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The Effects of Nearshore Forest Thinning on Upland Habitat Use by Pond-Breeding Amphibians in a Montane Coniferous Forest

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Abstract

Forest thinning treatments are expanding in scope and scale to counter increasing wildfire risk. Such treatments are being applied in aquatic-adjacent forests that provide a critical habitat for sensitive amphibians, yet little is known about the impact of these treatments. We used a 5-year (2017–2021) before–after–control–impact experiment to investigate the effects of hand-thinning on pond-breeding amphibian activity around an ephemeral lake in the southern Cascade Range of California. We found that hand-thinning had no detectable negative effects on long-toed salamanders (*Ambystoma macrodactylum*) and western toads (*Anaxyrus boreas*) and significantly increased adult Sierran chorus frog (*Pseudacris sierra*) activity ($\chi^2 = 4.70$, df = 1, $p = 0.030$) in upland habitats. These results are consistent with pre-treatment habitat associations—chorus frog activity was higher when tree density was lower, and the treatment reduced tree density; adult long-toed salamanders and western toads were positively associated with canopy closure, which was not significantly reduced by the treatment. In addition, late-season surface activity of adult long-toed salamanders and chorus frogs was strongly associated with fall rain events when they tend to cluster very near the lake edge. Hand-thinning in aquatic-adjacent habitat may have minimal negative impacts, and even some positive impacts, on pond-breeding amphibians in coniferous forests, especially if treatments are not implemented during periods of high amphibian activity and do not substantially alter canopy closure.

Keywords: pond-breeding amphibian; salamander; forest buffer; forest thinning

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1. Introduction

Wildfires have increased in size and intensity over the last half century as a result of climate change, fire suppression, past forestry practices, drought-induced diebacks, and an increase in anthropogenic sources of ignition [1–5]. This trend has led to a global rise in forest management practices aimed at removing woody fuels and increasing forest resiliency to severe wildfires, especially in temperate forests [6–9]. Thinning treatments that reduce the density of small trees linking the forest floor and canopy can reduce the occurrence of large-scale fires in coniferous forests [10–12], and are projected to increase in use as a means of fire prevention over the coming decades, particularly in areas that have recently experienced large-scale fires, such as western North America [13]. This uptick in forest thinning treatments increases the importance of understanding the effects of these treatments on wildlife. For example, Slauson et al. [14] used a modeling exercise to show that heavy thinning treatments may reduce short-term use by old-forest-associated predators but increase their long-term persistence by creating forest structure less susceptible to severe wildfire. Understanding how wildlife responds to fuel treatments will allow managers to decrease the negative effects and increase the beneficial effects of these treatments in high biodiversity areas or areas with sensitive species.

Aquatic-adjacent forest ecosystems form a transition zone between upland habitats and aquatic systems and provide critical habitat for numerous sensitive wildlife species [15–17]. The recognition of the importance of aquatic-adjacent forests has led to the development of forestry best management practices that maintain fixed-width buffer zones around headwater streams [18] and ponds, e.g., [19]. Limiting timber harvest in riparian buffers has proven important for supporting higher diversities and densities of fishes and other wildlife in streams by protecting habitat from the effects of intensive timber harvest [20,21]. However, in many cases, riparian buffer forests have not recovered from a legacy of forestry practices and are now decoupled from natural disturbance regimes – including fire – decreasing habitat heterogeneity and potentially limiting ecological benefits for sensitive wildlife [22–24]. In these cases, low-impact fuel treatments, such as hand-thinning, may be beneficial for reducing fire risk and improving conditions for wildlife [25–27]. However, there are few studies of the impacts of fuel treatments in aquatic-adjacent forests on sensitive wildlife whose life history spans the aquatic–terrestrial interface.

We investigated the effects of hand-thinning fuel treatments in an aquatic-adjacent forest buffer on pond-breeding amphibians that use aquatic habitats for breeding and adjacent upland forests for shelter and foraging. Amphibians are the most threatened class of vertebrates [28], play an important role in forest ecosystems [29,30], and are sensitive to a variety of forest management practices [31,32]. Primary concerns for pond-breeding amphibians include increased soil temperature, decreased moisture, and the removal or destruction of key habitat features such as coarse woody debris and animal burrows in forests adjacent to breeding ponds [33–35], though aquatic phases can benefit from canopy removal in smaller ponds [35,36]. However, there are few studies of the impacts of aquatic-adjacent thinning on pond-breeding amphibians in western North America, where wildfire risk and fuel treatments are both dramatically ramping up [13].

We worked with the Lassen National Forest in northern California, U.S.A. to apply hand-thinning treatments around a shallow, forested lake known to support high densities of pond-breeding amphibians. We applied a before–after–control–impact design to test whether nearshore forest thinning altered terrestrial habitat use by three species of amphibians and to characterize upland habitat use to help forest managers account for life history when conducting necessary fuel treatments in nearshore forest zones where amphibian densities are high. We focused efforts on long-toed salamanders (*Ambystoma macrodactylum*, Baird 1850), a California state species of special concern and USDA Forest Service sensitive species that lacks basic information about terrestrial habitat use [37]. We also collected data on western toads (*Anaxyrus boreas*, Baird and Girard 1852) and Sierran chorus frogs (*Pseudacris sierra*, Recuero et al. 2006) that occur in high numbers in the lake and use the surrounding upland habitats extensively. We predicted that hand-thinning would not have a negative effect on capture rates of adult or metamorphic amphibians unless canopy closure was greatly reduced so that the forest floor was more exposed to sunlight leading to drier soil and subsurface conditions [35]. We also predicted that clearing over-dense trees and shrubs in the understory might make dispersal movements away from the lake easier for newly metamorphosed amphibians resulting in increased juvenile captures in thinned plots following emergence from the lake. In addition, a common practice in forest thinning is gathering the logging slash into large piles for later burning, which may result in mortality for amphibians using these piles for cover. Given that few studies have assessed the effects of slash piles on vertebrates [38], we dissected five piles during a fall rain event to determine if the amphibians used them for refuge during fall migrations.

