



Experimental evidence indicates variable responses to forest disturbance and thermal refugia by two plethodontid salamanders

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ABSTRACT

Understanding how natural and anthropogenic disturbances affect sensitive species is critical to support conservation programs as land use activities and climatic conditions change. Forest management provides a range of ecosystem services to expanding human populations including production of substantial amounts of woody biomass, thereby reducing area under management and increasing opportunity for conservation designations. However, relatively little experimental information is available to describe how manipulating habitat at multiple scales may affect spatial and temporal variation in populations of climate-sensitive forest taxa. We conducted a Before-After Control-Impact experiment over seven years to evaluate responses of two species of Plethodontid salamanders in operational treatment (harvest, replanting, and herbicide application) and control units, Oregon, USA. In addition, we capitalized on existing variation in downed wood size and accounted for potential behavioral responses to evaluate the thermal refugia hypothesis. For Oregon slender salamanders (*Batrachoseps wrighti*), mean plot-level occupancy (90% CRI) was increased an estimated 11% (1.11; 0.62–2.1) and estimated mean abundance reduced 16% (0.84; 0.54–1.4) post-harvest. For *Ensatina* (*Ensatina eschscholtzii*), mean occupancy was reduced an estimated 80% (0.20; 0.08–0.47) and estimated mean abundance reduced 63% (0.37; 0.22–0.65) post-harvest. We found strong evidence of positive associations for both species with downed wood amount. As predicted, we found ambient temperatures to be higher in harvest than control units. Also, internal downed wood temperatures were warmer in harvested units, suggesting these structures may not have provided adequate thermal refugia. Application of an experimental framework provided evidence about both stand and structure level responses to active management. Habitat structures did not appear to buffer against substantial variation in local climate but evidence was equivocal about importance of these structures to population retention. Monitoring of recruitment and retention of downed wood through subsequent rotations can provide critical information to reduce trade-offs between wood production and conservation of climate sensitive taxa.

1. Introduction

Forests are vital reservoirs of biological diversity and provide essential services, including carbon sequestration and woody biomass, to expanding human populations (Meyfroidt and Lambin, 2011; Food and Agriculture Organization of the United Nations, 2012). Active management of forest ecosystems can alter abiotic and biotic factors, fragment landscapes, and lead to novel species assemblages. However, active management provides the opportunity to allocate required habitat features at different scales to support wildlife populations with low dispersal rates and high sensitivity to local climate. Given the prominent role of intensification in meeting global demand for forest

products (Meyfroidt and Lambin, 2011), and the challenge of maintaining supply under novel climatic variation, experimental evaluations of management effects on biodiversity and other ecosystem services are critically important (Bennett et al., 2009; Mace et al., 2012).

Altered vegetation diversity and structural complexity in intensively managed forests can reduce system capacity to withstand harvest- and climate-driven variation in temperature and precipitation (Semlitsch et al., 2009). The *thermal refugia hypothesis* posits that habitat structures can buffer species against temperature variation and are particularly important in the early stages of forest regeneration when dispersal limited species are exposed to novel, or more extreme, abiotic conditions (deMaynadier and Hunter, 1998; Chen et al., 1999; Hilmers et al.,

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2018). Structural components, such as leave trees or downed wood, can mitigate negative harvest impacts when they occur by providing refugia as units regenerate (Otto et al., 2013b). Coarse woody debris, primarily downed logs, is monitored under sustainable management guidelines and best practices (Objectives 4.1, 4.2, and 4.4; Sustainable Forestry Initiative, 2010; Forest Guild Pacific Northwest Biomass Working Group, 2013) and regulated under state forest practice rules in some regions (Cloughesy and Woodward, 2018). However, guidelines for efficient wood utilization, shorter rotation lengths, and worker safety requirements may reduce amounts, sizes and types of downed wood retained over time (Bunnell and Houde, 2010; Fletcher et al., 2011; Kroll et al., 2012). As a result, quantifying microclimate refuge capacity of coarse woody debris for forest-associated species can guide spatial and temporal allocation of these resources.

Amphibian species can be indicators of ecosystem health given their reliance on specific moisture and temperature characteristics (Davie and Welsh, 2004). For example, terrestrial salamanders can be sensitive to anthropogenic disturbance including timber harvest (Semlitsch et al., 2009; Homyack and Kroll, 2014). Douglas-fir production forests in western Oregon, USA, provide habitat for a diverse group of Plethodontid species including the endemic Oregon Slender (*Batrachoseps wrighti*) and Ensatina salamanders (*Ensatina eschscholtzii*) and are globally important sources of wood (Haynes, 2003). Although Ensatina are widespread and relatively well-studied, Oregon Slender salamanders have received less research attention due to restricted geographic distribution and reduced seasonal surface-activity (Vesely, 1999). Previous work suggests a strong association between this species and downed wood structures that reduce desiccation, provide escape cover, and enhance dispersal (Vesely, 1999). Due to concern over forest harvest effects, Oregon slender salamanders are classified as a G2/G3 species (Imperiled/Vulnerable; NatureServe) and are being considered for listing under the Endangered Species Act (<https://ecos.fws.gov/ecp0/profile/speciesProfile?slid=913>).

We conducted a seven-year, randomized experiment to quantify the role of forest harvest on occupancy and abundance of plethodontid salamanders in the Cascade Range, OR, USA. We evaluated treatment effect size using control (no harvest) and harvest (standard practices including clearcutting, planting of Douglas-fir seedlings, and herbicide applications) units. We expected negative harvest effects on Oregon slender salamanders given their strong association with mature forest conditions (Bury and Corn, 1988; Gilbert and Allwine, 1991). However, we did not predict negative effects for Ensatina due to the species' presence in a broad range of habitat types and successional stages throughout its geographic range (Olson and Kluber, 2014). Similarly, we predicted that downed wood acts as a thermal refuge for salamanders. As such, we predicted ambient temperatures would be higher in harvested than control units but that temperatures within downed wood would not differ substantially across treatments and should be cooler than ambient temperatures. We expected strong positive associations between downed wood amount and occupancy and abundance of Oregon slender and Ensatina salamanders. We interpret support for the thermal refugia hypothesis as evidence that coarse woody debris is a critical habitat element for both species and potentially associated with population performance.

