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Riparian buffer effects on headwater-stream vertebrates and habitats five years after a second upland-forest thinning in western Oregon, USA

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ABSTRACT

Riparian-management zones protect aquatic species and their habitats in managed forests, yet the effects of riparian-management alternatives warrant further study. We examined effects of alternative riparian-buffer widths on fish and amphibians in small headwater streams with upland forest thinning in western Oregon, USA. Previously, we reported apparent lag-time effects developing 10 years after thinning of upland second-growth forest, and additional effects 1–2 years after a second-thinning harvest. Here, we analyze effects on fish and amphibian abundances, body-size metrics, and habitats 5 years after the second thinning at 58 stream reaches across eight study sites. Riparian-buffer effects were evident for several species and species groups: higher densities of fish and amphibians (e.g., coastal giant salamander [*Dicamptodon tenebrosus*], torrent salamanders [*Rhyacotriton* spp.], sculpins [family Cottidae]) were detected in reaches with a no-entry one site-potential tree-height buffer (~70 m wide) in comparison with lower densities in two narrower no-entry buffers (6-m-wide, and a variable-width buffer with a 15-m minimum width) and a thin-through managed buffer (two site-potential tree-heights wide, ~140 m). In addition, indicator-species analyses showed that torrent salamander densities were positively associated with stream reaches in unmanaged controls. Some amphibians changed habitat affinities slightly, being found during the most-recent sampling in locations with habitats related to larger stream sizes (i.e., more-perennial stream flows) than they had been in earlier sampling. Analyses of body-size metrics showed associations with buffers across 42% of species × post-treatment years analyzed, yet patterns were inconsistent within species, and more consistent associations of body metrics were found with microhabitat types, finding larger animals in pools. Although the mechanism driving changes is unclear, the positive associations of species' densities with one-tree buffers suggest that either lag-time or cumulative effects of factors associated with treatments are developing, with benefits of wider streamside protections over longer time periods for headwater-associated fish and amphibians. Our findings of higher densities of headwater-reliant *Rhyacotriton* species in stream-reach treatments with the one-tree buffers, and affinities with unthinned control reaches, support the benefits of greater headwater-stream protections for that species complex, which includes species of conservation concern. The mix of different buffer widths and unmanaged units across our eight sites may be promoting site-scale persistence of a community of aquatic-vertebrate species—a mix of buffer widths with upslope forest management may be an alternative for larger-scale riparian forest-management objectives.

1. Introduction

Among global forest ecosystem services, two priority sustainability concerns can be at odds: wood-biomass production for socioeconomic viability; and forest biodiversity for services including ecological integrity, recreation, ethics, aesthetics, non-timber products, and cultural uses (Brockerhoff et al., 2017). The challenge to retain biota and timber production has led to development of forest ecosystem-management plans, ecological-forestry paradigms, forest-restoration approaches, and numerous habitat- or species-specific forestry × conservation measures (e.g., USDA and USDI, 1994; Lindenmeyer and Franklin, 2002; Lindenmayer et al., 2012; Puettmann et al., 2008, 2015; Franklin et al., 2018). Aquatic biodiversity in forests appears to be a subgroup in heightened peril, with multiple interacting stressors

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(Penaluna et al., 2017), especially as freshwater ecosystems are among the most threatened globally (IUCN, 2021a). Among aquatic biota, amphibians and fish top lists of threatened species from diverse threat factors, with 41% of world amphibian species (IUCN, 2021b) and >40% of freshwater fish species (McGregor Reid et al., 2013) designated at-risk. Habitat changes are a leading factor in these aquatic-dependent vertebrate concerns, with many occurring in forested ecosystems, for example: 68% of world amphibians are forest associated (Olson and Burton, 2014); 25% of US freshwater fishes are forest associated (Bury et al., 2021).

Timber-harvest effects on aquatic-dependent forest fauna have been ameliorated by implementation of streamside-management areas, often in the form of fixed-width riparian-buffer zones (Richardson et al., 2012). This practice was gaining widespread use in western North America by the 1960s (Richardson et al., 2012), leading to development of forestry Best Management Practices (BMPs) in the United States following the US Clean Water Act of 1972 and the US Endangered Species Act of 1973 (e.g., US EPA, 2001; USDA Forest Service, 2012), and Canada's Fisheries Act of 1985, which was amended in 2019 to strengthen fish and fish habitat protections: Imhof et al., 2021). Streamside-management zones have aimed to protect key aquatic species' habitat components. These include protection of water quality resulting from: 1) stream sedimentation by forestalling streambank erosion; 2) thermal pollution by provision of overstory shading and microclimate edge-effect buffering to retain cooler stream-riparian temperatures; and 3) uptake of chemical pollution from upland applications by streamside vegetation (Warrington et al., 2017). In addition, streamside riparian forests have provided standing trees for down-wood recruitment and litter inputs (USDA and USDI, 1993; Reeves et al., 2016), and other terrestrial subsidies for aquatic-dependent species (e.g., prey; Wipfli and Musslewhite, 2004; Baxter et al., 2005). However, relative to species, BMPs have generally been designed to mitigate effects on fish, whereas measures that go beyond these practices may be needed for protection of other aquatic-riparian denizens, especially amphibians that can have both aquatic and terrestrial life forms (Olson et al., 2007), and maintenance of ecological functions including transport of reciprocal subsidies between aquatic and upland ecosystems (Baxter et al., 2005).

In the Pacific Northwest of North America, timber-harvest effects on native amphibians have been an increasing concern owing to the region being a regional amphibian biodiversity hotspot and the number of endemic species reliant on moist coniferous forests and their embedded aquatic habitats (e.g., Blaustein et al., 1995; Jones et al., 2005; Ashton et al., 2006; Cafferata Coe et al., 2021). Three forest-obligate stream-breeding amphibian families unique to the region have biphasic life histories in which adults venture from natal streams into upslope forests for foraging and dispersal: tailed frogs (Ascaphidae)—a primitive lineage with their closest living relatives occurring in New Zealand; Pacific giant salamanders (Dicamptodonidae)—adults of which are among the world's largest terrestrial salamanders; and torrent salamanders (Rhyacotritondiae)—which rely on headwaters, including small perennial and intermittent stream reaches (Sheridan and Olson, 2003; Jones et al., 2005; Olson and Weaver, 2007). At this writing, two of the four torrent salamander species (*Rhyacotriton cascadae, R. kezeri*) are under status review for listing as Threatened or Endangered under the US Endangered Species Act (USFWS, 2021), adding to concern for threats including some forestry practices.

Management alternatives for small headwater streams in forests have been a specific focus of recent studies. These streams can be abundant, comprising up to 80% of stream lengths in a large, forested watershed (Meyer and Wallace, 2001; Gomi et al., 2002), with non-perennial headwater streams draining an average of 58% of US forested lands (Kampf et al., 2021). Historically, small streams have not been protected from forest management with buffers, and their current protections vary with landownership (e.g., Olson et al., 2007; Boisjolie et al., 2019; Kampf et al., 2021). Buffers are a trade-off with wood-production priorities, with headwaters being so potentially numerous that their designated buffers could cover large areas of forested land used for wood production. Because of this trade-off, over the last two decades, concerns for endemic headwater vertebrates have largely driven questions of the effectiveness of riparian buffer widths to ensure headwater-species protections. Consequently, numerous stream-riparian buffer studies have addressed timber-harvest effects on small-stream habitat conditions and species in the Pacific Northwest, including both fish and amphibians (Table 1). These studies have had different objectives, designs, and contexts, such that it may be difficult to reach broad-based conclusions from composite results—nevertheless, each has contributed a piece of the larger picture of how resilient the aquatic-riparian community may be under different management scenarios (Table 1). Also, as longer-term monitoring has been conducted, lag effects or cumulative effects on headwater-dependent amphibian species densities have emerged of experimental streamside riparian-management treatments with upslope timber harvest (Olson et al., 2014; Olson and Burton, 2014) such that studies examining only initial effects may miss longer-term patterns. The biphasic life history of stream-breeding amphibians may account for lag effects, as stream-riparian protections may directly affect only a portion of a population (e.g., aquatic larvae).

A common denominator of many Pacific Northwest studies of forest-management effects on aquatic-riparian communities is that species-abundance metrics are often the responses analyzed (Table 1). Because maintenance of well-distributed populations or species persistence is a goal for many land managers (e.g., USDA and USDI, 1993, 1994), abundance metrics are relevant gauges for understanding the efficacy of streamside-management alternatives. Studies that show the effects of forestry treatments in this context imply differential survival resulting in population fluctuations, although different dispersal, activity, or detectability levels also could account for differing abundances observed. In this vein, some studies of nonlethal effects of riparian forest management have been undertaken. For example, Johnston and Frid (2002) used radiotelemetry to compare movements of the terrestrial adult life-stage of coastal giant salamanders (*Dicamptodon tenebrosus*) in British Columbia, Canada at sites that were forested, clearcut to the stream margin, or clearcut with riparian-buffer strips. They found that salamanders in clearcuts without riparian buffers remained closer to streams, spent more time underground, and had smaller home ranges than salamanders in sites with the other two treatments. Similarly, other studies have found increased stream-riparian occurrences with timber harvest (e.g., western red-backed salamanders [*Plethodon vehiculum*] in second-growth compared to old-growth forests: Dupuis, 1997; coastal tailed frogs [*Ascaphus truei*] in clearcuts compared to old growth: Wahbe et al., 2004).