2. Materials and Methods

2.1. Study System

Our study was conducted at Big Lake, an ephemeral lake (or seasonally wet meadow) located at an elevation of ~1800 m in the southern part of the Cascades Range in the Lassen National Forest, Shasta County, CA, USA (latitude: 40.63024 degrees, longitude: −121.62881 degrees; Figures 1 and 2). This region is characterized by a warm summer mediterranean climate—summers are dry and most precipitation falls between October and May. Average precipitation is 1053 mm per year [39]. The "lake" is a 10.7 ha emergent wetland (depth < 0.5 m). It is fed by direct precipitation and a shallow, intermittent spring complex on the northwestern edge, and dries over the course of the summer, leaving minimal surface water by late summer/early fall.

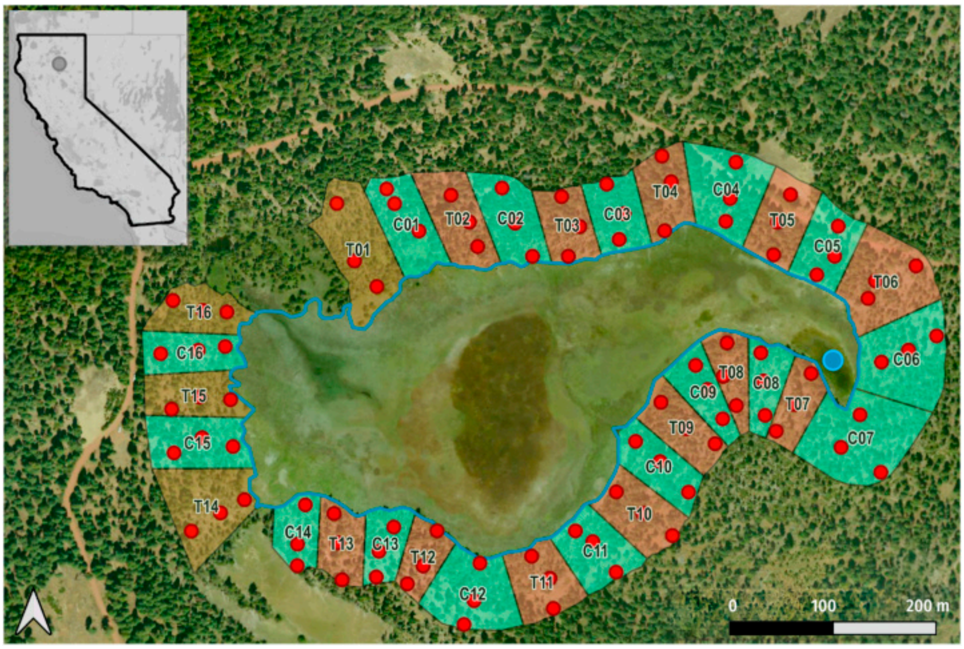

Figure 1. Site map and experimental design. Treatment–control plot design surrounding Big Lake Meadow, Shasta County, CA, USA. Shading indicates treatment (T) and control (C) plots. Red dots indicate locations of pitfall trap 2018–2021. All treatments were implemented in late summer or early fall 2019, except for plots T14 and T15 (implemented November 2019) and Plots T16 and T01 (untreated due to time and funding constraints). The blue dot shows the location of late-season larval habitat.

There is a remarkably distinct boundary between the "lake" and the surrounding forest. The silty-clay loam meadow (Aquoll) soils and meadow vegetation (mostly grasses, sedges, and forbs) suddenly give way to sandy loam upland (Yallani) soils and forest vegetation. Since this is also the general extent of early season water, we defined it as the edge of Big Lake. Lodgepole pines (*Pinus contorta* Douglas ex Loudon 1838) are the dominant tree species near this edge, with estimated pre-treatment densities up to 2500 stems/ha (1000 stems/acre). As the soils become drier further away from the edge, the dominant tree species becomes white fir (*Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr. 1874); other common trees include ponderosa pine (*Pinus ponderosa* Douglas ex Lawson 1836), sugar pine (*Pinus lambertiana* Douglas ex Don 1837), and red fir (*Abies magnifica* Murray 1858); understory vegetation is relatively undeveloped, though manzanita (*Arctostaphylos* spp.) are common in forest openings. Much of the forested uplands surrounding Big Lake were mechanically thinned by the U.S. Forest Service in 2016. The first 30–60 m of upland habitat immediately surrounding the lake was designated as a riparian conservation area and not subjected to mechanical thinning. At the beginning of the study, this area consisted of thick stands of young or stunted lodgepole pines and fir trees and downed woody debris (Figure 2A).

Figure 2. Big Lake and hand-thinning treatments. Big Lake early (**A**) and late (**B**) in the season, showing the seasonal dry-down. Forest surrounding Big Lake before (**C**) and after (**D**) treatment; note drift fence array at front left in panel (**C**) and slash piles in panel (**D**).

As annual dry-down prevents colonization by predatory fish, Big Lake is an important habitat for pond-breeding amphibians. Resident amphibians include western toads, Sierran chorus frogs, and long-toed salamanders, which are highly susceptible to fish predation [40–42]. At Big Lake, adults of all three species descend to the lake to breed at ice out in April/May and retreat to upland forests after breeding leaving large quantities of eggs behind to develop in the lake. While the timing of metamorphosis varies between years, the order of metamorphosis is relatively consistent, with toads beginning to metamorphose first (early/mid-June), chorus frogs next (early July), and long-toed salamanders last (late July/early August) (unpublished data). Surface water persists longest in the eastern portion of the lake, so this is where long-toed salamander larvae tend to be concentrated prior to metamorphosis, as it is often the only remaining aquatic habitat. Metamorphosed young of all three species move into upland forests surrounding Big Lake after emergence.

2.2. Experimental Design

We divided the uplands surrounding Big Lake into thirty-two 50 m wide plots that extended approximately 60 m outward from the lake edge (Figure 1). We did not include uplands adjacent to the northwest corner of the lake in the experimental design due to the presence of unique spring and meadow habitats. Prior to thinning, we designated equal numbers of treatment and control plots in an alternating design, with the first plot assigned randomly. However, due to implementation issues, we ended up with a total of 14 thinned and 16 control plots (Figure 1). Thinning for 12 of the treatment plots was implemented July through August 2019. Due to logistical constraints (e.g., funding and terrain accessibility) two planned treatment plots (T16 and T01) were not thinned until November 2019. Data from these two plots collected between July and November 2019 (i.e., prior to thinning) were not used as post-treatment data in analyses of treatment effects.