2. Methods

2.1. Study area

In cooperation with private and state landowners, we established 88 harvest units with an average size of 32.5 ha (SD: 17.4; range: 8.1–129 ha) in the Cascades, Oregon, USA (Fig. S1). Units were in the western hemlock zone (Franklin and Dyrness, 1973) at an average elevation of 588 m (SD: 205 m; range: 160–1045 m). Climate consists of cool, wet winters and mild, dry summers. Douglas-fir (*Pseudotsuga menziesii*) saplings, with minor components of grand fir (*Abies grandis*),

western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*), dominate tree plantations in the region. Common broadleaf species include California hazelnut (*Corylus cornuta* sub-spp. *californica*), ocean-spray (*Holodiscus discolor*), vine maple (*Acer circinatum*), big-leaf maple (*Acer macrophyllum*), cascara (*Rhamnus purshiana*), salmonberry (*Rubus spectabilis*), red alder (*Alnus rubra*), *Vaccinium* spp., salal (*Gaultheria shallon*), and Oregon grape (*Mahonia nervosa*). Numerous native and non-native plants occur in units with swordfern (*Polystichum munitum*) and brackenfern (*Pteridium aquilinum*) as the dominant species.

2.2. Experimental treatments

We selected 88 units randomly from the harvest plans of Weyerhaeuser, Port Blakely Tree Farms, Oregon Department of Forestry, and Bureau of Land Management for the experiment. Units were in two broad geographic blocks within the geographic range of Oregon slender and Ensatina salamanders (Fig. S1). To be included, units had to be greater than five ha in size, been harvested > 45 years previously, and have verified occurrence of Oregon slender salamanders. We conducted preliminary surveys to confirm Oregon slender salamander presence on all units. After harvest, units were replanted with Douglas-fir seedlings and received herbicide treatments to control herbaceous and woody vegetation (see Kroll et al., 2017 for an example of applications and timing). All study units were 2nd growth forests, allowing us to capitalize on existing variation in legacy habitat structures to evaluate predictions from the thermal refugia hypothesis.

2.3. Sampling

We began pre-harvest sampling in 2013. We note that we sampled only a portion of the units in the first year and that units were harvested in different years (Table 1). Each year, we sampled all units except those harvested within the previous 12 months (due to active regeneration efforts). The first surveys of harvested units occurred in 2015 (Table 1). During daylight hours each year from April–June, we sampled seven 81 m² plots selected randomly in each unit. We assigned a random starting point as the center for a single 81 m² plot. After the first plot was identified, six additional plots were established in a random direction with 40 m between them. We searched plots in three sequential 10 min intervals to estimate individual capture probabilities for each species (Kroll et al., 2015). During each 10 min interval, one observer searched the plot and we switched observers during each sequential 10 min interval. We used a “removal sampling” design: once both species were detected in a plot, additional 10 min sampling intervals for that plot did not occur. Observers used a light touch sampling protocol in which cover objects were returned to their original position and disturbance to habitat features, such as decayed logs, was minimized. During sampling, an observer counted coarse woody debris based on length (1–5, 6–15, > 15 m), width (large end; 25–50, > 50 cm), and decay (none, Stage 1, and Stage 2) classes (Maser and Trappe, 1984). In addition, an observer recorded abiotic variables, including air temperature, soil moisture (at each of four points within

Table 1

Number of total experimental units and harvested units surveyed for Oregon slender and Ensatina salamanders by year, Cascades, Oregon, USA, 2013–2019.

Year	Total units surveyed	Harvested units surveyed
2013	60	0
2014	56	0
2015	61	12
2016	76	22
2017	76	33
2018	78	41
2019	83	49

each plot), and date. We selected new plots each year to eliminate the possibility of confounding sampling and treatment effects on salamanders (Otto et al., 2013a; Kroll et al., 2015).

In 2016 and 2017, we deployed passive recorders to capture ambient and internal woody debris temperatures. We installed three temperature loggers (HOBO H8 Pro Series; Onset, Bourne, MA) in twelve units (six harvest, six control) to record data at 60-minute intervals from April–August. Within units, we selected randomly three downed logs > 30 cm in diameter and > 185 cm in length and inserted temperature loggers (TidbiT MX Temperature Data Logger; Onset, Bourne, MA) ~ 7.5–10 cm inside the approximate center of the log to record internal temperatures at hourly intervals from April–July. Due to decomposed state of logs, units could be pushed into wood or under bark plates. We bench-tested all temperature loggers prior to deployment. To compare temperatures at the harvest unit and downed log scale to regional temperatures, we downloaded data from the closest regional weather station (Stayton, OR; <https://www.usclimatedata.com/climate/stayton/oregon/united-states/usor0332>). At all three scales, we calculated the average (SD) high temperature for each day in April–June in 2016 and 2017 and for 2016 and 2017 combined.

Finally, we were interested in the relationship between total monthly precipitation and individual capture probability for both species. Plethodontid salamanders are lungless and require moist, moderate micro-climates. As such, we predicted both species were more likely to be active during periods of higher precipitation (Nussbaum et al., 1983; Connette et al., 2015). To evaluate this relationship, we calculated total precipitation for April–June annually with data from the Stayton, OR, weather station. We did not have unit-specific estimates of total precipitation and so could not model the relationship directly. Instead, we plotted model estimates of individual capture probability by month, year, and species against total monthly precipitation in each year.

2.4. Analysis

Our objective in formulating statistical models was to estimate patterns of occupancy and abundance associated with the treatment structure of this study while accounting for the experimental design and adjusting for imperfect detection based on captures of unmarked individuals. Our occupancy model used a modification of the MacKenzie model (MacKenzie et al., 2002) that follows closely from the “hierarchical single-scale model” described in Kroll et al. (2015). We used a similar approach to model abundance, applying an extension of the Royle-Nichols model (Royle and Nichols, 2003) for estimating abundance from presence-absence data.