Another nonlethal effect of forest management on stream-riparian vertebrates could be differences in body condition. This may be particularly important because body mass can relate to a suite of behavioral ecology and physiological responses, such as metabolic rate, energy intake, dispersal, and reproductive outputs (Brown et al., 2004; Adams and Church, 2008; Hillman et al., 2014). In managed forests, species energetics may be highly dynamic, varying with: 1) community interactions such as prey availability or predation rates, especially for main predators such as fish and salamanders that are central to food webs in small streams (Hawkins et al., 1983; Davic and Welsh, 2004; Kiffney and Roni, 2007); and 2) interacting effects of light availability and microclimate conditions (e.g., Anderson et al., 2007), which could alter stream productivity (Kaylor and Warren, 2017) as well as predator activity patterns such as time periods for foraging or surface activities (e.g., fish: Wilzbach and Hall, 1985; amphibians: Dupuis et al., 1995). For example, in northwest California, USA, Wilzbach et al. (2005) reported increased density and biomass of coastal cutthroat trout (*Onchorhynchus clarkii clarkii*) in streams with riparian forest-canopy removal compared to reaches with uncut riparian areas. In another study, coastal cutthroat trout biomass increased after an initial clearcut harvest in western Oregon, and then decreased to pre-harvest levels after a second harvest (Bateman et al., 2021). Also, in paired stream-reaches in old-growth and second-growth forests in western Oregon, Kaylor and Warren (2017) found that canopy openness explained 84% of the variation in fish and salamander biomass. In contrast, Corn and Bury (1989) reported greater aquatic amphibian biomass in streams in uncut forests, as compared to streams in clearcuts or with no buffers. Because body-mass patterns can vary with species and life stages, allometric relationships and body-condition indices of mass by body length have been proposed for use in fish and amphibians (Green, 2001; Stevenson and Woods, 2006; Santini et al., 2018). A scaled mass index as a measure of body condition may be relevant, as riparian and upland forest changes with forest-harvest practices could alter body allometric relationships, such as a change in body mass but not body length (Meiri and Dayan, 2003; Peig and Green, 2010). For example, MacCracken and Stebbings (2012) reported that starved amphibians in experimental feeding trials had a 17–32% lower scaled mass index than fed animals. Determining what factors may affect both abundance and food-web dynamics, including biomass or body condition of stream-riparian vertebrates is an emerging theme in contemporary forest-management studies, providing better assays of community-wide patterns (Bellmore et al., 2017; Kaylor and Warren, 2017).

The Density Management and Riparian Buffer Study of Western Oregon (DMS), conducted from 1994 to present, is among the longest-running studies examining the efficacy of alternative widths of streamside riparian buffers in protecting aquatic-dependent fauna in headwater forests. DMS was designed to address the aquatic conservation strategy objectives for US federal forest lands within the range of the northern spotted owl (*Strix occidentalis caurina*) as part of the Northwest Forest Plan (USDA and USDI, 1994), in the context of upland forest-harvest treatments of second-growth stands that aimed to accelerate the development of late-successional and old-growth forest conditions (Cissel et al., 2006; Dodson et al., 2012). In 1994, little was known about the utility of different riparian-buffer widths in the context of upland thinning, and buffers narrower than those developed for clearcut harvests (i.e., riparian-reserve widths in the Northwest Forest Plan: one to two site-potential tree-heights on each side of streams; USDA and USDI, 1994) were thought to be sufficient.

The DMS aquatic vertebrates and habitats study component (Cissel et al., 2006) included objectives to characterize headwater stream habitats and vertebrates (Olson and Weaver, 2007; old-growth forest comparison: Sheridan and Olson, 2003) and examine treatment effects of alternate buffer widths on stream habitats and vertebrates. Buffer effects appeared negligible at 1–2 y post-treatment (Olson and Rugger, 2007), and at 10 y post-treatment negative treatment effects were reported only for streambank-dwelling amphibians, with reduced densities of Dunn's salamanders (*Plethodon dunni*) in treatments with the narrowest buffer (6 m wide; Olson et al., 2014). A second-entry timber harvest was then conducted (in years 11–12 after the first thinning:

Table 1

Brief summaries of selected studies over last 35 years examining fish and stream-associated amphibian abundances in the context of managed moist coniferous forests of the Pacific Northwest of North America, with an emphasis on those examining effects of streamside riparian buffers. Locations: BC = British Columbia, Canada; CA = California, USA; OR = Oregon, USA; WA = Washington, USA; Species: ASTR = *Ascaphus truei*; DITE = *Dicamptdonon tenebrosus*; DIsp = *D. tenebrosus* and *D. copei*; ENES = *Ensatina eschscholtzii*; ONCL = *Oncorhynchus clarkii*; ONKI = *O. kisutch;* ONMY = *O. mykiss*; PLDU = *Plethodon dunni*; PLVA = P. vandykei; PLVE = *P. vehiculum*; RHsp = *Rhyacotriton* species; RHCA = *R. cascadae*; RHKE = R. kezeri; RHVA = *R. variegatus;* SAGA = *Salmo gairdneri*; SAMA = *Salvelinus malma*; TAGR = *Taricha granulosa*. * species names have changed over time, current names shown.

Study	Location	Management Context	Main Results*	References
Effects of clearcuts with and without buffers on fish	Southeast AK	18 streams sampled in old growth and clearcuts with and without stream buffers	ONKI, SAMA, SAGA, and ONCL sampled, but abundances in buffered reaches did not consistently differ from reaches in old-growth forest. In summer, in areas with underlying limestone, clearcut and buffered reaches with open canopy had more periphyton, benthos, and ONKI.	Murphy et al., 1986
Retrospective study of logging effects on amphibians	Western OR	Streams in uncut forests and in forests clearcut without buffers (14–40 y before the study)	Density and biomass of 4 species were greater in streams in uncut forests (DITE; RHsp; ASTR; PLDU)	Corn and Bury, 1989
Retrospective study	Western WA	Buffered vs unbuffered streams	More DIsp and ASTR in streams with riparian forest buffers, vs. unbuffered streams with timber harvest	Kelsey, 1995
Retrospective study of buffer strips and clearcuts vs unmanaged stands	Western OR	1st- to 3rd-order streams in managed forests with buffer strips and unmanaged forests.	Similar abundances of ENES PLDU and PLVE in riparian forests of managed and unmanaged sites; amphibian species richness lower in managed sites and richness correlated to buffer width	Vesely, 1996
Retrospective study of buffers, no buffers, and no management	Western BC	Streams without buffers and riparian-upland clearcuts, streams with 5–60-m-wide buffers with upland clearcuts, and unmanaged sites compared	Fewer larval ASTR in unbuffered streams compared to buffered streams with upland clearcuts and unmanaged sites.	Dupuis and Steventon, 1999
Retrospective study of riparian management	Olympic Peninsula, WA	Streams in managed forest stands without buffers, with buffers and in unmanaged stands compared	PLVA only found at unmanaged sites or sites with a riparian buffer, not at logged and unbuffered sites.	Bisson et al., 2002; Raphael et al., 2002
Retrospective study of amphibians in clearcut and late-successional forests	South western OR	Stream and terrestrial amphibians were sampled in clearcuts < 15-y-old (burned and planted) and uncut forest > 180 y old.	Abundance of larval ASTR and DITE in streams was markedly lower in clearcuts than mature forest stands. No differences in terrestrial amphibian sampling between treatments was reported.	Biek et al., 2002
Retrospective study of giant salamanders in 0–4-y-old forests	WA Cascade Range	Amphibian abundances and forest age examined in first-order streams	DIsp densities were unrelated to forest age, however DITE densities were negatively associated with riparian canopy cover in one year. RHCA captures were lowest in 0–24 y old forests, highest in 25–60 y old forests, and intermediate in forests ≥ 61 y.	Steele et al., 2002, 2003
Retrospective study of instream salamanders by	Northwest OR		Forest age or riparian forest composition did not affect RHKE distribution or relative abundance,	Russell et al., 2005

(*continued on next page*)

Table 1 (*continued*)

Study	Location	Management Context	Main Results*	References
forest age and habitat components.		Survey of RHKE in 119 headwater streams, with analyses of habitat and forest age and composition.	but geology, aspect, and elevation did at landscape scales, and stream gradient was in best reach-level model.	
Retrospective study of forest management with a variety of riparian buffer widths	Western OR	Streams in managed forests were sampled including 702 sample units in 16 randomly chosen basins. Analyses examined stream and riparian forest associations.	Wider streamside forest bands increased the odds of finding DITE, ASTR, RHsp; Buffers > 46 m recommended.	Stoddard and Hayes, 2005
Watershed amphibian distributions modeled, including forest seral stage	NorthernCA	Mattole watershed surveys	RHVA and ASTR occurred significantly more often in stream reaches within late-seral vegetation, compared to second growth and mixed grassland.	Welsh et al., 2005
Effects of riparian canopy opening on fish	Northwest CA	Six streams were treated with a 100-m riparian forest canopy opening, each matched with a reach having intact canopy	ONCL and ONMY density and biomass increased in reaches with the canopy opening.	Wilzbach et al., 2005
Retrospective study of stream amphibians in late-seral and second-growth forests	Northwest CA	Three matched pairs of streams in each of two blocks surveyed in 37–60-y-old forest (6 streams) and late seral forests (6 streams).	Amphibian species richness and abundance were significantly higher in late-seral forest streams. DITE, ASTR, RHVA dominated species encounters during surveys. Greater abundances of post-metamorphic ASTR, and all life stages of both DITE and RHVA were found in late-seral streams.	Ashton et al., 2006
Comparison of amphibian response in buffered, clearcut, and reference streams	Western WA	Pretreatment and immediate post-treatment effects were assessed for stream amphibians in clearcut, buffered and unmanaged reference streams.	Cleacutting to stream channels had short-term negative effects on DIsp and ASTR but not RHsp	Jackson et al., 2007
Stream buffers ameliorate timber harvest effects	Western WA	Stream amphibians were examined in 41 streams in 4 categories: clearcuts with and without buffers; 35-year-old second growth forests; and unmanaged forests.	RHCA and ASTR densities were 2–7 times lower in streams in managed forests vs. unmanaged forests; both spp were less abundant in streams without buffers or in unmanaged streams	Pollett et al., 2010
Basin-scale surveys of amphibian occupancy in managed forests	Western OR and WA	Amphibians in 1st-to 3rd-order streams in 70 randomly selected third order managed basins were sampled	In managed basins, occupancy probabilities were 0.99 for RHsp and DIsp, 0.95 for PLDU, and 0.60 for ASTR.	Kroll et al., 2010
Hinkle Creek Paired Watershed Study	Western OR	DITE densities were sampled in streams in a 3rd-order basin with clearcuts and no riparian buffers and streams in an unharvested basin.	Salamander density was associated with substrate, but there was no evidence of timber harvest effects.	Leuthold et al., 2012
Density Management and Riparian Buffer Study of Western Oregon	Western OR	Fish and amphibian density effects examined at years 1, 2, 5, 10 post-treatment of four riparian buffer management alternatives with upland forest thinning using a before-after-control-impact study design; and also 1 y after a 2nd thinning treatment.	Years 1–2 post-harvest: more TAGR on stream banks; more DITE in treatment reaches. At year 10 post-treatment using entire dataset in analyses: negative treatment effects on bank-dwelling and also a subset of Plethodontidae amphibians in narrowest two buffers, and on PLDU in narrowest 6-m buffer. Year 1 post 2nd thinning harvest: fewer RHsp in 6-m buffered streams; more PLDU and RHsp in 15-m minimum width buffer; fewer PLDU and DITE in case-study thin-through buffer. 5 y post 2nd thinning harvest: more fish and amphibians in 70-m buffer, RHsp associated with unharvested controls, body condition effects of buffers in some years.	Olson and Rugger, 2007; Olson et al., 2014; Olson and Burton, 2014; this paper.
Trask Watershed Study	Western OR	Before-after harvest experiment with model of survival, movement and capture probability of ASTR and DITE, and model of trout sensitivity to geophysical conditions and environmental change.	Increasing timber harvest intensity reduced downstream movement bias and reduced survival of DITE but not ASTR. ONCL models showed instream habitat variation mediated effects of forest harvest and climate change, with climate change having stronger effects on trout than forest harvest; also, trout biomass was most responsive to geophysical conditions of streams, suggesting geophysical habitat conditions render trout more or less sensitive to environmental change.	Chelgren and Adams, 2017; Penaluna et al., 2015a,b.
Type N Experimental Buffer Treatment Study	Western WA	Occupancy, density, and body condition responses of stream amphibians were examined in perennial streams with upland clearcuts and riparian buffers: WA Forest Practices buffer, a more extensive buffer (100%), no buffer (0%), unharvested reference.	In the two-year post-harvest period, negative effects on DIsp density were found in the forest practices buffer treatment, larval ASTR densities increased in two buffer treatments (Forest Practices, 100%) and post-metamorphic ASTR densities increased in one treatment (0%). No treatment response was detected for RHsp. Body condition treatment effects were not detected.	McIntyre et al., 2018
Alsea Watershed Study	Western OR	BACI design to examine effects of successive clearcuts on ONCL	ONCL biomass increased after first timber harvest, and decreased to pre-logging levels after second harvest.	Bateman et al., 2018, 2021