Within treated plots, lodgepole pine and white fir under 10 in. (25.4 cm) diameter were hand-thinned (i.e., cut down with a chainsaw) to densities of 440 trees per acre (1087 trees per hectare) at the lake's edge with a uniform transition to a density of 110 trees per acre (272 trees per hectare) 60 m from the lake edge (Figure 2B). Trees larger than 10 in. (25.4 cm) in diameter were left uncut. Treatments were implemented in all plots up to a minimum of 30 m from the lake; some plots required treatments up to 60 m from the lake based on density requirements. Crews collected cut trees and other woody debris under 15 in. (38.1 cm) in diameter into slash piles within treated plots (Figure 2C), most of which were >50 ft (15.2 m) from the lake. Piling did not include woody debris from the lakebed or debris that was significantly decayed. Collections resulted in 8–20 slash piles in each treatment plot, averaging 4–8 m in diameter and 1–2 m in height. Thinning treatments were implemented by the California Conservation Corps. Control plots were not disturbed during treatment implementation.

2.3. Habitat Characteristics

We conducted detailed habitat surveys in each of the 50 m wide plots. Habitat surveys were conducted in seven circular survey areas in each plot—one 2.5 m radius survey at each of the three trap locations and four 5 m radius surveys at randomly selected locations. We conducted surveys July to August of 2018 and repeated them in the same locations post treatment in August of 2019. Within each survey area we recorded litter depth and percent woody debris using established techniques [43] as indicators of cover available for amphibians in upland habitat. Litter depth measurements were taken by measuring the vertical distance from the litter surface to mineral soil using a ruler at five randomly selected points and averaged for each survey area. We assessed woody debris cover on the basis of ground cover percentage based on visual estimates. We used tree density and canopy closure as indicators of shade cover, an important factor in maintaining soil moisture and reducing temperatures on the forest floor [44]. All trees at or over breast height within the survey area were counted and used to calculate stem density (per m^2).

We assessed canopy closure with a spherical densitometer on a scale of 1–17, converting results into percent closure values [45,46]. We took four canopy measurements during each survey, each while standing in the middle of the survey area facing each of the four cardinal directions. Canopy closure measurements were then averaged for each survey area. We calculated plot-level habitat characteristics as the mean values from the four 5 m radius vegetation surveys in each plot.

2.4. Amphibian Surveys—Drift Fence Arrays

To assess amphibian movement and surface activity in the nearshore upland habitat, we erected drift fence arrays with pitfall traps (Figure 2C) [47]. A drift fence array included a 5 m long section of shade cloth positioned parallel to the lake shore with the bottom buried roughly 10 cm deep leaving about a 45 cm high fence held in place by 5 wooden stakes. Two pitfall traps (no. 10 metal food cans) were buried at each end of the fence so that the rim abutted the fence and was level with the soil surface. Traps were covered by wooden lids held about 5 cm above the rim and contained moist sponges to prevent mortality due to desiccation or predation [48]. To prevent amphibian escape, we fit funneled plastic collars on the inside of each tin. To aid in the escape of incidental rodent captures, we hung a string from the coverboard into the tin [49].

We checked open pitfall traps daily and recorded all captured vertebrates by species and life stage; captured animals were quickly released. We classified amphibians into three life stages: (1) newly metamorphosed young (metamorphosed in that year), (2) subadults, and (3) adults. We measured physical characteristics for salamanders including snout-to-vent length (SVL, in mm), total length (mm), and weight (grams). On extremely large salamander capture days (>150 captures), we were unable to measure all salamanders captured; instead, we only categorized by life stage. We released salamanders under a nearby log avoiding areas directly behind or in front of traps to avoid affecting recapture probability. On occasion, a few traps were significantly damaged overnight by wildlife or heavy rains; these were marked ‘unavailable’ and treated as closed in analyses.

Drift fence arrays were deployed during five summer/fall seasons (2017–2021). In 2017 we erected a total of 94 drift fence arrays placed around the perimeter of the lake at various distances from the lake edge. Most traps (89) were placed 3–50 m from the lake, while another 5 traps were located at distances of 53–114 m. In 2018–2021, after plots were delineated, we erected the arrays at distances of 3 m, 30 m, and 60 m from the lake in each of the 32 plots for a total of 96 traps (Figure 1).

In 2017, pitfall traps were opened during periodic weeks in June, most of August, and three days in September. In 2018, we opened traps from late May through mid-August, as well as one week in both September and October. Low capture rates early in the season and between rain events in 2017 and 2018 emphasized the need to open traps during late-season rain events, especially for long-toed salamanders. In 2019, we opened traps during most of August, September, and for one week in October. Limited breeding due to low water levels and a lack of fall rain events limited trap opening to 6 days in 2020, including the two days following small rain events in late July, mid-October, and early November; a similar lack of fall rain limited trap opening to two days in 2021 (22 and 23 Oct). Trapping was not possible during the spring breeding migration due to snow and saturated soil. It is possible that focusing on late-season trapping to maximize salamander captures in 2019–2021 may have led us to miss the movement of some metamorphic toads and frogs. Our procedures for the use of drift fences and pitfall traps were reviewed and approved by the Washington State University Institutional Care and Use Committee (protocols 4749 and 6339).

2.5. Amphibian Surveys—Time- and Area-Constrained Surveys

We conducted time-constrained and area-constrained searches with the goal of assessing upland habitat use by amphibians that may not be captured in pitfall traps. Time-constrained searches [47] assessed adult surface activity in May and early June of 2019 when upland habitat still contained significant snow cover. During surveys, we flipped cover objects for a period of one hour and recorded all amphibians detected; all surveys were conducted by a single person. We conducted 48 time-constrained searches on the north, east, and west sides of Big Lake in 2018 and 36 searches in 2019. Area-constrained searches [50], conducted from June through early August in 2017 and 2018, assessed surface activity during summer months. For these searches, we generated randomly placed 5 m radius survey areas in the uplands directly adjacent the lake, flipped all cover objects in the plot, and recorded all amphibians found. A total of 63 area-constrained searches were conducted in 2017 and 64 in 2018.