For the occupancy model, we let Z_{ijk} denote the occupancy of plot k in year j from harvest unit i , which takes the value of 1 when the plot is occupied and 0 otherwise. We assume that plot-level occupancy follows a Bernoulli distribution $Z_{ijk} \sim \text{Bern}(\psi_{ijk})$ where ψ_{ijk} is the probability that plot k of harvest unit i during year j is occupied. Within-plot occupancy is assumed to be closed across all visits within a year. We let y_{ijkl} denote the detection status of plot k from harvest unit i during year j and visit l , taking the value of 1 when the species is detected and 0 otherwise. We considered species detection to also follow a Bernoulli distribution $y_{ijkl} \sim \text{Bern}(Z_{ijk} \cdot p_{ijk})$ with detection probability p_{ijk} , conditional on plot occupancy.

We parameterized the occupancy probability model based on the treatment and design structure, with main effects for block (north and south blocks) and year, and a harvest-unit random intercept. We allowed the occupancy probability of treatment and control sites to differ in both the pre- and post-harvest periods with separate treatment-unit fixed effects in each period. The difference in these terms provides an estimate of the putative harvest effect on occupancy probability. In addition to the design-based terms, we include a plot-level covariate for downed wood count, as prior results found this covariate to be associated with Oregon slender salamander occupancy (Kroll et al., 2015).

The mean occupancy model for both Oregon slender and Ensatina occupancy probability was:

$$\begin{aligned} \text{logit}(\psi_{ijk}) = & \beta_{0i} + \beta_1 \text{Block}_i + \beta_2 2014_{ij} + \beta_3 2015_{ij} + \beta_4 2016_{ij} + \beta_5 2017_{ij} \\ & + \beta_6 2018_{ij} + \\ & \beta_7 2019_{ij} + \beta_8 \text{Pre-Treatment}_{ij} + \beta_9 \text{Post-Treatment}_{ij} \\ & + \beta_{10} \text{Downed Wood}_{ijk} \end{aligned} \quad (1)$$

We parametrized the detection probability for occupancy as a quadratic function of air temperature. We included random effects for all detection coefficients to allow the association with temperature to vary by year, thus allowing for different trends in pre-harvest and post-harvest control plots:

$$\begin{aligned} \text{logit}(p_{ijk}) = & \alpha_{0j} + \alpha_{1j} \text{Post-Treatment}_{ij} + \alpha_{2j} \text{Air Temperature}_{ijk} \\ & + \alpha_{3j} \text{Air Temperature}_{ijk}^2 + \\ & \alpha_{4j} \text{Post-Treatment}_{ij} \cdot \text{Air Temperature}_{ijk} + \alpha_{5j} \text{Post} \\ & - \text{Treatment}_{ij} \cdot \text{Air Temperature}_{ijk}^2 \end{aligned} \quad (2)$$

Salamander abundance was modeled from the same repeated presence-absence detections used for occupancy by assuming the probability of detecting occupancy on a sampling unit can be expressed as a function of plot-level abundance, N_{ijk} , and individual detection probability θ :

$$p_{ijk} = 1 - (1 - \theta)^{N_{ijk}} \quad (3)$$

We further assumed that abundance varied among sites according to a Poisson distribution, such that $N_{ijk} = \text{Poisson}(\lambda_{ij})$. Under these assumptions, we account explicitly for heterogeneity in occupancy detection due to variation in abundance (Royle and Nichols, 2003). The model for mean plot-level abundance followed a similar structural form to the model used for occupancy probability except the logit-link was replaced with a log-link:

$$\begin{aligned} \log(\lambda_{ijk}) = & \beta_{0i} + \beta_1 \text{Block}_i + \beta_2 2014_{ij} + \beta_3 2015_{ij} + \beta_4 2016_{ij} + \beta_5 2017_{ij} \\ & + \beta_6 2018_{ij} + \\ & \beta_7 2019_{ij} + \beta_8 \text{Pre-Treatment}_{ij} + \beta_9 \text{Post-Treatment}_{ij} \\ & + \beta_{10} \text{Downed Wood}_{ijk} \end{aligned} \quad (4)$$

We modeled individual detection probability θ using the same covariate structure as Eq. (3) and included random effects for model coefficients to allow the association between individual detection probability and temperature to vary by year:

$$\begin{aligned} \text{logit}(p_{ijk}) = & \alpha_{0j} + \alpha_{1j} \text{Post-Treatment}_{ij} + \alpha_{2j} \text{Air Temperature}_{ijk} \\ & + \alpha_{3j} \text{Air Temperature}_{ijk}^2 + \\ & \alpha_{4j} \text{Post-Treatment}_{ij} \cdot \text{Air Temperature}_{ijk} + \alpha_{5j} \text{Post} \\ & - \text{Treatment}_{ij} \cdot \text{Air Temperature}_{ijk}^2 \end{aligned} \quad (5)$$

We fit both the occupancy and abundance models in a Bayesian framework. We chose prior probabilities for model parameters to allow for a broad range of species responses. Each model was fit using MCMC in JAGS (Plummer, 2003) by running four chains of 10,000 iterations each, after a 1000 sample burn-in and 1/10 thinning. We assessed model convergence with R-hat values and visual inspection of the MCMC chains, and model fit using posterior predictive checks (Gelman et al., 2004). JAGS code for models, including prior distributions, is in Appendix S1. We used 90% credible intervals to indicate a likely range for the parameters (Kroll et al., 2016; Kozma et al., 2017).