Table 2) to further reduce overstory tree density because canopy closure was occurring and was expected to slow growth of those larger trees; accelerated overstory growth to attain late-successional and old-growth forest conditions was the upland forest objective. At 1 y after this second harvest, Olson and Burton (2014) reported additional negative effects on stream vertebrates: 1) decreased occurrences of torrent salamanders in streams with the narrowest buffer width (6 m); 2) both Dunn's and torrent salamander abundances increased in reaches with moderate-width buffers (variable-width, 15-m minimum width); and 3) Dunn's and coastal giant salamander densities decreased in case-study stream reaches with buffers that had permitted thinning harvests to the streambank. Hence, as time passed and with the second-entry thinning, increasing negative effects on aquatic-dependent vertebrates emerged. However, trend assessments spanning at least one generation time are likely needed to document population abundance patterns such as potential population declines (Blaustein et al., 1994). Although it is unknown whether the first 10 y of this study matched lifespans of amphibians in our sample, stream-breeding amphibians have delayed maturity (e.g., 1- to 4-y larval periods in *Ascaphus truei*: Brown, 2005), and some individuals likely are very long lived (tailed frogs may live to 14 years: Bull and Snook, 2005; some large aquatic salamanders live to 25 years or more: Welsh, 2005). Population responses may still have been developing after the first harvest, and only a single year had passed after the second harvest, which would not allow detection of potential lag effects.

Herein, we examine DMS treatment effects on fish and amphibian densities, stream habitat components, and body conditions at the time-period of 5 y after the second-thinning harvest. We were interested in whether effects of buffer treatments on animal abundances observed at 10 y after the first thinning (Olson et al., 2014) or 1 y after the second thinning (Olson and Burton, 2014) prevailed at the next time-period sampled. Additionally, we hoped continued monitoring of habitat conditions would provide insight to mechanisms driving observed changes, which had remained elusive previously. To examine sublethal effects, we conducted exploratory analyses of associations between animal body-size metrics, habitat type, and buffer treatments. Larger-sized animals in post-treatment time periods may represent a positive response to treatments, for example from an altered food web where increased light from upland thinning increases productivity of lower trophic levels, including increased invertebrate prey availability (e.g., Wilzbach et al., 2005; Kaylor and Warren, 2017). Conversely, smaller-sized animals in treatment units may represent a negative effect, again possibly from an altered food web but with reduced prey availability or microhabitat changes that stress instream vertebrates, resulting in lower feeding rates. An initial analysis of microhabitat type (i.e., pool, riffle units) was added as a possible interacting variable, as instream vertebrates in our study have had significant relationships with microhabitat components, including pool and riffle units within reaches (Olson and Burton, 2014).

2. Materials and methods

2.1. Study sites

We conducted a Before-After-Control-Impact (BACI) study design at 58 stream reaches at eight forested study sites (Fig. 1) on lands administered by the U.S. Department of Interior Bureau of Land Management (BLM) as part of the DMS (Cissel et al., 2006). Five sites were located in the Coast Range and its foothills, and three sites were in the Cascade Range. Mean annual rainfall in the study area ranges from 1351 to 2192 mm (USDA-NRCS-NWCC, 1999), and soils are well to poorly drained ultisols and inceptisols (Soil Survey Staff, 1999). Each study site had at least 81 ha of contiguous second-growth forest. At the start of the study prior to the first thinning in 1997, forests were dominated by 30–70-year-old Douglas-fir *(Pseudotsuga menziesii)* trees with varying abundances of western hemlock (*Tsuga heterophylla*). Hardwood trees were a minor component of the overstory stands. Forest understory communities have been richer in diversity than the overstory, with more than 300 vascular plant species identified (Ares et al., 2009, 2010).

Forest-stand conditions were described in more detail previously (Cissel et al. 2006; Olson and Burton, 2014; Burton et al., 2016). Briefly, at each site, one 16- to 25-ha unthinned control upland area was preserved with 430–600 trees ha^{-1}. As part of the main riparian buffer study component, an initial thinning treatment was implemented with a moderate-density (main study, eight sites) tree retention that removed over half the overstory to ~200 trees ha^{-1}. However, thinning at the Perkins Creek site occurred 20 years prior to this study, to 250 trees ha^{-1}, hence the first entry for this study was the second thinning at this site, and the harvest similarly removed over half the overstory, leaving a density of 100–150 trees ha^{-1}. A second thinning (third for Perkins Creek) was implemented at harvest units between 2009 and 2011 (~12 years after the initial thinning), reducing overstory tree densities to around 85 trees ha^{-1}.

Three of four no-harvest riparian-buffer treatments were retained from the original study design along headwater streams at the sites (Table 2): 1) a one site-potential tree-height buffer (1-Tree, ~ 70 m on each side of streams); 2) a variable-width buffer (VAR, 15-m minimum width on each side of streams), and 3) a streamside-retention buffer (SR, ~ 6 m on each side of streams). Reach lengths ranged from 70 to 875 m. The distance from the outer edge of buffers to ridgelines was designed to be at least 60 m to permit upland forest thinning.

The original 4th buffer width was a two site-potential tree-height

Table 2
Dates of first and second forest thinning treatments, sampling dates before and after the second thinning, and replication of riparian buffer treatments for the Density Management and Riparian Buffer Study sites in western Oregon, USA. Buffers: C = Control; 1-Tree = one site-potential tree height, ~70 m; Var = Variable-width buffer (15-m minimum); SR: Streamside retention (6-m wide); TT = Thin-through two site-potential tree-height buffer (~145-m). Controls and unthinned buffers were 430–600 trees ha^{-1}; TT buffers in main study were thinned to 150 trees ha^{-1}; 2nd thinning reduced upland forest from ~ 200 to 85 trees ha^{-1}. Sites: CC: Callahan Creek; DC = Delph Creek; GP = Green Peak; OM = O.M. Hubbard; KM = Keel Mountain; PC = Perkins Creek; NS = North Soup Creek; TH = Ten High (all for moderate density thinning treatments), KMHD = Keel Mountain, High Density thinning treatment wherein TT buffers were previously Var widths (15-m minimum) and thinned to 150 trees ha^{-1}, and the 2nd thinning reduced upland forest from ~ 300 to 150 trees ha^{-1}.

Site	Thinning Dates		Sampling Dates		Riparian Buffer Treatment				
	1st Thinning	2nd Thinning	Before the 2nd thinning	~5-yrs after 2nd Thinning	C	1-Tree	Var	SR	TT
CC	1998	2010	2007	2014	2	1	2	2	2
DC	2000	2011	2010	2016	2	0	1	1	0
GP	1999–2000	2011	2010	2016	2	1	1	1	0
OM	1997	2009	2008	2014	3	2	2	0	0
KM	1997–1998	2009	2007	2014	2	1	1	1	3
PC	1999–2000	2011	2008	2016	2	0	2	2	0
NS	1997–1998	2010	2009	2015	2	1	1	1	0
TH	1999–2000	2011	2009	2016	2	1	3	2	0
KMHD	1997–1998	2009	2007	2014	2	0	3	0	4

buffer (2-Tree, ~ 145 m on each side of streams). As only two sites with 2-Tree buffers had been retained in the study by the time of second-thinning treatment, and no effect of 2-Tree buffers had emerged to this time (Olson and Burton, 2014; Olson et al., 2014), a new treatment was developed. Stream reaches within the former 2-Tree buffers were transformed to a thin-through (TT) riparian-buffer treatment that reduced riparian-zone overstory tree density from 430 to 600 trees ha^{-1} (unthinned second growth) to 150 trees ha^{-1} without a no-harvest zone along streambanks (five reaches implemented, Table 2). During harvest, thinning operations were directed to avoid ground disturbance to stream channels and to fell trees away from streams. The upland thinning density was the same as for the other three buffer treatments, 85 trees ha^{-1}.

In addition, a case study was conducted at the time of the second thinning entry at one site, Keel Mountain, due to the number of stream reaches occurring in a high-density tree-retention treatment which had been thinned to 300 trees ha^{-1} during the first thinning entry. Headwater streams were frequent at the Keel Mountain site, and numerous reaches in the high-density upland treatment had been buffered with a variable-width buffer (VAR) during the first thinning entry. During the second thinning of these upland forests, where thinning reduced overstory trees from 300 to 150 trees ha^{-1}, half the reaches in the high-density treatment with VAR riparian buffers were thinned-through (TT), reducing their overstory density from 430–600 trees ha^{-1} (unthinned second growth) to 150 trees ha^{-1} without a no-harvest zone along streambanks (Table 2). This enabled a comparison of animal densities and stream metrics with three contrasting riparian forest configurations: High density upland–TT buffer (variable-width buffer [≥15 m] thinned to 150 trees ha^{-1} within the buffer and in uplands), High density upland–VAR buffer (variable-width buffer [≥15 m] with 430–600 trees ha^{-1} within the no-entry buffer and uplands thinned to 150 trees ha^{-1}), and Controls (no harvest [~200 m or more to ridgeline] with secondary forest, 430–600 trees ha^{-1}).