2.6. Slash Pile Surveys

We assessed slash pile use by amphibians by dissecting five piles on 18 October 2019 during the fall migration period; a heavy rain event led to the capture of 181 amphibians in pitfall traps on the morning of 17 October and another 60 amphibians on the morning of pile searches. We selected piles in treatment plots on the north, east, and southeastern portions of the lake where pitfall trap captures indicated high levels of amphibian activity. We surveyed piles located 15–45 m from the lake, between 3 and 4.5 m in diameter, and 1–2 m in height; (Figure 2D). Slash pile surveys included removing individual logs until the entire pile was disassembled and remade in a nearby location. All litter and cover objects located beneath the pile were searched for amphibians.

2.7. Statistical Analyses—Summary

We conducted analyses to evaluate (1) the effect of hand-thinning on upland habitat characteristics and amphibian activity, (2) within-season spatiotemporal patterns in surface activity of amphibians, and (3) pre-treatment associations between upland habitat variables and surface activity. The analyses of the effects of hand-thinning were focused on determining whether there was an effect of treatment, so we used a null hypothesis testing approach. The analyses of spatiotemporal patterns and habitat associations were focused on determining which variables had an important influence on amphibian activity, and so we applied an information-theoretical approach to determining variable importance and impact. Our analyses focus on drift fence pitfall trap data; data from area-constrained and time-constrained searches were only used to provide qualitative support due to the paucity of individuals observed with these methods. We only used surveys in which at least 10 animals in the focal group were captured to avoid an excess of uninformative zeros, which eliminated most sampling dates from early in the season and dry periods (Table S1).

All analyses were conducted in R version 4.3.1 (R Foundation for Statistical Computing, Vienna, Austria). We fit generalized linear mixed models (GLMMs) using the ‘glmmTMB’ command in the {glmmTMB} package [51]. All continuous predictors in GLMMs were centered and scaled to a standard deviation of one prior to analyses. For all GLMMs we used the {performance} package [52] to assess overdispersion and examined residuals using the DHARMa package [53] to assess consistency with model assumptions. We used Poisson GLMMs unless there was evidence that these models were overdispersed, in which case we used negative binomial GLMMs [54]; a log link function was used in both cases.

2.8. Hand-Thinning Treatment Effects

To evaluate the effect of hand-thinning treatments on upland habitat characteristics we ran a multivariate analysis of variance (MANOVA) comparing habitat characteristics in control and treatment plots after the treatment had been implemented. The predictor variable was treatment; response variables were tree density, woody debris cover, canopy closure, and litter depth. We log-transformed tree density in order to meet assumptions of normality and standardized each of the four response variables using a Z score transformation [55]. We used the Shapiro–Wilk test to assess multivariate normality of dependent variables and Levene's test to confirm the assumption of equal variances. To confirm that pre-treatment habitat conditions were not significantly different across plot type, we ran a preliminary MANOVA test assessing differences in pre-treatment habitat conditions (2018) between control and treatment plots. This analysis found that pre-treatment habitat conditions did not differ between treatment and control plots.

To assess the treatment effect on the upland amphibian activity, we ran separate analyses for long-toed salamander metamorphs, long-toed salamander adults, Sierran chorus frog metamorphs, Sierran chorus frog adults, and western toad metamorphs (there were not enough captures to model adult western toads, or subadults of any species). The response variable in these models was the number of amphibians caught in each individual trap during a survey period, where survey periods were defined as periods of continuous sampling, and we included the number of trap-days for each trap in each survey period as an offset to account for variation in survey effort. Plot and trap were included as random predictors to account for non-independence. Treatment was a fixed predictor, as was the trap's distance from lake edge. We included mean plot-level pre-treatment daily capture rates (from 2017 and 2018) as a predictor to account for pre-existing variation in amphibian activity between plots. We also included year for species and life stages with multiple years of post-treatment data (salamander and chorus frog adults). Year*treatment interactions were included in preliminary models for species with data from multiple years; these were dropped from the final models as they were not significant ($p > 0.3$ in all cases). The significance of fixed effects was evaluated using chi-squared likelihood ratio tests.

2.9. Spatiotemporal Patterns and Habitat Associations

For the analyses of spatiotemporal patterns, we only used data from 2019, the year with the most captures over multiple survey periods. As with the analyses of treatment effects, we ran separate models for each species–life-stage combination that had sufficient data, and the response variable in these models was the number of amphibians caught in each individual trap during a survey period, with the number of trap-days as an offset to account for variation in survey effort. Plot and trap were included as random predictors to account for non-independence. The other predictor variables were ordinal date (day of year), distance from lake, distance from late-season water, ordinal date*distance from lake interaction, ordinal date*distance from late-season water interaction, slope, and geolocation (latitude, longitude, and their interaction). These variables were selected because they represent important spatial and geographic components of the habitat that are unlikely to be affected by forest conditions. Correlations between predictor variables were generally low ($r < 0.35$) except in the case of longitude and distance from late-season water. We ran all possible combinations of the predictor variables, ranked them using Akaike information criterion corrected for small sample size (AICc), and calculated model weights [56]. We then calculated relative variable importance for each predictor as the sum of model weights over all models including the focal variable using the {MuMIn} package [57]; we also report output from the top model, which we considered to be the model with the least parameters within 2 AICc units of the best AICc score.

To evaluate upland habitat associations of the amphibians, we used only pre-treatment data (2017 and 2018) because we were concerned that the hand-thinning treatment could disrupt pre-existing habitat associations. We used the same species-life stage groups described above as response variables. The other predictors were distance to lake, distance to late-season water, tree density, canopy closure, litter depth, woody debris cover, slope, and geolocation (latitude, longitude, and their interaction). Plot, trap, and survey period were included as random effects to account for non-independence; year was included as a fixed effect as there were only 2 years. As in the analysis of spatiotemporal patterns, correlations between continuous predictor variables were generally low to moderate ($r < 0.52$) except in the case of longitude and distance from late-season water. We ran all possible combinations of predictor variables and calculated AICc, model weights, relative variable importance, and output from the top model.

3. Results

Across the five years (2017–2021) and 94 nights of active drift fence-pitfall trap arrays we captured a total of 1748 long-toed salamander adults, 4081 metamorphs, and 72 subadults; 227 Sierran chorus frog adults, 3105 metamorphs, and 8 subadults; and 16 western toad adults, 763 metamorphs, and 33 subadults. There was substantial variation between years in the timing and magnitude of amphibian activity and the presence of young-of year (Table S1).

