged frogs are noted as a species of special concern across multiple jurisdictions throughout their range.

Obligate riparian breeders

Obligate riparian breeders depend on the 'stream effect' of cool, moist conditions that permeate upslope (Olson et al., 2007), as they and their eggs are highly susceptible to desiccation and warmer temperatures. In the PNW, all of the species in this group belong to the genus *Plethodon*: lungless salamanders that are terrestrial (or semi-terrestrial) throughout their lives. Plethodontids in this group are considered stream-adjacent and have a strong association with riparian habitat as they are rarely found away from streambanks, seeps, waterfalls, and other habitats with permanent ground- or surface-water sources. They're known to lay eggs inside downed wood and talus alongside streams and the nests often have an attendant adult. This reliance on the unique microclimates and habitat features found at the interface between aquatic and terrestrial systems potentially makes them indicator species for intact riparian ecosystems of the PNW. As with most amphibian species occupying headwaters in the PNW, habitat loss and degradation are key threats, as are any compounding effects of climate change.

*Van Dyke's salamander (*Plethodon vandykei*)*

The Van Dyke's salamander (Fig. 5) is endemic to Washington and found in three disjunct regions: the Olympic peninsula, the Willapa Hills, and the southern extent of the Cascade Range in Washington. As with other members of the genus *Plethodon*, this species is terrestrial throughout its life, but is considered semiaquatic. Van Dyke's salamanders are highly associated with seeps, saturated rock faces, waterfall splash zones, and streambanks. They show a unique association with *headwall seeps* more so than high-gradient streams. Headwall seeps appear to be relatively rare on the landscape, which may contribute to the rarity of *P. vandykei*. Habitat loss and degradation from logging and road building are the largest threats to this species, particularly in the Willapa Hills, which has significantly less protected land than the other two regions. The habitat between the three ranges was clearcut in the 19th and 20th centuries, and it is thought that this may have contributed to the fragmentation of the species range. Van Dyke's salamanders are a candidate species of conservation concern in the state of Washington.

Facultative riparian breeders

Facultative riparian breeders include species who can breed on or near streambanks but can also use a diverse array of other habitats. In the PNW, this includes many species of salamanders which, with one exception, belong to the family Plethodontidae. Some

Fig. 4 Photo of Northern red-legged frog (*Rana aurora*). © Christopher Cousins.

Fig. 5 Photo of Van Dyke's salamander (*Plethodon vandykei*). © Christopher Cousins.

members of the family, such as the Larch Mountain salamander (*Plethodon larselli*) and Siskiyou Mountains salamander (*P. stormi*), primarily utilize talus slopes where animals can take advantage of the cool, moist interstices of rock and gravel. For slender salamanders in the genus *Batrachoseps*, downed wood provides these refugial conditions (Garcia et al., 2020). Timber harvest is the primary threat to this group, as most of the species rely on forested habitat, and some are reliant on the downed and living wood of old-growth forests.

*Clouded salamander (*Aneides ferreus*)*

Clouded salamanders (Fig. 6) are endemic to the PNW, occupying coastal forests and forests of the west slope of the Cascade Range in Oregon and northern California. Few data exist on the abundance of clouded salamanders throughout their range, but they are thought to occur in high densities in old-growth forests. Historically believed to be largely terrestrial and associated with downed wood, they have recently been found to utilize tree vole nests in the living canopy and have been found as high as 75 m up in tree cavities. This use of both terrestrial and arboreal habitat potentially makes them an important species for nutrient transfer in the tree canopy; more research is needed to fully understand their role in forest food webs. Key threats to this species include logging and habitat loss, with logging on short cycles considered particularly harmful to clouded salamander populations. Clouded salamanders are listed as Oregon state-sensitive.

Fig. 6 Photo of Clouded salamander (*Aneides ferreus*). © Christopher Cousins.

A path forward

Like many imperiled taxa, HSA amphibians are still plagued by a dearth of basic ecological information, likely contributing to the lag in allocation of conservation resources. Reconciling the myriad data deficiencies for these species continues to be a priority and is helping to strengthen the breadth of information used in conservation planning and decision-making as we prepare for an uncertain future. Conservation planning tools such as Climate Change Vulnerability Assessments (CCVAs) are uniquely suited to providing practitioners with the necessary guidance for adaptive (or risk-based) management of imperiled species or, more specifically, climate adaptation and preparedness. CCVAs are useful tools for evaluating extinction risk in amphibians because of their sensitivity to climate-related threats like warming and drought. The traditional CCVA framework evaluates three components of vulnerability: exposure, sensitivity, and adaptive capacity. Exposure reflects the type and magnitude of climatic changes that a species will experience. Sensitivity refers to the degree to which a species is affected by or susceptible to climate change. Adaptive capacity refers to the ability of a species to cope with, adjust to, and persist in the face of climate change. Recently, separate research efforts focusing on climate vulnerability have put HSA amphibians of the PNW under the spotlight. First, Case et al. (2015) assessed sensitivity to climate change for 195 northwestern USA plant and animal species, including 17 headwater-stream associated amphibian species. Nine factors pertaining to species' life history, ecological relationships, climatic and non-climatic threats were assessed. The median sensitivity score for amphibians was 77 (out of 100), higher than all other taxa assessed, suggesting high sensitivity to climate change for this group. Second, Mims et al. (2018) developed a combined rarity and climate-sensitivity index for rapid assessment of all Oregon fishes, amphibians, and reptiles. Several HSA amphibians, such as Columbia torrent salamanders, were among the highest risk for rarity and climate change concerns. More recently, Thurman et al. (2020) developed a framework for evaluating the adaptive capacity of species to climate change through a similar trait-based assessment of their ability to persist in place and/or shift in space. This framework is currently being applied to priority species of conservation concern in the PNW, including HSA amphibian species like the Cascade torrent salamander, Rocky Mountain tailed frog, and coastal tailed frog. Collectively, these assessments provide much needed information in support of conservation decision-making, for example, in response to petitions for listing by the U.S. Endangered Species Act and other state- or provincial-level assessments.