Fig. 1. Locations of eight Density Management and Riparian Buffer Study sites in western Oregon.

2.2. Field data collection

One year before the second thinning (the "Before" data in our BACI design) and five years after the second thinning (third thinning for Perkins Creek; the "After" data), we conducted stream-reach habitat and animal (amphibians and fish) surveys during rainy spring conditions at the 58 study reaches. First, habitat surveys were conducted along entire reach lengths using the Hankin and Reeves approach (Hankin and Reeves, 1988) modified for small streams (Olson and Weaver, 2007). Within reaches, streams were classified into units by surface streamflow category (e.g., pool, riffle, dry channel). Unit dimensions were measured (length, width, depth) and average dimensions for reaches were calculated. Stream substrate and down-wood data were collected and characterized for study reaches. Per unit, percent substrate composition was characterized in the spring season by particle size category: bedrock cobble (>64 to 256 mm in particle size); large gravel (>8 to 64 mm); small gravel (>2 to 8 mm); sand (>62.5 µm to 2 mm); and silt (3.9 µm to 62.5 µm). Per reach, the diameter and length of down-wood pieces ≥ 10 cm in diameter were estimated visually, and each piece was categorized into one of five decay classes. During each survey, width and length of a subsample of pieces were measured, accounting for a total of 18% of the total number of pieces recorded. To correct for potential error in estimates and differences among observers, we adjusted estimates using regression linear relationships between measured and estimated values (r^2 = 0.98 and 0.97 for length and diameter, respectively). We recorded the percentage of down-wood volume present in reaches within the current wetted channel (Zone 1); outside the wetted channel and within the estimated channel at bankfull stages of streamwater (Zone 2); above the stream prism at the estimated bankfull stage and outside Zones 1 and 2 (Zone 3). We present results for total and stream wood volumes added across Zones 1–3 for early (Classes 1–2) and late (Classes 3–5) stages of decay, assuming a cylindrical geometry for the debris pieces.

Initial analyses of pre-treatment survey data collected at stream-unit scales characterized reaches by surface-water flow patterns in both spring and summer seasons into five "hydrotypes" (Olson and Weaver, 2007): 1) perennial reaches with surface flow in spring and summer; 2) summer-intermittent reaches with continuous flow in spring and discontinuous surface flow in summer (some units being characterized as dry channel, with wet channel units up- and down-slope); 3) perennial-ephemeral reaches, having continuous flow in spring, but being continuously dry channels upslope in the summer; 4) intermittent reaches with discontinuous surface flows in spring and summer; and 5) intermittent-ephemeral reaches with discontinuous flow in the spring and no flow in summer. We examined instream microhabitat and instream and stream-bank species patterns for intermittent and perennial hydrotypes 1, 2, and 4, because classes 3 and 5 were formerly represented by only one reach apiece. For context, hydrotype 4 was the most frequent reach type in our initial study sample (Olson and Weaver, 2007), and for a watershed context, such intermittent streams translated to an average subdrainage area of 12.6 ha (median = 10 ha; Olson and Burton, 2019).

In the wet spring season, after habitat surveys were completed, stream-associated vertebrate species were surveyed in streams and along streambanks in a subsample of at least 10 units per reach. Reach segments located approximately 15 m from the bottom- and top-most portions of the reach were excluded from sampling. Reach units were classified as either slow- (pools) or fast-water (riffles, cascades), and the selected units for animal sampling were in proportion to their frequency in the sampled reach (Hankin and Reeves, 1988). The first unit was selected randomly from the first five units included at the downstream end of the reach. Moving upstream, subsequent units were selected such that every n^{th} unit of a type (slow, fast) was sampled, where n = the number of units by type in the remaining upstream reach to be sampled, divided by the remaining total number of units.

Stream and streambank sampling were conducted separately per selected unit. For stream animal sampling, units were either sampled by hand or by electrofishing. Electrofishing was restricted to fish-bearing streams because it was not effective to catch fish by hand. However, electrofishing may underestimate amphibian occurrences, as amphibians may hide in stream substrate crevices, and hence search method was included as a factor in the analyses. For hand sampling, amphibians were captured using dip nets placed downstream from cover objects and gathered into nets as cover was examined or moved. Once captures were identified to species and measured, they were returned to the unit. Unit length and width were determined and animal density per square meter was calculated per reach for analyses. Streambank surveys were conducted for 5 min on each side of the sampled unit within 2 m of the water's edge. Animals were placed in plastic bags upon capture, identified, measured, and released to the capture location. Similar to stream surveys, search areas were estimated, and species densities were calculated on a per-square-meter basis per reach. Animal lengths and weights were measured: total length and snout-vent length were measured to the nearest 0.1 mm with rulers or rulers mounted in half-PVC pipes, and weight was recorded to nearest 0.01 g with an electronic balance (A&D Engineering HL-100, 0.01 g scale; San Jose, CA, USA). Larval tailed frogs were not measured. For analyses, the two species of *Rhyacotriton* in our sample, *R. variegatus and R. cascadae*, were combined (*Rhyacotriton* spp.: RHsp) to bolster sample sizes for analyses. Sculpins also were combined for analyses (Cottidae spp.: COsp) as species were difficult to distinguish during field sampling, as were age 0+ years salmonids. All 1+ years salmonids were *O. clarkii clarkii* (ONCL), suggesting that young-of-the-year 0+ years salmonids likely were ONCL as well

2.3. Statistical analyses

2.3.1. Instream habitat components, animal densities, and treatment effects

We conducted non-metric multidimensional scaling ordination (NMS: Kruskal, 1964; Mather, 1976) on all data (main and case-study data combined; data: animal densities, habitat components, treatments) to assess effects of upland thinning and riparian-buffer treatments on key habitat features and amphibian and fish community composition at stream reaches five years after the second thinning. We included the habitat characteristics: reach-scale average stream width and depth, pool depth, riffle depth, patterns of surface streamflow (i.e., % riffle and % pool by reach length and area per reach, pool:riffle ratio by reach length, % dry length), substrate (i.e., percentage fine, small gravel, large gravel, cobble, boulder, and bedrock), and total volume of down wood and volumes in early stages (1–2) and late stages (3–5) of decay.

For the NMS analyses, we used the Sorensen distance measure with the ''slow-and-thorough'' autopilot settings with 30 runs of 50 iterations. Plots were ordinated in amphibian and fish species space for all sites. Associations between individual species and species groups with reach-scale habitat characteristics were assessed by examining the correlations of species densities with ordination axes.

For stream reaches in the moderate-density thinning main study, to further examine temporal changes in animal abundances and habitat associations between one year before the second thinning and five years after the second thinning, we conducted a principal coordinate analysis (Gower, 1966) using the Sørenson distance. In comparison to the NMS analysis, principal coordinate analysis is more sensitive at detecting extent and direction of changes in animal abundances between the two time periods.

We also conducted multi-response permutation (MRPP) analyses using all data (main study and case study, combined) to test for differences in species composition among reaches with different buffer treatments and hydrotype conditions. This procedure is an alternative to analysis of variance for non-parametric data and tested for differences in species composition based on the average within-group Sorensen distance. In assessing results of this analysis, a more negative T would indicate greater differentiation among reaches for a given effect and an A-stat close to 0 would signal higher heterogeneity among reaches.

Indicator species analysis (ISA; Dufrêne and Legendre, 1997) was conducted to calculate indicator values for amphibian and fish species. Indicator values relate to the fidelity of a species to a given treatment and are calculated from species' relative frequency and abundance within a given treatment. All the previous analyses were performed using PC-ORD 4.0 (McCune and Mefford, 1999).

2.3.2. Body-size relationships with buffer treatment and microhabitat type

Sufficient data across treatments and years for body-size analyses were available for two fish species and six amphibian species (Supplemental Table S1). Most equations included ln transformations of weight (i.e., mass), total length and snout-to-vent length except for BAWR relationships, for which polynomial cubic functions fit the data better.

We calculated the scaled mass index (SMI) following methods outlined by Peig and Green (2009, 2010). The procedure included: 1) assessing the relationship between mass and length and screening the data for outliers by examination of scatter plots; 2) fitting a line to the mass and length data on a natural log–log scale, and using the slope estimate of that line as the power function in the SMI calculation; 3) estimating the mean length for each group, the value of which is used as the constant in the SMI calculation; then 4) calculating SMI for each individual.

We estimated the scaling exponent for the SMI equation as the slope of an ordinary least-squares regression of ln mass and ln length, divided by the Pearson correlation of ln mass and ln length (Peig and Green, 2009). We used t-tests to compare the mean mass and SMI estimates between control and treatment groups for before and after the second thinning time-periods, where appropriate. SMI estimates were based on either total length (SMITL) or snout-vent length (SMISVL). We used Pearson correlations to assess relationships between each body component measure (scaled and raw absolute mass, and percent total mass) and the corresponding SMI for each species with sufficient data for analyses. All analyses were performed with SYSTAT 12 (Systat Software, Inc., Chicago, IL).

Riparian buffer, habitat, and buffer × habitat treatment effects on body metrics were analyzed using a mixed-model analysis of variance, conducted in SAS 9.1 (SAS Institute, Inc, 2013) with buffer as fixed effect and habitat as random effect (Littell et al., 1996). In these analyses, microhabitat of instream animal locations within study reaches was used, distinguished by microhabitat units having fast water flow (riffles) or slow water flow (pools). Animal interactions may result in assortment of instream individuals by size in pools or riffles within reaches, and frequency of those units could interact with buffer patterns, hence these factors were teased apart here. Because we had sampled the study sites in multiple years after the first thinning and before the 2nd thinning (Supplemental Material Table S1), we examined data from each post-treatment year separately to see if trends developed over time or persisted with time. We determined the effect of buffer treatment and habitat on total length (TL), weight (mass), and SMITL for five species that had sufficient sample sizes for analyses (ONCL, COsp, transformed ASTR juveniles and adults [total length effects not assessed], DITE, and PLDU) and on snout-vent length (SVL) and SMISVL for ASTR, DITE, and PLDU. Habitat and buffer × habitat effects were not analyzed for bank-dwelling species (BAWR, ENES, and PLDU).

3. Results

3.1. Instream habitat components, animal densities, and treatment effects

The two-dimensional NMS ordination of 58 reaches in vertebrate-species space explained 81% of the variability in the distance matrix (73% for axis 1, 8% for axis 2; Fig. 2). The most prominent reach-level differences in habitat and vertebrate species were among hydrotype classes (1, 2, 4: perennial, intermittent, summer intermittent, respectively), rather than among thinning (moderate or high density) or buffer treatments (Fig. 2). Axis 1 contrasted habitat composition of the two main hydrotypes, perennial stream reaches with greater area, average width, depth, pool length, down wood, proportion of gravel, cobble, and boulder substrates against intermittent stream reaches which were associated with smaller stream unit sizes, less down wood, and a greater proportion of fine substrates (Table 3).