3.1. Effect of Hand-Thinning on Habitat Characteristics

The MANOVA on post-treatment habitat conditions revealed a significant effect of treatment on overall habitat conditions ($F_{4,23} = 6.26$, $p = 0.001$). Tree density was 73.6% lower in treated plots than in control plots ($F_{1,26} = 16.98$, $p < 0.001$; Figure 3), percent woody debris cover was 32.1% higher in treated plots ($F_{1,26} = 4.92$, $p = 0.03$), and litter depth was 17.4% higher in treated plots ($F_{1,26} = 3.60$, $p = 0.07$). We did not detect a significant effect of treatment for canopy closure ($F_{1,26} = 0.57$, $p = 0.45$).

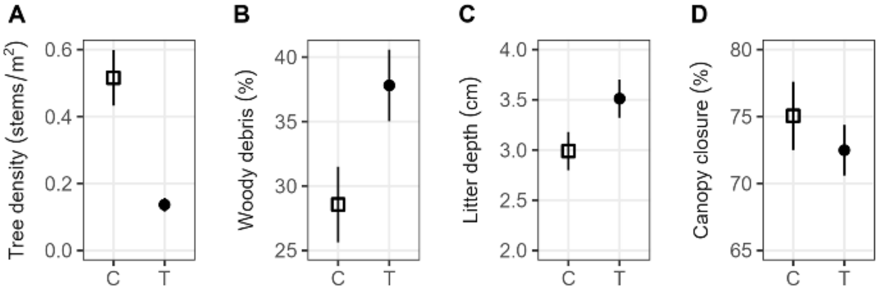

Figure 3. Effect of thinning treatments on upland habitat conditions. C = control plots (open squares), T = treatment plots (filled circles). The means and standard errors of post treatment habitat measurements are shown by treatment type. Values were calculated based on plot-level averages of 5 m radius vegetation surveys conducted post treatment (2019). Units vary for each habitat variable and include (**A**) tree density (trees/m^2), (**B**) woody debris cover (% ground cover), (**C**) litter depth (depth in centimeters), and (**D**) canopy closure (% closure).

3.2. Effects of Hand-Thinning on Amphibian Activity

There were no detectable effects of hand-thinning on long-toed salamander activity for both adults ($\chi^2 = 0.65$, df = 1, $p = 0.42$) and metamorphs ($\chi^2 < 0.001$, df = 1, $p = 0.98$) (Figure 4; Table S2). For Sierran chorus frogs model-estimated marginal means indicated a 107% increase in adult activity in hand-thinned plots ($\chi^2 = 4{,}70$, df = 1, $p = 0.030$; Figure 4; Table S2), and a marginally significant trend for increased metamorph activity in hand-thinned plots ($\chi^2 = 2.77$, df = 1, $p = 0.096$). There were no detectable effects of hand-thinning on toad metamorphs ($\chi^2 = 0.15$, df = 1, $p = 0.70$). A detailed search beneath five slash piles on 18 October 2019, during the fall movement period, revealed no long-toed salamanders, western toads, or Sierran chorus frogs using the slash piles as cover.

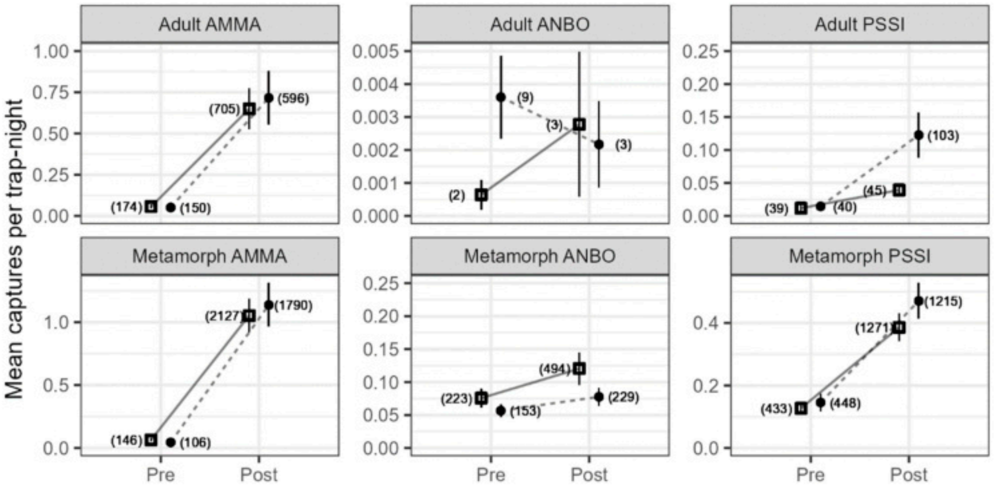

Figure 4. Effects of hand-thinning on amphibian activity. Mean captures per trap-night (±SEM) of different life stages of three amphibian species: *Ambystoma macrodactylum* (AMMA), *Anaxyrus boreas* (ANBO), and *Pseudacris sierra* (PSSI). Plot-level means and standard errors from before (pre; 2017–2018) and after (post; 2019–2021) treatment in control (open squares, solid lines) and treatment (filled circles, dashed lines) plots are shown. Sample sizes (n) indicate the total number of captures for each species and life stage in each treatment and time period. Symbols for different treatments are offset on the x-axis to avoid overplotting. The y-axis scale varies among panels to accommodate differences in capture rates among species and life stages.

3.3. Spatiotemporal Patterns in Amphibian Activity

Periods of high surface amphibian activity occurred after metamorphosis and during late-season rain events (Figure S1); surface activity in upland habitats between breeding and metamorphosis was limited. In 2017 and 2018 drift fence arrays were active earlier in the season (starting in early June in 2017 and late May in 2018). These surveys showed that while metamorph activity in upland habitats frequently occurred shortly after metamorphosis for each species, adult long-toed salamanders and Sierran chorus frogs were most commonly captured during fall rain events (Figure S1). Area-constrained searches revealed low levels of surface activity by all three species in upland forests during mid-summer months (4 June–17 Aug; 2017 and 2018); mean densities were 0.01 m^{-2} for all species combined and 0.003 m^{-2} for long-toed salamanders. Time-constrained searches revealed relatively low levels of long-toed salamander activity in upland habitats during spring (15 May–5 June; 2018 and 2019) with 0.72 salamanders found per hour of searching.