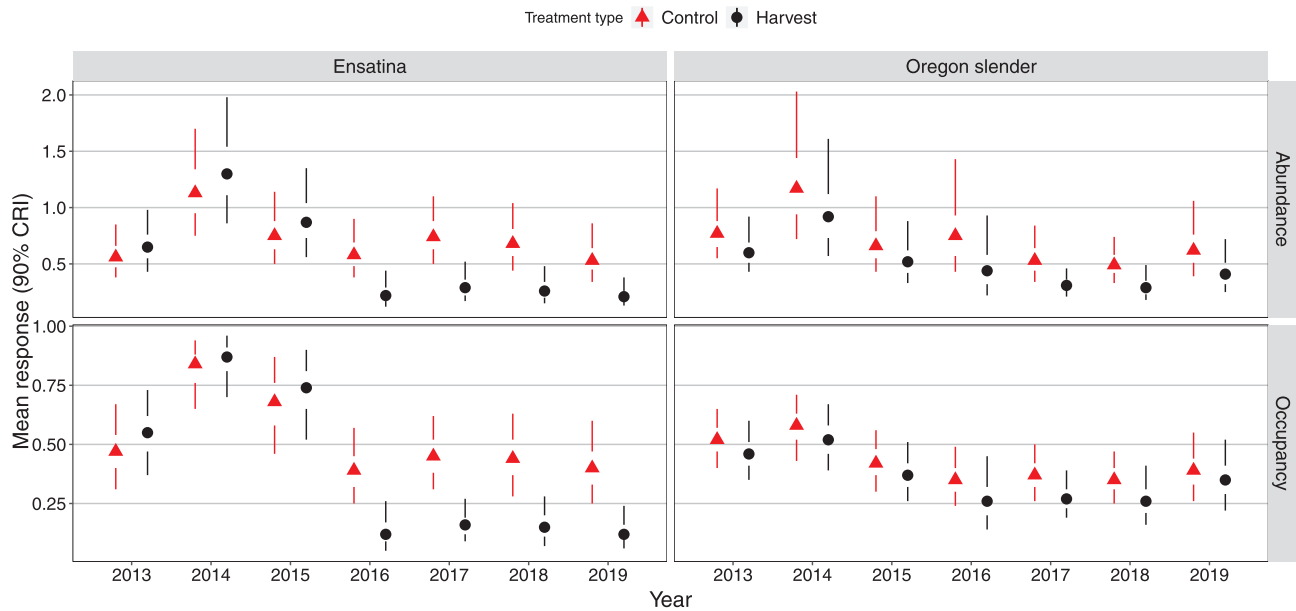


Fig. 1. Abundance and occupancy estimated responses for *Ensatina* and Oregon Slender salamanders by treatment and year, Cascades, Oregon, USA, 2013–2019. For each estimate, the 50% (inner ends of vertical lines) and 90% credibility intervals (outer ends of vertical lines) are displayed. For display purposes, 2013–2015 are based on pre-treatment occupancy and abundance estimates while 2016–2019 are based on post-treatment estimates.

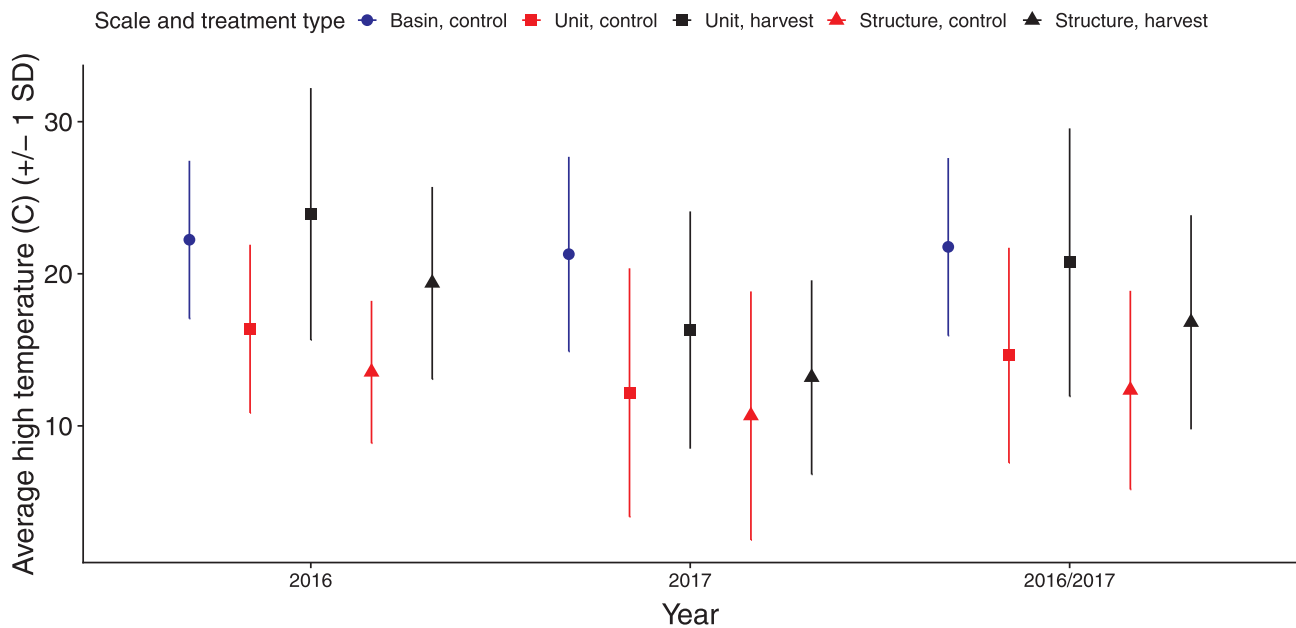


Fig. 2. Average high temperature from April–June by year (2016 and 2017) or averaged across years (2016–2017) at three scales: basin, experimental unit, and structure (downed logs), Cascades, Oregon, USA, 2016–2017. At the basin scale, only controls exist. Basin data are from the Stayton, Oregon, USA, weather station (<https://www.usclimatedata.com/climate/stayton/oregon/united-states/usor0332>).