More specifically, hydrotype 4 stream reaches in our sample tended to be smaller (mean width = 0.69 m) in comparison to hydrotype 2 (1.44 m) and hydrotype 1 (1.68 m). All three hydrotypes were represented in our different buffer treatments, except there were no hydrotype 4 stream reaches in our thin-through buffers for the high-density thinning case study; these were formerly variable-width buffers in our first-thinning treatment. Additionally, there was variation in stream size by buffer type. In descending order by average stream width, 1-tree buffers tended to be a similar width (mean width = 1.47 m) to thin-through buffers which were former variable-width buffers in our high-density thinning case study (1.45 m), and slightly wider than variable-width buffers (1.31 m), control stream reaches (1.23 m), thin-through buffers which were former 2-Tree buffers in our moderate-density thinning main study (1.22 m), and streamside-retention buffers (1.05 m).

In NMS ordination analyses, perennial stream reaches corresponded to larger abundances of ONCL, COsp, ASTR, DITE, and all stream-breeding amphibians (Table 4). Axis 2 was positively correlated to pool:riffle ratio, bedrock substrate, and abundance of ENSE, PLDU, and terrestrial-breeding amphibians (Tables 3, 4).

The principal coordinate ordination revealed two patterns of species abundances with time, from one year before the second thinning to five years post-thinning. First, fish and most stream-breeding amphibians showed relatively small changes in ordination space between time periods (length of arrows and axis position change in Fig. 3), and most clustered together toward the right end of Axis 1 (Fig. 3), which was positively associated with habitat components characterizing the larger perennial streams in our headwater sample. Of note, COsp were detected at only 2 of 8 study sites, so the inference of our findings relative to sculpins is restricted to one site in the Cascade Range with limited captures (Delph Creek: 48 and 33 individuals analyzed in before and after thinning years) and one site in the Coast Range with many captures (Callahan Creek: 293 and 510 individuals). RHsp also showed a small change in ordination space over time but was located toward the left end of Axis 1 in association with a negative axis value and locations in intermittent streams. This part of the axis was positively associated with smaller stream-habitat units with finer substrates (Table 5), consistent with smaller headwater streams. Only 1% of RHsp individuals were found on streambanks, so the analyzed population of RHsp largely represented aquatic forms. In addition, we only detected RHsp at 4 of 8 study sites in the before and after thinning years analyzed here, with only incidental captures ($\leq$6 individuals per site per year) at two sites within the range of *R. cascadae* (Delph Creek, Keel Mountain); hence our habitat associations are more representative of *R. variegatus* at two sites in the Oregon Coast Range (Green Peak, Ten High) where observations were higher ($\sim$30–60 individuals per site per year). Second, terrestrial-breeding amphibians (BAWR, ENES, PLDU, and *Plethodon vehiculum* [PLVE, western red-backed salamander]) and the pond-breeding rough-skinned newt (Fig. 3: *Taricha granulosa,* TAGR*)*, showed much more change in ordination space between time periods (longer arrows and greater axis position changes in Fig. 3), with a stronger rightward trend along Axis 1 and a slight downward trend along Axis 2. Numerous habitat metrics were correlated with Axis 1 (Table 5; note similarity to Table 3), suggesting stronger associations of these salamanders five years after the second thinning with larger, more-perennial stream-habitat units having larger substrates, more down-wood volume, and down wood in later stages of decay.

Results from the MRPP analysis confirmed the greater effect of stream hydrotype on animal species and habitat characteristics, compared to thinning intensity or buffer type (T: −9.1 A: 0.09 for hydrotype, T: −2.6, A: 0.02 for thinning intensity, T: −0.1, A: −0.002 for buffer configuration). These results corroborated patterns from the NMS Ordination (Axis 1, Fig. 1; Table 3).

In the main study (moderate density thinning), abundance of all fish, COsp, all amphibian species, stream-breeding amphibians, DITE, and RHsp were significantly related to riparian-buffer treatments (MRPP covariance analyses: Table 6). This reflected greater densities of these species and groups in the 1-Tree buffer treatment compared with lower

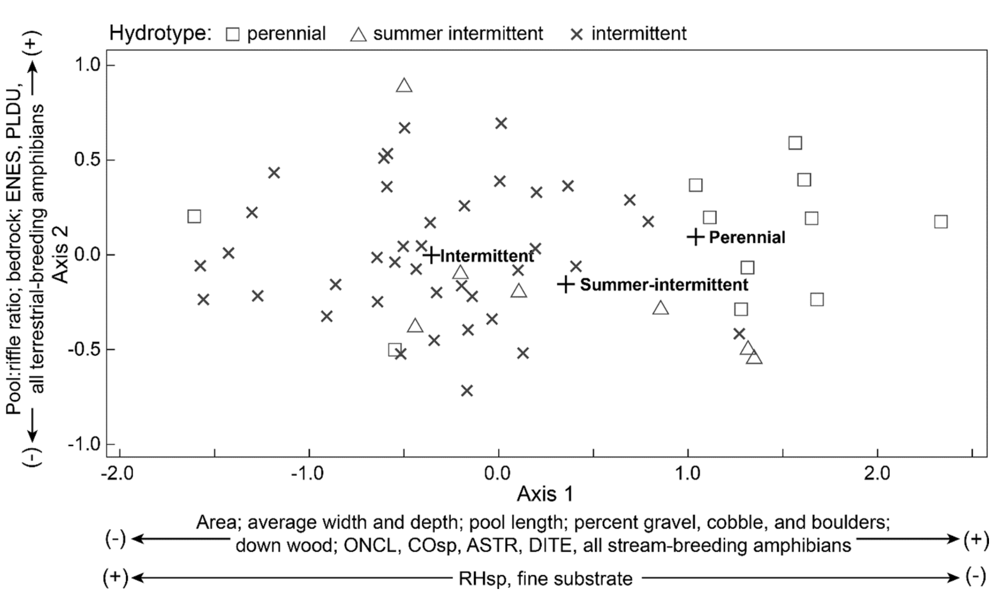

Fig. 2. Results of non-metric multi-dimensional scaling (NMS) ordination analysis of reach-scale habitat and animal density data 5 years after the second thinning harvest from 58 stream reaches at 8 sites in western Oregon as part of the Density Management and Riparian Buffer Study (81% of variatiability in distance matrix explained: Axis 1, 73%; Axis 2, 8%). Symbols represent three stream types by surface streamflow (hydrotype: perennial = constant surface flows; summer intermittent = perennial in spring wet season and spatially discontinuous in summer dry season; intermittent = spatially discontinuous in spring and summer). Axis habitat and species correlations are shown. Amphibian and fish species acronyms: ONCL = *Oncorhyncus clarkii clarkii*; COsp = Cottidae spp.; ASTR = *Ascaphus truei*; DITE = *Dicamptodon tenebrosus*; ENES = *Ensatina eschscholtzii*; PLSU = *Plethodon dunni.*

Table 3
Correlation of microhabitat characteristics with non-metric multi-dimensional scaling ordination (NMS) axes 1 and 2 (Fig. 2) five years after a second forest thinning harvest with alternative riparian buffer widths. *, **, *** symbols indicate significant correlations at P ≤ 0.05, 0.01, and 0.001, respectively.

Reach characteristics	Correlation with ordination axes	
	Axis 1	Axis 2
Habitat unit dimensions		
Length	0.287**	−0.008
Area	0.590***	0.015
Average width	0.714***	−0.135
Average depth	0.485***	0.163
Riffle average depth	0.315**	0.056
Proportion of habitat units		
Pool length (%)	0.377***	0.198*
Pool:Riffle ratio	0.061	0.345**
Substrate cover (%)		
Fine	−0.653***	−0.132
Small gravel	0.415***	−0.004
Large gravel	0.630***	0.156
Cobble	0.417***	−0.128
Boulders	0.334***	0.163
Bedrock	0.223**	0.313**
Stream wood		
Early stages of decay	0.282**	−0.146
Late stages of decay	0.308**	0.191*
Total volume	0.318**	0.180*

Table 4
Correlation of animal groups and individual species with non-metric multidimensional scaling ordination (NMS) axes 1 and 2 (Fig. 2) five years after a second thinning. *, **, *** symbols indicate significant correlations at P ≤ 0.05, 0.01, and 0.001, respectively. ^{2} symbols indicate significant correlations at P ≤ 0.010.

Species/Group	Correlation with ordination axes	
	Axis 1	Axis 2
All amphibian and fish species	0.840***	0.216
All stream-breeding amphibians	0.829***	0.126
Fish species		
All species	0.575***	−0.253*
Oncorhyncus clarkii	0.567***	−0.273*
Cottidae spp.	0.549***	−0.241
Stream-breeding amphibians		
All species	0.830***	0.123
Ascaphus truei	0.605***	0.008
Dicamptodon tenebrosus	0.611***	0.246
Rhyacotriton spp.	−0.222*	0.022
Terrestrial-breeding amphibians		
All species	0.264*	0.724***
Ensatina eschsholtzii	−0.052	0.300*
Plethodon dunni	0.279*	0.701***
Pond-breeding amphibians		
Taricha granulosa	−0.045	−0.235^2
Rana aurora	0.274*	0.231^2

densities in the VAR, SS, and TT treatments. As noted above, the COsp and RHsp findings largely reflect occurrences at two sites. DITE were found at 7 of 8 sites overall, but at only three sites in both before and after thinning samples, and one of those sites had <9 individuals captured; hence inference for buffer treatment effects stemmed from two Cascade Range sites (Delph Creek, Keel Mountain).

Species detections by sampling method also were differentiated by MRPP analyses. Abundances of total fish species, ONCL, COsp, all amphibian species, stream-breeding amphibians, ASTR, and DITE five years after the second thinning were significantly affected by sampling method (Table 6). This reflected the larger numbers of individuals of ONCL, COsp, and ASTR caught by the electrofishing method at three sites where most sampling units were electrofished due to larger stream units with fish presence (e.g., at 5 yrs post thinning, 99% of units were electrofished at Callahan Creek, 90% at Delph Creek, and 66% at Ten High), compared with the hand-capture, rubble-rouse procedure that dominated sampling at 5 sites (86% of units at Perkins Creek; 100% of units at OM Hubbard, Green Peak, Keel Mountain, and Soup Creek). Our results of species-habitat and -buffer associations likely reflected a signature of method and site, as well as stream size and hydrotype as reaches with fish were larger perennial streams. Because fish occurrences prompted sampling by electrofishing, fish associations with habitat components and buffer types were not confounded by sampling method. Over 98% of RHsp and 91% of DITE were captured by hand sampling, so different sampling methods likely did not affect RHsp and DITE results, but as noted above, COsp and RHsp were largely found at two sites (COsp: Delph Cr., Callahan Cr.; RHsp: Green Peak, Ten High), so those species results are reflective of site-specific effects.