Within-season spatiotemporal patterns in upland habitat use varied by species and life stage. The most important predictors for adult long-toed salamanders included ordinal date, distance to the lake, and their interaction (Table 1), with adult activity increasing near the lake later in the season (Figure 5). For long-toed salamander metamorphs, these same variables were important, but so was distance to late-season water (Table 1)—metamorph activity was concentrated close to the location of late-season water when they first appeared and subsequently spread out over the upland habitat, with activity generally moving away from the lake edge as the season progressed (Figure 5). Sierran chorus frog metamorph activity decreased as the season progressed and became increasingly concentrated near the lake and the location of late-season water; activity was highest in the northeast part of the study site. The activity of western toad metamorphs also decreased as the season progressed and was concentrated near the lake edge (Table 1). There were not sufficient data to characterize within-season spatiotemporal patterns in activity for other species and life stages.

Table 1. Weights and top model output for spatiotemporal analyses.

	AMMA Adult		**AMMA Metamorph**		**PSSI Metamorph**		**ANBO Metamorph**	
Predictor	**Weight**	**IRR**	**Weight**	**IRR**	**Weight**	**IRR**	**Weight**	**IRR**
Ordinal date	1.00	2.93 ***	1.00	1.25 **	1.00	0.71 ***	1.00	0.53 ***
Distance to late-season water	0.62	-	0.94	0.60 ***	1.00	1.03	0.83	5.04 †
Distance to lake edge	1.00	0.48 ***	1.00	0.89 ***	1.00	0.67	1.00	0.45 ***
Slope	0.26	-	0.41	-	0.27	-	0.28	-
Latitude	1.00	1.50 ***	0.32	-	0.74	1.11	1.00	1.38 †
Longitude	0.35		0.33	-	0.86	1.16	0.98	3.86
Latitude * Longitude	0.10		0.03	-	0.63	1.47 **	0.97	0.38 ***
Ordinal date * Distance to late-season water	0.48	-	0.54	-	1.00	0.83 ***	0.55	-
Ordinal date * Distance to lake edge	0.90	0.84 **	1.00	1.14 ***	0.99	0.92 ***	0.35	-

AMMA = *Ambystoma macrodactylum* (long-toed salamander); PSSI = *Pseudacris sierra* (Sierran chorus frog); ANBO = *Anaxyrus boreas* (western toad). Weight is the sum of all model weights for models including the focal variable; IRR = incidence rate ratio from the top model; values > 1 indicate increasing captures; values < 1 indicate decreasing captures (see Section 2.9 for details); asterisks indicate significance based on WALD z-tests: *** $p < 0.001$, ** $p < 0.01$, † $p < 0.1$.

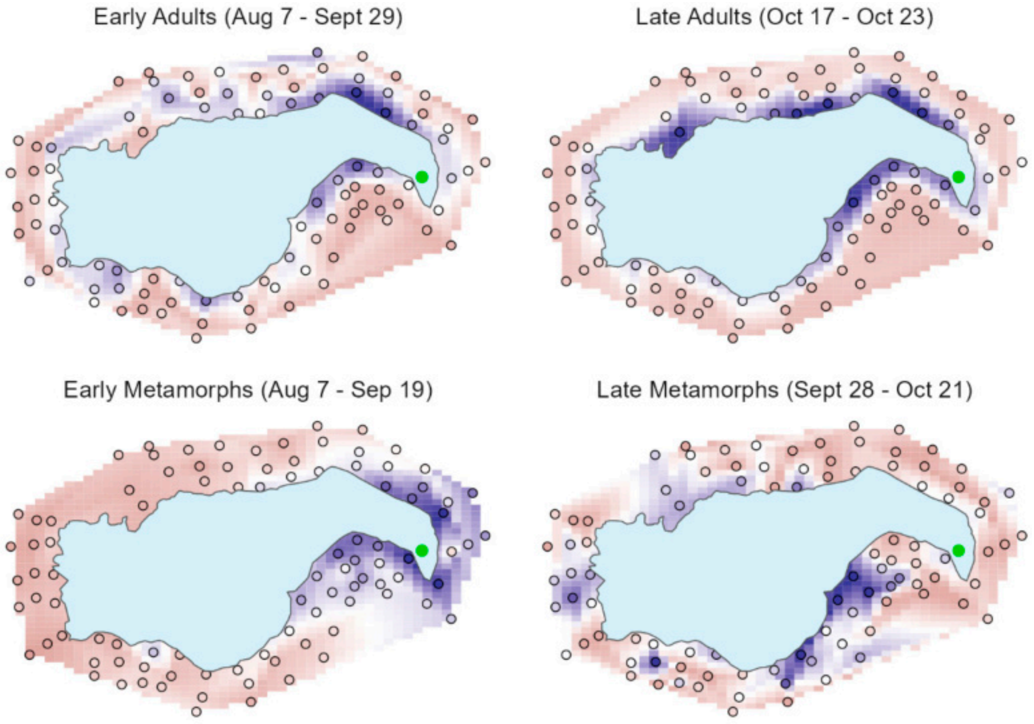

Figure 5. Spatial distribution of adult and metamorph Ambystoma macrodactylum. Data are from pitfall traps in the early and late portions of the 2019 and 2021 survey seasons. Interpolated heatmaps of z-scaled abundance across the study area split into four categories: early season adults, late-season adults, early season metamorphs, and late-season metamorphs, with trap locations overlaid. Abundances are scaled within each category with red values indicating densities lower than the average and blue indicating densities higher than the average. The lake is shown in blue and late-season larval habitat is shown with a green dot.

3.4. Upland Habitat Associations

For adult long-toed salamander adults canopy closure was the most important habitat-related predictor of activity (Table 2), with increasing canopy closure associated with increased adult salamander activity. For salamander metamorphs, tree density was the most important habitat-related predictor (Table 2), with salamander metamorph activity decreasing as tree density increased. A similar pattern was observed for adult chorus frogs (Table 2). Habitat associations for metamorphic chorus frogs and western toads were generally weak, though there was a trend for increasing toad captures with increased canopy closure (Table 2).