Information synthesis, and particularly the reconciliation of information gaps, is critical for ensuring effective conservation action. The emergence of new tools and techniques, such as inventory and monitoring via *environmental DNA* (eDNA), holds promise for improving knowledge of the occurrence of rare or elusive species like HSA amphibians. Since many stream amphibian species of the PNW are also data deficient, eDNA may offer an efficient tool for gathering much needed information on their distribution, abundance, genetic diversity, and habitat associations. In turn, these data gathering efforts can be used to refine the science in support of conservation planning for imperiled species, such as through State Wildlife Action Plans (SWAPs). SWAPs identify Species of Greatest Conservation Need (SGCN) and are used across all states and territories in the U.S. to assess the status of wildlife and habitats, identify key threats, and provide a comprehensive strategy to conserve them before they become too rare or costly to restore. In the PNW, SWAPs have been used to identify threats such as invasive species, disease, and climate change, and associated mitigation strategies for several HSA species. For example, each state has identified at least one amphibian pathogen as a disease of management concern. Actions include developing or expanding disease surveillance and mapping in targeted regions or amphibian populations. Additionally, some states are focusing on ecosystem health to promote disease resiliency in susceptible populations by implementing management approaches that maintain high habitat quality, generally improve ecosystem function, and prevent the spread of pathogens to new populations. Establishment of standard and enhanced biosecurity procedures to reduce human-mediated spread of amphibian diseases is an emerging priority (Olson et al., 2021). Most SWAPs acknowledge the intersection of habitat disturbance or climate change with disease susceptibility. However, the incorporation of disease management, unless the primary concern, is seldom given consideration in climate adaptation planning and is an actionable pathway for conservation that is ripe for further investigation.

Meanwhile, practitioners are looking towards other conservation opportunities that may act as stop-gaps or buffers to prevent species extinctions in the face of climate change and continued habitat loss. For instance, the identification of *climate-change refugia*—locations relatively buffered from climate change that are likely to facilitate species persistence—may offer significant conservation potential, particularly for less studied species (Morelli et al., 2020). The conservation of climate-change refugia represents a valuable opportunity to preserve unique biodiversity and maintain ecosystem function in a rapidly changing environment. For HSA amphibians, this could involve a local approach to identifying refugia specific to the ecological needs of a given species (e.g., via mapping of surface and subsurface hydrogeological structures for seep-associated species). Alternatively, broader-scale refugia can offer amphibians a slow lane within a landscape where faster climatic changes occur, particularly for species that are dispersal limited and require connected networks of headwater streams to facilitate climate tracking (e.g., Olson and Burnett, 2009). Protection of adequate riparian forest area, coarse stream substrate and clean, cool water to sustain HSA amphibian communities represent potentially important refugial characteristics. As an example of application, the Partners in Amphibian and Reptile Conservation (PARC) organization has begun an initiative to designate Priority Amphibian and Reptile Conservation Areas (PARCAs) that support species rarity, richness, and landscape integrity (e.g., climate change refugia) and complement existing local-to-regional conservation efforts.

Updates to IUCN Red List assessments for HSA amphibians are also critically needed. Currently, about half (24) of the 52 HSA species are indicated as needing updates (**Table 1**). These assessments are important barometers of the health of biodiversity. For those species where assessments are based on limited information, there is an even greater need for additional research to inform and catalyze action for conservation. In addition to more baseline information on species life-history and ecology, research is needed on the potential synergistic effects of the numerous threats to this imperiled group. For instance, the interactive effects between disease and climate change—two stressors having significant impacts on amphibians globally—are largely unknown for most (if not all) HSA species yet could threaten their persistence into the future. Collecting baseline and continuous data for HSA species will allow us to track and monitor changes to populations, communities, and ecosystems over time, elucidating the importance of various factors like canopy cover and topographic complexity for mitigating stream temperature changes. Increased allocation of research effort and conservation resources will, therefore, ensure that headwater stream-associated amphibians continue to play a vital role in sustaining forest ecosystem health.

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