In the high-density thinning case study, there was no significant relationship between buffer treatment and either habitat conditions or vertebrate abundances (MRDP analysis; data not shown). There was a significant effect of sampling method on RHsp abundance (P ≤ 0.001); i. e., there were fewer captures of RHsp with the electrofishing method than with the hand-capture rubble-rouse procedure.

Indicator species analyses showed that the fish ONCL and COsp, the stream-breeding amphibians ASTR and DITE, and the pond-breeding northern red-legged frog (*Rana aurora*, RAAU) were significantly positively associated with perennial streams, whereas PLDU was linked to summer-intermittent streams (Table 7). ASTR showed the greatest affinity to perennial streams and RAAU the lowest. Also, abundances of these three amphibian species had significant associations with buffer treatments (Table 7): RHsp densities were positively associated with control streams; RAAU were positively associated with streamside-retention buffers; and BAWR were positively associated with thin-through buffers. Three amphibians were positively associated with the high-density thinned treatments (Table 7: versus moderate-density thinned treatments or controls): PLDU, BAWR, and RAAU. The BAWR species range is restricted to the Oregon Cascade Range, where the HD case study was conducted and most of the thin-through buffers occurred, likely accounting for these associations for that species. All RAAU detections were at the Keel Mountain study site, and 46% of them were in the high-density thinning case-study treatments—hence a signature of a site-specific pattern may have emerged for that species as well. Similarly, most PLDU (55%) were caught at the Keel Mountain study site, and 92% of those were in the high-density treatments. These site-specific detections are likely contributing to the PLDU, BAWR, and RAAU treatment patterns.

3.2. Body size relationships with buffer treatment and microhabitat type

Species length-weight allometric relationships are reported in Supplemental Material Table S2. Species body-size metrics were associated with riparian-buffer treatments and/or habitat types (pool, riffle) in some years for five species (ONCL, COsp, DITE, ASTR group 1, and PLDU). There were no buffer or habitat effects with body size for RHsp, BAWR, and ENES. Overall, there were 8 of 19 (42%) body size × buffer × year effects across all species analyzed, and 7 of 19 (37%) species body size × habitat-type × year effects (Supplemental Material Table S3). For example, for ONCL, a buffer effect was detected in 1 of 5 years tested, with greater cutthroat trout total length and weight in the 1-Tree buffer width, compared to the 2-Tree and Variable-width buffer in 2003. Other species had significant buffer effects with body-size metrics in one-third (COsp, ASTR) or one-half (DITE, PLDU) of years examined, but consistent trends were not apparent. All body-size × habitat relationships supported larger-bodied animals in pools compared to riffles, and these effects were observed in three of five years for ONCL, one of three years for COsp, and three of four years for DITE (Supplemental Information Table S3).

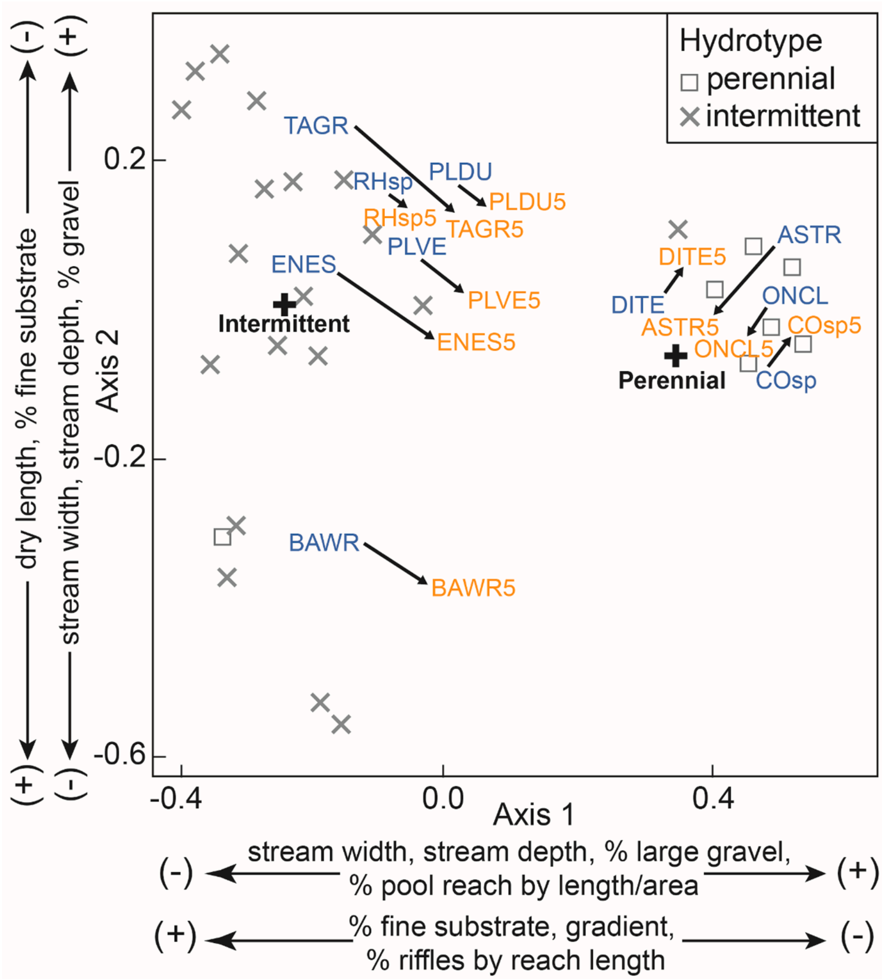

Fig. 3. Results of principal components analysis showing changes in species space between time-periods one-year before (blue) and five-years after (orange, also indicated with "5″ per species) the second-thinning harvest at 58 stream reaches with alternative stream buffers as part of the Density Management and Riparian Buffer study of western Oregon. Headwater streamflow hydrotype is indicated: perennial = constant surface flow; intermittent = spatially discontinuous surface flow. Amphibian and fish species acronyms: TAGR = *Taricha granulosa*; PLDU = *Plethodon dunni*; PLVE = *P. vehiculum*; ENES = *Ensatina eschscholtzii*; BAWR = *Batrachoseps wrighti*; RHsp = *Rhyactotriton* spp.; DITE = *Dicamptodon tenebrosus*; ASTR = *Ascaphus truei*: ONCL = *Oncorhynchus clarkii clarkii*; COsp = Cottidae spp. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 5
Correlation of habitat metrics with principal coordinate ordination analysis axes 1 and 2 at the time period of five years after a second thinning. *, **, *** symbols indicate significant correlations at P ≤ 0.05, 0.01, and 0.001, respectively.

Reach characteristics	Correlation with ordination axes	
	Axis 1	Axis 2
Dimensions of habitat units		
Length	0.388*	0.095
Area	0.809***	0.029
Average width	0.898***	−0.043
Average depth	0.716***	−0.077
Riffle average depth	0.496**	−0.041
Proportion of habitat units		
Pool length (%)	0.545**	0.064
Pool area (m^2)	0.681***	−0.069
Substrate cover (%)		
Fine	−0.800***	−0.051
Small gravel	0.569**	0.029
Large gravel	0.850***	−0.158
Cobble	0.647***	−0.158
Boulders	0.462*	−0.153
Stream wood		
Late stages of decay	0.427*	0.061
Total volume	0.436*	0.053

4. Discussion

We examined the effects on headwater stream habitats and vertebrates of alternative streamside riparian-buffer widths in second-growth forest stands with upland-forest thinning treatments that aimed to accelerate development of late-successional and old-growth forest conditions. Herein, we report results at the time-period of five years after a second thinning harvest, with findings both contrasting and consistent with earlier time-steps in effects monitoring. In contrast to earlier reports (Olson et al., 2014; Olson and Burton, 2014), in our main study with a moderate-density upland thinning treatment and four experimental riparian buffers plus an unmanaged control, we found significantly greater densities of sculpins, coastal giant salamanders, and torrent salamanders in stream reaches with 1-Tree buffers (~70 m wide on both sides of the stream) compared to narrower 6-m and 15-m minimum-width buffers, and a thin-through buffer lacking a no-entry zone along streams. In our case study with a high-density upland-thinning treatment, we found no associations between buffer treatments and animal densities, a finding similar to the earlier time-step at one year after the second thinning (Olson and Burton, 2014). A new finding was that torrent salamanders were positively associated with streams in our unthinned control units (Indicator Species Analysis, ISA). Two other species showed buffer-treatment associations in ISA results— northern

Table 6
Probability levels from the multi-response permutation (MRPP) covariance analysis for the significance of sampling method, habitat and buffer effects on amphibian species and groups in the moderate-density upland treatment five years after a second thinning. Bold indicates P < 0.05. ONCO = *Oncorhynchus clarkii clarkii*; COsp = Cottidae spp.; TR0 = Unknown trout 0 + yrs; AllAm = All amphibian species; StrAm = Stream-breeding amphibians; TerAm = Terrestrial-breeding amphibians; PonAm = Pond-breeding amphibians; ASTR: *Ascaphus truei;* DITE = *Dicamptodon tenebrosus* (instream); RHsp = *Rhyacotriton* spp.; PLVE = *Plethodon vehiculum*; PLDU = *P. dunni;* TAGR = *Taricha granulosa*.

	All fish	ONCO	COsp	TR0	AllAm	StrAm	TerAm	PonAm	ASTR	DITE	RHsp	PLVE	PLDU	TAGR
Sampling method	**<0.001**	**<0.001**	**<0.001**	0.08	**<0.001**	**<0.001**	0.54	0.81	**<0.001**	**0.02**	0.65	0.27	0.32	0.81
Habitat (H)														
Buffer (B)	0.89	0.93	0.85	0.78	0.14	0.13	0.33	0.39	0.50	0.13	0.66	0.57	0.41	0.46
H × B	**0.02**	0.70	**<0.02**	0.08	**0.004**	**0.01**	0.47	0.46	0.13	**0.001**	**<0.04**	0.44	0.65	0.39
	0.84	0.91	0.90	0.99	0.87	0.87	0.56	0.38	0.69	0.93	0.96	0.31	0.79	0.38

Table 7
Indicator species values (IV) associated with hydrotype conditions and thinning and buffer treatments 5 years after a second thinning. IV combines the relative abundance and frequency of each species in the hydrotypes and treatments. The higher the IV, the greater the association of the species to a given treatment; P values indicate significant relationships.