Table 2. Weights and top model output for pre-treatment habitat association analyses.

	AMMA Adult		AMMA Metamorph		PSSI Metamorph		PSSI Adult		ANBO Metamorph	
Predictor	**Weight**	**IRR**	**Weight**	**IRR**	**Weight**	**IRR**	**Weight**	**IRR**	**Weight**	**IRR**
Distance to lake edge	1.00	0.58 ***	0.94	0.62 ***	0.77	-	0.48	-	0.52	-
Distance to late-season water	0.24	-	0.36	-	0.32	0.75 ***	0.35	-	0.53	-
Canopy closure	0.90	1.35 **	0.28	-	0.31	-	0.51	-	0.62	1.34 †
Tree density	0.47	-	0.89	0.65 **	0.62	-	0.76	0.32 **	0.29	-
Litter depth	0.43	-	0.28	-	0.29	-	0.27	-	0.32	-
Latitude	1.00	1.67 ***	0.81	1.33 **	0.94		0.99	1.54 **	0.92	
Longitude	1.00	1.18	0.81	1.07	0.94		0.99	0.65 **	0.92	
Latitude * Longitude	1.00	1.23	0.81	0.81	0.94		0.99	0.94	0.92	
Woody debris	0.28	-	0.34	-	0.34	-	0.38	-	0.42	-
Slope	0.78	1.33 *	0.34	-	0.27	-	0.36	-	0.31	-

AMMA = *Ambystoma macrodactylum* (long-toed salamander), PSSI = *Pseudacris sierra* (Sierran chorus frog), ANBO = *Anaxyrus boreas* (western toad). Weight is the sum of all model weights for models including the focal variable, IRR = incidence rate ratio from the top model, values > 1 indicate increasing captures, values < 1 indicate decreasing captures (see Section 2.8 for details); asterisks indicate significance based on WALD z-tests: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, † $p < 0.1$.

4. Discussion

Consistent with our expectations, we found that hand-thinning had no detectable negative effects on long-toed salamanders and western toads and positive effects on the activity levels of Sierran chorus frogs in upland habitats. The most robust positive effects were observed for Sierran chorus frog adults, though there was a marginally significant positive effect for chorus frog metamorphs as well. These results are consistent with pre-treatment habitat associations—prior to hand-thinning, Sierran chorus frog activity (for both adults and metamorphs) was higher when tree density was lower. One of the most pronounced effects of hand-thinning on habitat was reduced tree density, which suggests that increased chorus frog activity in treated plots was driven by reduced tree density. The absence of a detectable treatment effect for adult long-toed salamanders and western toads may reflect the fact that the treatment did not significantly reduce canopy closure, which was positively associated with activity for these two groups.

Amphibian species and life stages differed in their spatiotemporal patterns of upland surface activity, which suggest distinct seasonal patterns of movement. Surface activity of adult long-toed salamanders is strongly associated with fall rain events, when they tend to cluster very near the lake edge. In contrast, salamander metamorph activity is initially clustered near the last part of the lake to dry up (which is likely where they metamorphose) and moves farther into the upland habitat as the season progresses. Sierran chorus frog and western toad metamorphs were not as strongly associated with late-season water. Furthermore, slash piles did not seem to be extensively used for cover by amphibians during the fall migration period directly following hand-thinning. Taken together, these findings suggest that carefully implemented fuel treatments can have minimal negative impacts on upland habitat for pond breeding amphibians. In order to minimize impacts, treatments should emphasize the maintenance of canopy closure and at least some woody debris and avoid periods of high surface activity such as fall rain events.

4.1. Effects of Hand-Thinning and Upland Habitat Associations

The positive effects of hand-thinning on the activity of Sierran chorus frogs, and the lack of negative effects on long-toed salamanders and western toads, is consistent with known habitat associations for these species as well as previous studies of forest management practices on amphibians. Increased activity of Sierran chorus frog adults in thinned plots is consistent with their association with lower tree density prior to hand-thinning in the current study, as well as previous studies showing associations with more open upland habitats [58–60]. Sierran chorus frog metamorph activity also tended to increase in thinned plots, but we did not find strong evidence for pre-treatment associations with tree density, which may explain the weaker treatment effect for this life stage. In contrast, there were strong pre-treatment associations between the activity of long-toed salamander metamorphs and lower tree density, but no evidence for treatment effects. This difference may be due to stronger trade-offs for long-toed salamander metamorphs between ease of movement and protection from desiccation [61], especially in the two drought years following treatment. Long-toed salamander adults were strongly associated with canopy closure prior to treatment. We hypothesize that this group was not impacted by the thinning treatments at least in part because these treatments did not cause major reductions in canopy closure (Figure 3).

In general, it appears that the hand-thinning treatment did not alter aquatic-adjacent forest habitats in a way that negatively impacted pond-breeding amphibians in our study. Decreases in local amphibian abundance after thinning treatments in previous studies were associated with forest floor disturbance [32,62], a loss of woody debris [63], or a decrease in canopy closure [33,62,64]. Such disturbances are often associated with mechanical thinning and piling treatments that degrade soils and necessitate heavier thinning to allow room for large machines [62,65]. Treatments at Big Lake were implemented via chainsaws and were able to preserve litter depth, removing only understory trees and leaving overstory pines that provide shade cover. Though tree density decreased after treatment, such declines may be more likely to be associated with a decrease in amphibian abundance when treatments are heavy enough to reduce canopy closure [66]. Thus, thinning treatments within aquatic-adjacent habitat may not affect abundance or survival of amphibians in the short-term when treatments result in minimal ground disturbance or changes to other key upland habitat conditions.

Importantly, there are some caveats associated with this general finding of no negative impacts on amphibians. For example, the treatment may have altered the detectability of some species, confounding our ability to evaluate its impacts (or lack thereof) on amphibian activity. In addition, while our study included three years of post-treatment data, there may be longer-term consequences of the treatment that were not detectable within the span of our study. The potential for undetected effects is also increased by environmental variability. The year in which treatments were implemented (2019) featured multiple late summer and fall precipitation events in which there were thousands of amphibians captured within a few months of thinning, whereas the next two years (2020 and 2021) were dry, with limited metamorphosis and surface activity in both years (with the exception of a late-season pulse of adult Sierran chorus frog and long-toed salamander activity in 2021) (Table S1). Finally, our study of patterns in upland activity does not provide any direct insight into the impacts of thinning treatments on population viability.