3. Results

We captured 615 *Ensatina* and 923 Oregon slender salamanders with an average (standard deviation; SD) of 0.18 (0.48) and 0.27 (0.62) individuals captured per plot, respectively. We detected at least one salamander of either species on 29% of the plots. Over seven years, we detected *Ensatina* only, Oregon slender salamanders only, or both species on 8%, 14%, and 6% of the plots. The maximum number of individuals detected on a single plot were three *Ensatina* and four Oregon Slender salamanders. Between 2013 and 2019, 86/88 (98%) units had at least one Oregon slender salamander; 85/88 (97%) units had at least one *Ensatina*; and 87/88 (99%) units had at least one

Oregon slender or *Ensatina* salamander.

In contrast to our predictions, we found evidence (non-overlapping post-harvest credible intervals) of a negative harvest effect on *Ensatina* and a lack of clear evidence for a harvest effect on Oregon slender salamanders (Fig. 1). For Oregon slender salamanders, estimated average plot-level occupancy (90% CRI) was 0.42 (0.35–0.51) and 0.45 (0.30–0.62) in control and harvested units, respectively; average plot-level abundance was 0.69 (0.54–0.88) and 0.58 (0.37–0.97). For *Ensatina*, estimated average occupancy was 0.57 (0.43–0.71) and 0.21 (0.10–0.39) in control and harvested units, respectively; average abundance was 0.66 (0.48–0.91) and 0.25 (0.15–0.43).

We found that the estimated mean odds of occupancy (90% CRI) for

Oregon slender salamanders was 11% higher (1.11; 0.62–2.1) in the post-harvest period compared with the pre-harvest period, after adjusting for imperfect detection and pre-post changes in control unit occupancy probabilities. Correspondingly, we estimated a 16% reduction in mean abundance (0.84; 0.54–1.4) after adjusting for control unit changes and imperfect detection. For *Ensatina*, mean odds of occupancy was estimated to be 80% lower (0.20; 0.08–0.47) and mean abundance 63% lower (0.37; 0.22–0.65) on harvest units in the post-harvest period, after adjusting for temporal changes in control units and imperfect detection. For both species, occupancy and abundance on control units were generally higher in 2013–2015 than 2016–2019 (Fig. 1). We note that effect estimates and inference for the occupancy models are given on the odds-scale due to the use of a logit-link function in our modeling.

We calculated temperature differences between treatment types and found ambient April–July temperatures were 19% higher in harvested units than in control units (Fig. 2). Average temperatures were 14% and 23% warmer in 2016 than in 2017 for control and harvest units, respectively. Annual variation in control and harvest units did not resemble variation at the Stayton station (Fig. 2). We note that 2016 appeared to be the warmest year of the study (Fig. S2).

We found treatment differences for within structure temperatures. April–July temperatures within downed logs were, averaged across daily highs, 15% higher in harvested units than in control units (Fig. 2). Average daily high temperatures within downed logs were 10% and 20% warmer in 2016 than in 2017 for control and harvest units, respectively.

Across treatments, we found evidence of a positive association between occupancy and abundance of Oregon slender and *Ensatina* salamanders with downed wood count (Fig. 3). For Oregon slender salamanders, the model estimates indicated an expected 1.2 (90% CRI: 1.1, 1.3) times greater odds of occupancy for each unit difference in wood

count and a 1.08 (90% CRI: 1.05, 1.10) times higher abundance for plots with a unit higher count in downed wood. Similarly, for *Ensatina* salamanders, the model estimates indicated an expected 1.1 (90% CRI: 1.0, 1.2) times greater odds of occupancy for each unit difference in wood count and a 1.06 (90% CRI: 1.03, 1.09) times higher abundance in plots for each unit difference in downed wood. We sampled an average (SD) of 3.1 (2.5) and 3.6 (3.1) pieces of downed wood on control and harvested plots, respectively.

For both species, we did not find evidence of an association (based on over-lapping credibility intervals) between individual capture probabilities and ambient air temperature at time of sampling (Fig. 4). In addition, we did not find evidence of higher capture probabilities for Oregon slender salamanders than *Ensatina* in either control or treatment units (Fig. 4). Using among-year random effect means (β_{0i} , α_{0j}) and median air temperature, estimated individual capture probabilities (90% CRI) for *Ensatina* on control and treatment plots were 0.10 (0.07, 0.13) and 0.10 (0.04, 0.21), respectively. For Oregon slender salamanders, estimated probabilities were 0.13 (0.06, 0.24) and 0.16 (0.11, 0.23) for control and treatment plots, respectively.

In general, total monthly precipitation declined in each year across the three months in which we sampled plethodontid salamanders (Fig. 5). However, we did not find consistent relationships between total monthly precipitation and individual capture probabilities for either species. For example, we found that capture probabilities and total monthly precipitation were associated positively for Oregon slender salamanders in 2015 but in other years clear relationships did not exist (Fig. 5). Similarly, we did not find any variation in capture probabilities for *Ensatina* in 2015–2019 and inconsistent relationships in 2013 and 2014.