Species	Hydrotype/Treatment	IV	P
	Hydrotype		
O. clarkii clarkii	Perennial	52.4	≤ 0.001
Cottidae spp.	Perennial	45.5	0.001
A. truei	Perennial	71.2	0.01
P. dunni	Intermittent	55.1	0.01
D. tenebrosus	Perennial	25.5	0.02
R. aurora	Perennial	18.2	0.04
	Upland treatment		
P. dunni	High density	48.6	0.04
B. wrighti	High density	56.7	0.002
R. aurora	High density	38.6	0.01
	Buffer treatment		
B. wrighti	Thin-through	27.9	0.04
R. aurora	Streamside	44.7	0.001
Rhyacotriton spp.	Control	49.3	≤ 0.001

red-legged frogs were associated with 6-m buffers, and Oregon slender salamanders were associated with thin-through buffers. These two species were primarily found at a single site: a single-site effect may foreshadow patterns that could be observed elsewhere in areas where these animals occur.

Overall, narrower buffers in our study treatments have been previously associated with reduced densities of some species (Olson et al., 2014; Olson and Burton, 2014), and current findings show potentially cumulative effects of two thinning harvests developing between time-periods one- and five-years post-harvest. Specifically, reduced densities of giant and torrent salamanders and sculpins in 6-m and 15-m minimum-width buffers at 5 y after the second thinning suggests that these narrower buffers may be associated with risks to these taxa. Considering the complex life history of stream-breeding giant and torrent salamanders, having both instream and upland-forest life stages, a time-lag in effects is not surprising. Instream larvae and a subset of metamorphosed juveniles and adults are likely sampled by our stream-survey methods, and an unaccounted-for subpopulation of transformed juveniles and adults occurs in upland forests, some of which may occur within the harvested portion of the upland outside the riparian buffer. The narrower two buffers (6-m and 15-m) correspond to upland thinning occurring closer to streams, with corresponding altered ground conditions from harvest activities as well as warmer, dryer riparian forest microclimates (Anderson et al., 2007). These factors can have potential adverse effects on upslope life forms of instream-breeding amphibians.

Although the mechanism behind reduced sculpin, giant salamander, and torrent salamander densities in streams with the narrower buffers is not known, several interacting factors could be at play. First, streamside retention buffers were on-average narrower streams with smaller-sized substrates, and sculpins, giant salamanders and torrent salamanders are benthic, relying on substrates for foraging and substrate interstices for refuge (e.g., from predators or episodic higher water currents with storm events); so such habitats could be limiting in the narrower streams with streamside retention buffers. However, the smaller substrates were documented pre-treatment, and we have no support for a treatment effect of increased sedimentation with narrow buffers. Nevertheless, this habitat condition could interact with other factors. In addition to assessing riparian forest microclimates as mentioned above, Anderson et al. (2007) reported slightly higher instream temperatures with narrower buffers and upslope thinning. Furthermore, Olson and Burton (2019) reported stream-flow reduction in warm-dry years in spatially intermittent streams, which are narrower stream reaches further up headwater drainages. And, on average, our narrowest buffer type was implemented along smaller streams. Warm-dry years across our long-term study could also magnify warming edge effects of narrow stream buffers. Assembling these factors, smaller drying and warmer streams with fewer substrate interstices for refugia could result in adverse effects for these species. More specifically, the lower densities of giant and torrent salamanders and sculpins in streams with narrower buffers at year 5 after the second thinning harvest may be a sign of lethal, sublethal, or behavioral responses to our experimental harvest treatments along smaller streams subject to warming and drying. For example: there could be differential survival and reproduction among streams with different buffer widths; animals may have moved to different stream reaches or in/out of the study site (e.g., Johnston and Frid, 2002); or they may be more detectable during survey efforts in some streams (e.g., possibly being more active on the ground surface under some local conditions, such as those with cool wet conditions).

Some elements of our study design warrant emphasis. Our study has: 1) optimized between-year consistency in survey methods since pre-treatment surveys began in 1994 using the same field technician collecting most data to reduce variation in observer bias; 2) maximized detection of amphibians when they are surface-active by conducting surveys during wet-spring seasons; and 3) maximized stream-reach replication where we have sampled as many stream reaches per year as field crews can manage, with the consequence of logistical and budgetary constraints precluding multiple surveys of streams within years. Hence, we have not incorporated repeated measures to enable calculation of occupancy or detection probabilities. Yet at one site, we previously reported occupancy for our hand-sampling method to be 0.45 to 0.85 for Dunn's salamanders on streambanks, 0.83 for instream coastal giant salamanders, and 0.90 for instream southern torrent salamanders, and detection probabilities were 0.3 to 0.45 for Dunn's salamanders, 0.35 to 0.53 for giant salamanders and 0.65 for torrent salamanders (Olson et al., 2014). Hence, our hand-sampling results should be couched relative to likely imperfect detection, yet greater detection probability of torrent salamanders is notable given their higher densities in stream reaches with 1-Tree buffers in our current analyses. As previously mentioned, we also suspect imperfect detection of amphibians by electrofishing, and those results are consequently considered to be conservative estimates of amphibian densities in those reaches. In particular, the DITE results of greater densities in 1-Tree buffered reaches could have been a conservative result due to low detections by electrofishing in reaches with fishes.

In addition to examining buffer effects on animal abundances, we conducted exploratory analyses of body-size metrics as a non-lethal response to our buffer alternatives. Although we did not find a consistent signal of buffer effects on body size or scaled mass indices within or among species or years (Supplemental Information), buffer × size effects were significant in 42% (8 of 19) of all species × year combinations analyzed (Supplemental Information Table S3). Inconsistent patterns may signal biological relevance. Interspecific interactions (i.e., predation, competition) might affect size assortment of species by reaches, resulting in these patterns. For example, larger cutthroat trout and both larger-bodied and higher densities of coastal giant salamanders in 1-Tree-buffered reaches may have had effects on other organisms to avoid aggressive interactions with trout and giant salamanders resulting from predation attempts or competition for space or food resources. Direct and indirect community-level interactions might also be affected by the larger-bodied trout, giant salamanders, and sculpins occurring more often in pool microhabitat units within stream reaches, a pattern seen in 7 of 12 (58%) years analyzed for those three species. Untangling complex relationships among buffer treatments, microhabitats, species by body size, and species interactions is beyond the scope of the current study. Rundio and Olson (2001, 2003) previously reported interspecific interactions between members of this stream community, suggesting this effect may result in microhabitat segregation within or among reaches. Roon (2021) recently accounted for significant predation among these animals in a northern California study of small streams with riparian management treatments. Owing to our observations of buffer × body size patterns and microhabitat × body size patterns occurring in over one-third of analyses, such community interactions and habitat associations may merit follow-up assessments. Food-web and energetics analyses might contribute to understanding these potentially complex patterns (Bellmore et al., 2017; Kaylor and Warren, 2017).

Habitat and microhabitat conditions in headwater streams have many dimensions. In addition to the stream-buffer associations of some species and the species' body-size associations with pool habitat units discussed above, a variety of habitat associations with animal densities were evident for all species in our sample (stream-size metrics, pool length, substrate composition, stream-wood metrics; Figs. 2 and 3; Tables 3, 4, and 5). In particular, stream hydrotype along a continuum of surface flow conditions from perennial to intermittent reaches continued to be a key factor assorting instream vertebrate communities in our study (pre-treatment: Olson and Weaver, 2007; post-treatment: Olson et al., 2014; Olson and Burton, 2014; results herein), with torrent salamanders having a clear association with the intermittent headwater streams, and perennial streams being occupied by cutthroat trout, sculpins, giant salamanders, and tailed frogs. These patterns are consistent with communities described from western Oregon old-growth forests (Sheridan and Olson, 2003). We also found that Dunn's salamanders were significantly positively associated with summer-intermittent streams, which were streams with continuous flow in the wet spring and discontinuous flow in the summer (Indicator Species Analysis). In our current results, hydrotype had a greater effect on animal densities and habitat characteristics than buffer width or thinning intensity (moderate or high density). As the objectives of the current study were focused on assessing effects of buffer type with upland thinning, more focused attention is warranted to understand ecological complexities of hydrotype associations, especially as narrower buffers can be applied to smaller streams with intermittent flow and be prone to warming and drying (Anderson et al., 2007; Olson and Burton, 2019).

New findings show some terrestrial- and pond-breeding amphibians in the intermittent stream assemblage with altered habitat associations between before the second thinning and 5 y after the second thinning—moving in ordination space toward more-perennial stream reaches (Fig. 3). These species included Dunn's salamanders, western red-backed salamanders, ensatina, Oregon slender salamanders, and rough-skinned newts. A small-scale movement of torrent salamanders from intermittent toward perennial stream ordination space was also evident. These small-scale changes in habitat associations could reflect reduced surface streamflow of the uppermost headwater streams in warm, dry years (Olson and Burton, 2019). Moisture needs of terrestrial-breeding amphibian species, not just the stream-breeders, suggest that they track moisture gradients. Increased amphibian occurrence and movements in riparian forests near streams that have cool, moist "stream effects" (Anderson et al., 2007; Rykken et al., 2007) has been supported previously at our study sites (e.g., Kluber et al., 2008; Olson and Kluber, 2014). However, it should be noted that our sampling for the current study was conducted during cool-and-wet spring conditions, so that this potential explanation is likely not capturing animal responses to acute conditions at the time of sampling, but potentially longer-term conditions inclusive of interannual variability in warm-dry summers. Also, Olson and Burton (2019) found some climate metrics and stream drainage area were associated with reduced surface flow in summer, but they reported that buffer treatments were not a significant factor in stream drying. Nevertheless, additional study is warranted to see if stream-, terrestrial-, and pond-breeding amphibians have differential dispersal patterns in response to interannual microclimate patterns related to management effects or climate change, or alternatively, have differential survival or surface activities resulting from these effects.