Despite high amphibian surface activity during the week of slash pile surveys, evidence that amphibians used newly formed slash piles was absent. Western toads, Sierran chorus frogs, and long-toed salamanders all use woody debris for cover and foraging when in upland habitat [44,67]. However, amphibians in coniferous forests often select cover objects showing moderate levels of decay as these logs and stumps provide increased moisture and microhabitat opportunities over freshly fallen debris [68,69]. Though slash piles may conserve soil moisture during dry summer months, the slash piles at Big Lake did not appear to offer increased soil moisture levels in October when surrounding soils were cool and wet (pers. obs.). The ground beneath slash piles also revealed a layer of pine needles several inches thick that may represent a physical obstacle for amphibians. Following fuel treatments, most slash piles are left for 1–2 seasons for wood to dry and are burned outside of peak fire season (in fall or winter) when conditions are wet and fires may be controlled. This period of settling and decaying may make these logs more desirable cover objects for amphibians, making slash piles a potential hazard to individuals seeking cover prior to burning. Future research should emphasize the degree to which amphibians use slash piles as cover in the years following fuel treatments.

4.2. Temporal and Spatial Patterns of Activity and Upland Habitat Use

The surface activity of pond-breeding amphibians in upland habitats was strongly tied to life history events and precipitation events. The movement of metamorphs into upland habitats corresponded to the timing of metamorphosis (June to September, with toads tending to emerge first, followed by frogs, followed by salamanders). Pulses of high surface activity were associated with rains that occurred during this period, but such events were rare and there was measurable surface activity outside of precipitation events. In contrast, the surface activity of adult Sierran chorus frogs and long-toed salamanders tended to occur later in the season (September to October) and was strongly tied to significant precipitation events, with little evidence of surface activity outside of these events (including surveys in which we looked under cover objects). We suspect that after the spring breeding season and during the dry summer months adult frogs and salamanders stay well below the surface in burrows, consistent with known patterns of behavior for these species [70,71]. We were somewhat surprised to find little evidence for adult and subadult movement associated with the spring season (May to June), when upland habitats were still moist due to snowmelt. We suspect that adults may be concentrated in burrows very near the lake edge before and after breeding (see below for details), limiting our ability to detect them with surveys oriented towards cover objects (saturated soils prevented the use of pitfall traps in spring). In fall, the surface movement of all amphibians ceased when nighttime temperatures consistently dropped below freezing (late October or early November during the study period).

Activity levels for all amphibian species and life stages decreased with distance from the lake, but there were important differences between species and life stages in the strength and temporal dynamics of this relationship, especially for long-toed salamanders. Adult long-toed salamanders were strongly clustered near the lake edge, and increasingly so as the fall movement season progressed (Figure 5). This suggests that breeding adults move towards the lake in fall where they likely overwinter within meters of the lake edge, and is consistent with previous studies of montane populations of long-toed salamanders that found high abundances near the lake shore [72–74]. Adult long-toed salamanders at Big Lake may overwinter close to the lake edge to facilitate early arrival during the breeding season. In contrast to adults, the surface activity of long-toed salamander metamorphs shifted away from the lake as the season progressed (Figure 5). This movement of metamorphs away from the lake is consistent with the species' life history, where juvenile long-toed salamanders disperse away from their natal wetland and spend 1–3 years in upland habitats, mostly within 100 m of the wetland, before returning to breed as adults [70]. The movement of salamander metamorphs away from the lake edge may also be driven, at least in part, by intraspecific competition with resident adults for space in burrows near the lake. Intraspecific competition for burrows has been documented in studies of other *Ambystoma* species, e.g., [75].

For Sierran chorus frog metamorphs, upland surface activity decreased over the course of the season and became more concentrated closer to the lake and the location of late-season water. We suspect this is driven by ongoing metamorphosis later in the season, as this species appears to metamorphose over a relatively long period of time. Upland activity of western toad metamorphs tended to be concentrated farther away from late-season water. This species metamorphoses early in the season, when a greater portion of the lake is wetted, so it is not surprising that metamorph upland activity is not tied to late-season water.

5. Conclusions and Management Implications

Hand thinning in aquatic-adjacent habitat may have minimal negative impacts, and even some positive impacts, on pond-breeding amphibians in coniferous forests. While mechanical thinning often results in ground disturbance that negatively affects habitat conditions for amphibians, hand thinning methods can avoid such disturbance and may be useful in sensitive aquatic-adjacent habitat. Some amphibian species may benefit from the thinning of overgrown stands near breeding ponds if implementation avoids substantial ground disturbance and canopy reduction. Upland habitat associations for amphibians are often species and life-stage-specific; management decisions should consider the biology and life history of local species.

Wetland hydrological characteristics and timing of work should also be taken into consideration to minimize direct contact with surface-active amphibians. For example, upland habitat surrounding the location of late-season water may be particularly important for amphibians that have longer larval development stages. Near-shore forest work in areas adjacent to known areas with late-season water could be timed to occur ahead of or after late summer and fall periods of metamorphosis to avoid direct impacts to dispersing metamorphs. We observed that metamorphosis occurs regardless of weather patterns but metamorphs find refuge under nearby cover objects during warm and dry periods and move to safer upland burrows during moist and cool periods. They are likely highly susceptible to ground disturbance during this period. Our findings that adult amphibians are minimally active on the forest floor during summer dry periods, tend to move towards breeding ponds during fall rain events, and overwinter close to shore to facilitate early breeding in spring suggest that they are fairly safe from thinning treatments that do not compress topsoil and do not occur during significant precipitation events.

The burning of slash piles following thinning treatments may be a concern for amphibians, especially when treatments include the piling of existing woody debris. We found no amphibians using slash piles as cover in the year these piles were created. However, slash piles often sit for multiple years prior to burning, during which time they could be colonized by amphibians. In addition, the timing of pile burning may be tied to weather conditions that are particularly conducible to amphibian surface activity (e.g., fall rain events).

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f16071059/s1, the Supplementary_File_Descriptions document contains descriptions of the remaining supporting files.

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