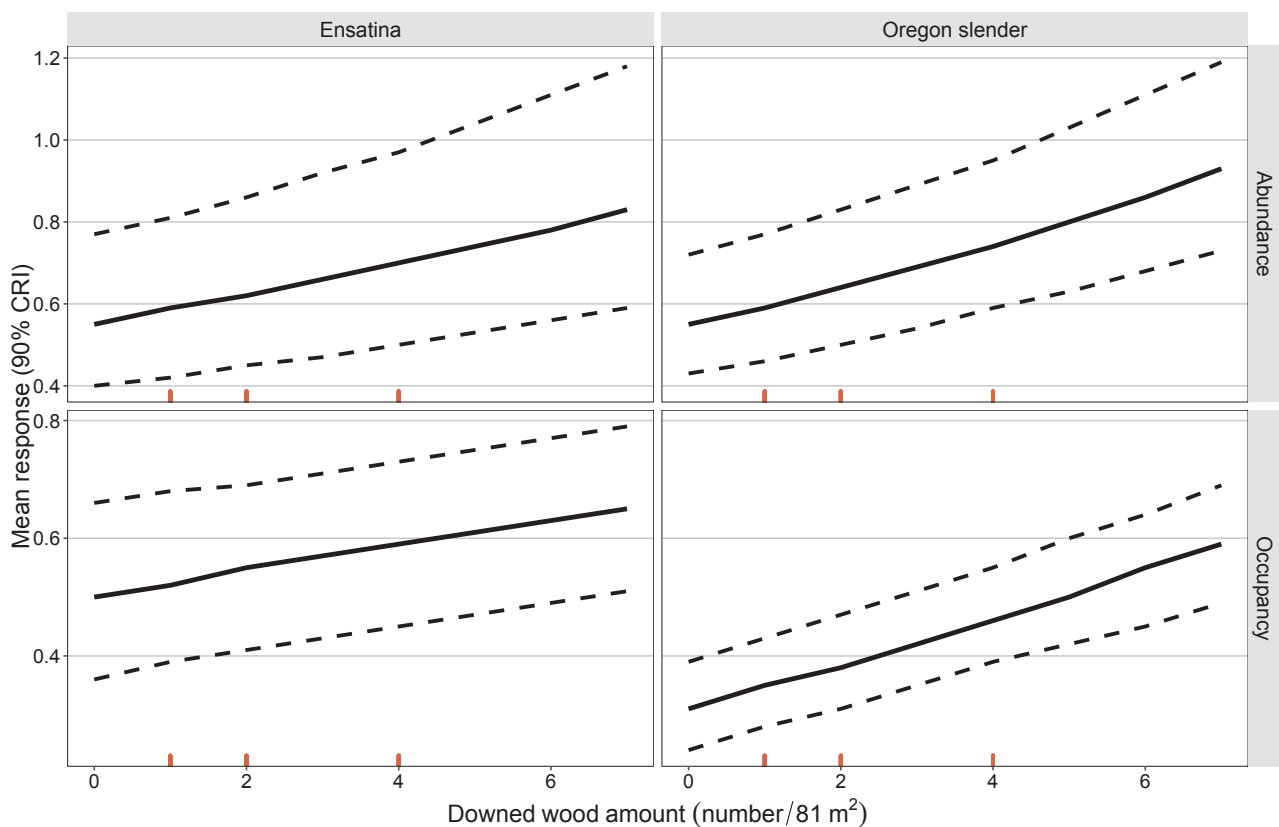


Fig. 3. Estimated association between estimated abundance and occupancy for *Ensatina* and Oregon Slender salamanders and downed wood count at the plot level, Cascades, Oregon, USA, 2013–2019. The rug plot shows the median and 25% and 75% quartiles of downed wood count.

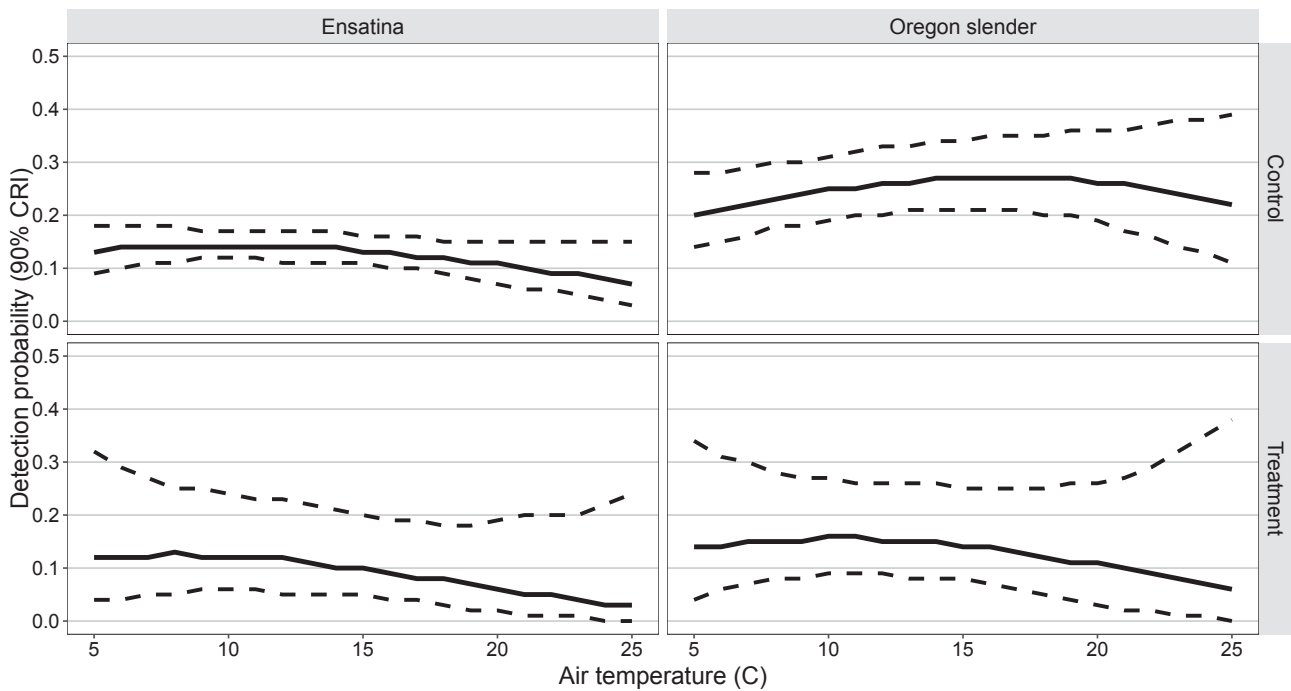


Fig. 4. Estimated association between air temperature at time of sampling and detection probabilities (probability of detecting at least one individual) for Ensatina and Oregon Slender salamanders by treatment, Cascades, Oregon, USA, 2013–2019.