Complex interactions between hydrotype, stream size, buffer treatment, sampling method, species occurrence, and study site may underly some of our results – with important lessons learned regarding study designs of large-scale forest-management experiments. First, during our study design and buffer assignment to stream reaches in 1994, sites were chosen due to homogeneity of upland forest conditions, with the stream study component being of secondary importance. We had no knowledge of stream heterogeneity during study design. Hence buffer assignment was blind to ecological variation of small headwater stream habitats and their vertebrates, which was an initial study objective to characterize from pretreatment data (Olson and Weaver, 2007). The depth of knowledge of stream size, hydrotype and related physical habitat components, and species associations revealed in our body of work (this paper, Olson et al., 2014; Olson and Burton, 2014) could inform future site selection for examining buffer effects on more targeted species and assemblages. In particular, we now know much more about stream heterogeneity (Penaluna et al., 2017), relative to species and habitat conditions. For example, COsp occurred at only 2 of 8 sites and RHsp occurred at 4 of 8 sites in the samples analyzed for this paper, supporting more limited site-scale inference of our findings for those two taxa. As there were buffer treatment effects for both those taxa, our findings herein may be important to inform future studies of these targeted species. Second, stream geometry drove upland forest-treatment designations (Cissel et al, 2006) and spatial logistics affected stream-buffer assignments. Upland blocks with more streams were designated as control or moderate-density thinning treatments, the main thinning context for the riparian buffer study component. As feasible, stream sizes were matched between these blocks and a coin flip was used to add a random element to block assignments if only two of four upland blocks (Cissel et al., 2006) had streams. In thinned blocks, study stream reaches required sufficient upland forest outside of buffers for thinning treatments to be implemented. Along some stream reaches in smaller drainages, the initial 2-Tree buffer width or the 1-Tree buffer width did not fit with space between the outer edge of the buffer and ridgelines to allow an upland thinning treatment. Our replication of these wider buffers was consequently reduced, and complete random selection of buffer types with stream reaches was not possible at some sites. If there were multiple reaches that could accommodate a wider buffer at a site, randomization was used to assign buffer widths – for example a coin toss may have assigned a 1-Tree or 2-Tree buffer to a specific reach, and another coin toss may have assigned a variable-width or a streamside retention buffer to a reach. Yet despite an element of randomization, this approach still likely tended to assign wider buffers to larger streams, as we discussed above. Future studies could match stream sizes and species compositions during the site selection.

4.1. Management implications

Forest-management advances to sustain natural resources including biodiversity during timber harvest continue to be a topic of keen interest, especially as the Earth's 6th mass-extinction event unfolds from a variety of causes including species' habitat loss and fragmentation (Stuart et al., 2004; Wake and Vredenburg, 2008; IPBES, 2019; Tsing et al., 2020). Proactive measures for biodiversity retention have been instituted on US federal forests in the US Pacific Northwest where over 1,000 species are positively associated with late-successional and old-growth forest conditions (Thomas et al., 1993; USDA and USDI, 1993, 1994; Molina et al., 2006; Raphael and Molina, 2007; Olson et al., 2017). In addition to larger reserved land-use allocations, biodiversity in forested lands with timber harvest is addressed by stand-scale mitigations, including streamside riparian-forest buffers to protect aquatic resources. For the high-density stream network embedded within the Northwest's west-side mesic forests, streamside riparian buffers aim to retain water quality and the integrity of stream ecosystems, including endemic species. Small streams in headwater catchments can make up 80% of stream lengths (Meyer and Wallace, in press; Gomi et al., 2002), and host a unique community of fish and amphibians (Sheridan and Olson, 2003; Olson and Weaver, 2007). The three families of stream-breeding amphibians iconic to Northwest forested headwaters, giant and torrent salamanders and tailed frogs, have been a particular focus of research and management, with members of each family occurring on local or national at-risk species lists. Two regional torrent salamanders are under status review at this time for US Threatened and Endangered listing. Can stream-riparian buffers maintain well-distributed populations of these animals with upland timber harvest for either restoration or commodity production?

In western Oregon secondary forests that were thinned in two iterative harvests over 10 years, we found significantly higher densities of sculpins, torrent salamanders, and coastal giant salamanders in headwater stream reaches with a one site-potential tree-height buffer, ~70 m wide on both sides of streams, five years after the second harvest. Conversely, reduced densities of these three aquatic vertebrates occurred in reaches with the three alternative buffers in which timber harvest occurred closer to streams: a 6-m-wide buffer; a 15-m minimum-width buffer; and a 2-Tree riparian-management zone that was thinned without a streamside no-entry zone. Torrent salamanders also showed a significant association with unthinned control streams. These findings support a more-resilient fish-and-amphibian community in the 1-Tree-buffered stream reaches compared to reaches with narrower no-entry or managed buffers; and resilience of torrent salamanders appeared to be related to unmanaged controls.

Of more importance than buffers, animals sampled in and along the 58 streams in our study had strong associations with stream-habitat conditions, especially relative to hydrotype, the periodicity of surface streamflows. Torrent salamanders occurred in spatially intermittent streams, whereas sculpins, trout, giant salamanders, and tailed frogs occurred in perennial stream reaches. We noted a trend for small hydrotype-association changes of some species with affinities to the intermittent streams toward conditions with more-perennial habitat conditions: Dunn's salamanders, western red-backed salamanders, ensatina, Oregon slender salamanders, rough-skinned newts, and torrent salamanders. This could suggest responses to warm, dry conditions and consequent drying of the uppermost stream reaches, a finding reported in a recent companion study conducted with retrospective data from our study sites (Olson and Burton, 2019). Olson and Burton (2019) modeled headwater stream flows under future climate change projections. Within the range of the Cascade torrent salamander alone, modeling results predicted a 4.5% to 11.5% loss in headwater surface streamflows, with 597 to 2058 km of headwater streams becoming dry channels in years 2055 to 2085. Riparian buffer protection of tomorrow's retained surface streamflows seems imperative for these taxa, hence areas which may coincide with today's perennial headwater reaches (Olson and Burton, 2019); it is possible that our data are already showing changes in species-hydrotype associations in response to warming climates over the course of our study.

At the larger project-scale, in forest stands that had been clearcut without buffers, followed by repeated thinning with a mix of riparian buffer widths and unthinned control units, persistence of stream-breeding and streambank species is supported. There could be local risks of narrower and managed buffers for this fish-amphibian community, as results reported here suggest, but they could be offset at the larger site scale by protections offered by the 1-Tree buffers in the moderate density thinning main study, the variety of buffers in the high density thinning case study, and the control units. The aim of stream protections in forest-management contexts warrants consideration of the mosaic of conditions beyond a single-stream reach, the spatial scale of effects, the time scale of effects, and also weigh the benefits and costs of heterogeneous conditions. Although the mechanism driving effects is not disentangled, our work provides evidence for adverse stream-reach effects on aquatic species of narrow and managed riparian buffers, increasing effects with time with moderate upland thinning densities as studied herein, but increasing benefits of wider buffers and uncut control units with time. If some objectives of forest restoration are being met better in areas of the site with narrower buffers, and aquatic species persistence is retained by offsets of wider buffers and no harvest elsewhere, site-scale heterogeneity of prescriptions may have both aquatic and upland justifications. The narrower 6-m buffer and 2-Tree thin-through buffer are examples of prescriptions that could have both upland and aquatic benefits over time. For example, if tree growth is accelerated in the thinned buffer or upland thinning with a narrower buffer, and trees attain larger sizes faster for accelerated development of large down wood, an instream habitat component associated with pool habitats and both amphibian and fish populations, then there could be long-term gains for fish and amphibian stream habitats and communities. If higher densities of aquatic species can be retained in a portion of sites, a mix of buffers might be useful to consider for attainment of long-term benefits at larger site scales. Mixed widths of buffers can also hedge prevailing uncertainties in buffer efficacies for aquatic protections (Olson et al., 2014).

Consideration of the spatial scale at which aquatic populations function is an important corollary to this concept of providing a mix of habitat conditions at a larger site scale. Are populations restricted mostly to single reaches, or do they span larger areas? Stream-breeding amphibian life history supports a biphasic aquatic and terrestrial life cycle, and dispersal and gene flow knowledge supports movements among stream reaches (e.g., Emel et al., 2019; Olson et al., 2007) hence there is reason to believe that these populations function at a scale larger than a single headwater reach. Hence, if a mix of buffers were to be applied to a larger site, more than one stream reach with a conservative buffer is supported for better protection of aquatic organisms. Such a design of redundant conservative protections of headwater stream reaches could benefit at-risk torrent salamanders as well, especially if warmer, dryer years are projected with consequent shrinking of intermittent stream surface flows (Olson and Burton, 2019), habitats with which they are particularly associated.

Our focus has been on the stream and streambank aquatic vertebrate communities, and in our study terrestrial- and pond-breeding amphibian captures are lower, precluding some statistical analyses. Site-specific detections of larger numbers of northern red-legged frogs and Oregon slender salamanders in our study may reflect sites within their species ranges and/or locally suitable habitats. For example, the abundance of legacy large down wood from the initial clearcut harvest at the Keel Mountain site may explain Oregon slender salamander occurrence there (Rundio and Olson, 2007). That site may also have a nearby breeding pond for northern red-legged frogs, explaining their local occurrence.

Importantly, our current study was not designed to address effects of the dual thinning harvests on these other amphibian assemblages. A case study at two of our sites previously examined terrestrial amphibians before treatment and in the first two years after the first thinning, showing decreased detections of ensatina and western red-backed salamander post-treatment (Rundio and Olson, 2007). At five to six years after the first thinning, Kluber et al. (2008) reported no effects of thinning on terrestrial salamanders at three of our study sites, but they suggested that site conditions such as rocky substrates may have ameliorated harvest effects. They found that distance-from-stream was associated with amphibian abundance, with more animals within 15 m of streams, supporting riparian-buffer benefits for upland amphibian assemblages. Olson and Kluber (2014) similarly reported more surface movements of amphibians within 15 m of streams, supporting riparian areas as likely dispersal corridors. Additionally, Anderson et al. (2007) reported that a stream effect of cooler, moister microclimate conditions occurred within 15 m of streams at the Density Management and Riparian Buffer Study sites. These studies show that riparian buffers have more ecological significance than provision of habitats for instream and streambank assemblages, as they may be tied to upland habitat functions for distinct communities. It is relevant to note that an earlier report from the current study, 10 years after the first thinning Olson et al. (2014), supported a 15-m buffer for stream salamanders. The concepts of providing either wider streamside buffers (e.g., 1-Tree buffers) on headwater streams or a mix of buffer widths at the site scale should be weighed within the context of the upland harvest treatment(s) and the broader forest-dependent fauna and ecological processes and functions at stake.

CRediT authorship contribution statement

Deanna H. Olson: Conceptualization, Project administration, Funding acquisition, Writing – original draft. **Adrian Ares:** Formal analysis, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120067.

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