4. Discussion

We present evidence from a manipulative experiment to indicate variable effects of timber harvest on occupancy and abundance of two plethodontid salamanders in Douglas-fir plantations. Contrary to our predictions, we found relatively strong evidence of negative harvest effects on occupancy and abundance of Ensatina salamanders. After accounting for uncertainty in our estimates, our model results indicate a drop in the odds of Ensatina occupancy of 50% or more, corresponding to a reduction in mean plot-level occupancy from approximately 57% pre-harvest to a likely range of 8–37% post-harvest. We did not find

clear evidence of a harvest effect on Oregon slender salamander occupancy and abundance. Results from occupancy and abundance models suggest relatively small harvest impacts; however, our estimates do not preclude modest increases or decreases in post-harvest populations. The estimated odds ratio of 1.11 (0.62–2.1) corresponds to a post-harvest plot-level mean occupancy range of 31%–60%, given a pre-harvest plot occupancy rate of 42%. Although a harvest-driven decrease in plot-level occupancy of approximately 10 percentage-points is consistent with our data, so too were increases of up to 20 percentage-points. Our results suggest that it is unlikely that the Oregon slender salamander experienced the level of impact observed for Ensatina over the time period of

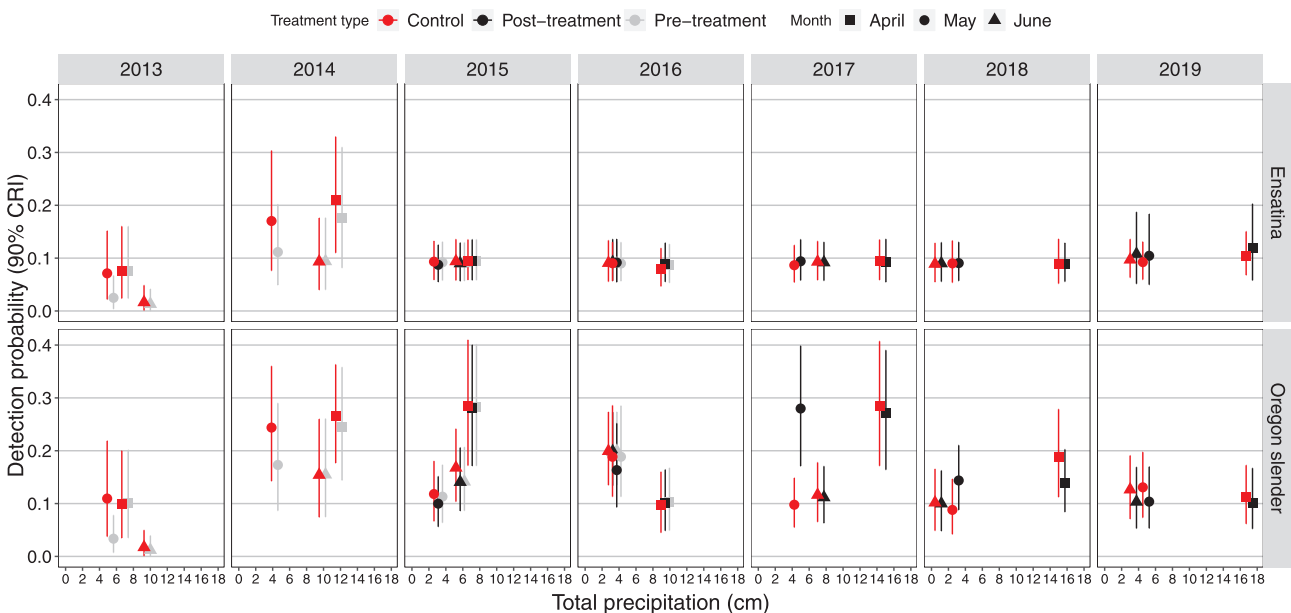


Fig. 5. Individual capture probabilities (based on counts of unmarked individuals) by species as a function of total monthly precipitation for control and treatment units, Cascades, Oregon, USA, 2013–2019. We separated treatment units (units to be harvested eventually) into pre- and post-treatment. Symbols are dodged for over-plotting: in each year, total monthly precipitation does not differ in each month for control, post-treatment, and pre-treatment units.

this study.

Species differences in occupancy and abundance across control and harvest treatments may be a function of habitat selection and dispersal ability. *Ensatina* salamanders have larger dispersal distances relative to Oregon slender salamanders (Miller et al., 2005; Olson and Kluber, 2014) and, in fragmented landscapes, will choose patches with higher vegetation cover (Rosenberg et al., 1997). As such, habitat disturbance could initiate *Ensatina* emigration from harvested plots. In the southeastern United States, Todd et al. (2009) found that ambystomatid salamanders in forests were more likely to emigrate from a clear-cut patch rather than immigrate into one. Further, soil moisture and temperature can be predictors of plethodontid occurrence (Farallo and Miles, 2016; Baecher and Richter, 2018). Canopy removal can cause substantial variation in surface and soil temperature and moisture conditions in harvested units (Harper and Guynn, 1999; Homyack et al., 2011; Otto et al., 2013b) and may increase the likelihood of individuals dispersing into adjacent plots, using thermal refugia such as downed logs, or retreating underground. Therefore, the reliance of *Ensatina* and Oregon Slender salamanders on local coarse woody debris may contribute strongly to their conservation status and persistence in these managed landscapes.

We found mixed support for the thermal refugia hypothesis. First, at the unit scale (large scale), we found that, relative to controls, harvested units had higher average temperatures in the first two years post-harvest. We also found that average temperatures within downed logs (small scale) were lower compared to ambient temperatures in the units. Contrary to our prediction, downed wood temperatures were higher in harvest units than in control unit (Fig. 2), most likely due to complete removal of canopy cover. However, these structures were still cooler than ambient temperatures within harvested units. Additional information is needed to understand relationships between downed wood size and thermal refuge potential. Salamanders are ectothermic poikilotherms and changes in micro-climatic temperatures are likely to affect physiological processes such as metabolism and respiration (Rome et al., 1992). If larger structures buffer temperature changes better than smaller downed logs, they may harbor more salamanders. The positive associations between downed wood and estimates of occupancy and abundance suggest that these structures are important habitat elements for both species. Additional information is needed to understand the complex relationships between downed wood size and thermal refuge potential.

The lack of evidence for a strong negative harvest effect on Oregon slender salamanders suggests several alternatives: thermal refugia were adequate; other thermal refugia (e.g., sub-surface locations) were available and used in addition to or instead of downed wood; or individuals were resilient for at least 4 years to fluctuations in temperature and soil moisture conditions. Given the widespread occurrence of Oregon slender salamanders in 2nd growth units created by harvest, all three of these alternatives are likely to influence occupancy and abundance patterns. In contrast, we found fewer *Ensatina* in harvested units relative to controls. If thermal refugia are critical to maintain populations of *Ensatina*, adequate amounts of these features may not have been present. This difference in responses across species may be a function of regeneration practices: specifically, herbicide applications to reduce competing vegetation. Herbicides will alter vegetation cover and species composition dramatically but not affect downed wood and salamanders therein (Kroll et al., 2017). We often detected *Ensatina* either on the ground or under vegetation, while Oregon slender salamanders were found almost exclusively under bark plates or moss mats on downed logs. Collectively, harvest and regeneration effects may have decreased habitat suitability for *Ensatina* salamanders and caused short-term declines in occupancy and abundance. However, we note that, in a study of plethodontid salamander responses to a forest fire, Chelgren et al. (2011) found occupancy probabilities were > 90% for *Ensatina* in both burned and unburned plots while Oregon slender salamander occupancy was twice as great in unburned plots. Whether

these results, from a study conducted due south of our study area in the Oregon Cascades, are indicative of variable responses to natural vs. anthropogenic disturbances, or reflect variation in local population sizes and behavior, is a question that merits additional investigation.

We cannot dismiss the possibility that *Ensatina* used sub-surface habitat more frequently in harvest units than controls, and could be present but unavailable (Chelgren et al., 2011). Use of sub-surface habitat by Plethodontid salamanders is well-documented (Davies and Welsh, 2004) including in response to anthropogenic and natural disturbances (Zalisko and Sites, 1989; Pilliod et al., 2003). For *Ensatina*, changes in occupancy and abundance could represent behavioral responses rather than absolute changes in the population size or shifts in distribution (Kroll et al., 2009). Importantly, equivalent capture probabilities in both control and harvest units indicate an ecological response and not sampling variation (Fig. 5).

In our study, we found negative annual trends in occupancy and abundance estimates for both species regardless of harvest condition. We cannot attribute this temporal decline across experimental treatments to annual variation in either precipitation or temperature (Figs. 5 and S2). Emigration from the plot due to sampling-induced habitat disturbance is also unlikely as individual plots were repeatedly sampled during a single visit each season (Chelgren et al., 2011). Further exploration of more detailed climate variables or other covariates may provide associative evidence to explain these declines.

Similar to other studies of plethodontid salamanders, we found evidence for both abiotic and biotic variation in capture probabilities (Bailey et al., 2004b; Kroll et al., 2009; Roloff et al., 2011). We did not find strong associations between capture probabilities for either species and harvest treatment or air temperature at the time of sampling (see Chelgren et al., 2011 for a different result). Also, we did not find an association between monthly total precipitation and capture probabilities despite the oft-noted tendency of plethodontid salamanders to be surface active when favorable moisture and temperature conditions prevail (Bailey et al., 2004a). Unsurprisingly, capture probabilities for Oregon slender salamanders were higher in control units where intact canopies kept ambient temperatures and temperatures within downed wood lower than those in harvest units. However, we did not find a similar effect for *Ensatina*. Finally, we reiterate that our sampling design eliminated confounding between treatment and sampling effects. We urge other investigators to consider design-based rather than model-based solutions to the problem of potential confounding of sampling and treatment variation for sensitive taxa such as plethodontid salamanders.

Despite needing to characterize thermal refugia across a broader range of wood sizes, decay classes, and soil layers, we emphasize that both species were associated positively with amount of downed wood. Current forest management practices regulate downed wood retention based on size and spatial distribution (Cloughesy and Woodward, 2018). Downed wood is habitat for numerous forest-associated species and adequate types and amounts of downed wood are critical to retain species after timber harvest (Bunnell and Houde, 2010). Our experiment found occupancy and abundance for both salamander species were associated positively with amount of coarse woody debris. Quantity and quality of coarse woody debris may therefore regulate salamander population dynamics over time by maintaining temperature and moisture refugia conditions through the early successional stages of forest regeneration. Although we do not know if the amount of downed wood will retain populations as units regenerate, we emphasize that all units in our study had confirmed populations of Oregon slender salamanders and over 85% of the units had confirmed populations of *Ensatina* during preliminary surveys. These results indicate that both species were retained after previous harvests, recolonized units as suitable habitat developed over time, or colonized units after harvest (i.e., the species was not present before harvest). However, we emphasize that previous harvests were of mature forest stands and, frequently, these harvests produced a large amount of coarse woody debris in

various size classes. Whether contemporary management prescriptions produce downed wood of similar quality and quantity as previous management, and how underlying demographics of salamander populations vary in response, are questions that require additional monitoring to resolve.

CRedit authorship contribution statement

Tiffany S. Garcia: Conceptualization, Methodology, Investigation, Writing - review & editing, Supervision, Project administration, Funding acquisition. **Josh Johnson:** Conceptualization, Methodology, Investigation, Data curation, Supervision, Project administration. **Jay Jones:** Software, Validation, Formal analysis, Writing - review & editing. **Andrew J. Kroll:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - review & editing, Visualization, Supervision, Funding acquisition.

Declaration of Competing Interest

A.J. Kroll, Josh Johnson, and Jay Jones are employed by Weyerhaeuser, which provided some funding to undertake and publish the research.

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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.2020.118045>.

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