



Herbicide Application Improves Plethodontid Salamander Habitat Conditions in Regenerating Clear-cut Forests

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1 **Herbicide Application Improves Plethodontid Salamander Habitat Conditions in**
2 **Regenerating Clear-cut Forests**

3 **Sara E. Leslie**, Department of Biology, Mount Allison University, Sackville, NB, Canada;
4 Current: Faculty of Forestry, Department of Natural Resource Management, University of
5 British Columbia, Vancouver, BC, Canada; sara.leslie@student.ubc.ca

6 **Christopher B. Edge***, Natural Resources Canada, Canadian Forest Service, Fredericton, NB,
7 Canada; christopher.edge@nrcan-rncan.gc.ca

8 **Julia L. Riley**; Department of Biology, Mount Allison University, Sackville, NB, Canada;
9 jriley@mta.ca

10

11 *Corresponding Author: Christopher B. Edge (christopher.edge@nrcan-rncan.gc.ca)

12

13 Abstract

14 Forestry activities, including harvesting and herbicide application, alter both overstory
15 and understory vegetation communities, reshaping ecosystem structure and condition. These
16 changes likely impact wildlife sensitive to environmental change, such as the Eastern Red-
17 backed Salamander (*Plethodon cinereus*). We compared canopy cover, soil temperature, soil
18 moisture, soil pH, and salamander abundance across unharvested reference stands and clear-cut
19 harvest blocks treated and untreated with a glyphosate-based herbicide. Overall, reference stands
20 exhibited the highest canopy cover and soil moisture, and lowest soil temperature. Herbicide-
21 treated blocks showed decreasing soil temperature and increasing moisture with time since
22 harvest, whereas untreated blocks exhibited the opposite trend. Salamander abundance in
23 reference stands was 4 and 18 times higher than in herbicide-treated and untreated blocks,
24 respectively, and 3 times higher in herbicide-treated than untreated blocks. Greater canopy cover
25 and soil moisture in herbicide-treated blocks likely improve habitat suitability, promoting higher
26 salamander abundance compared to untreated blocks during forest regeneration. Our study
27 suggests that herbicide application in clear-cut forests may accelerate the recovery of
28 microhabitat conditions to preharvest levels, partially mitigating the impacts of harvesting on
29 forest specialists like salamanders. We emphasize the need for holistic approaches in forestry
30 management to sustain biodiversity and ecosystem integrity in increasingly changing landscapes.

31

32 **Keywords:** Acadian Forests, indicator, clear-cutting, forest ecology, forest management,
33 glyphosate-based herbicide, Plethodontid, lungless salamander, silviculture, reproduction

34

35 **Introduction**

36 The degradation, conversion, and fragmentation of habitats are some of the main causes
37 of biodiversity loss worldwide (Newbold et al. 2015). Reversing past impact, limiting future
38 impact, and potentially providing a benefit to forest habitats are considered within contemporary
39 forest management planning and silviculture (Jung et al. 2023). Forestry operations often involve
40 large-scale spatial disturbances and reshape forest dynamics, including age, structure,
41 composition, and both biotic and abiotic conditions (Kuuluvainen et al. 2021). The biotic and
42 abiotic changes that follow tree harvesting have a strong influence on the quality and quantity of
43 habitat for a variety of species, especially those that make use of interior forest habitat (Keenan
44 and Kimmins 1993). The direct (e.g., habitat loss) and indirect (e.g., changes to forest structure)
45 effects of forestry on biodiversity have led to calls for ecosystem-centered approaches to forest
46 management. Such approaches aim to balance timber harvesting with environmental
47 conservation, including ecological preservation (Venn 2023). In navigating towards this balance,
48 ecosystem-centered strategies must account not only for the impacts of harvesting and
49 subsequent regeneration but also for the modifications to forest structure induced by post-harvest
50 silvicultural interventions. Assessing these impacts requires reliable ecological indicators,
51 particularly species that are highly sensitive to environmental change and are closely linked to
52 forest ecosystem health.

53

54 Given the resource-intensive nature of evaluating multiple species, researchers often rely on
55 bioindicator species, which are living organisms used to assess and monitor the health and
56 quality of ecosystems or environments. The Eastern Red-backed Salamander (*Plethodon*
57 *cinereus*), a terrestrial lungless salamander common in the Acadian Forests of eastern North

58 America, is an ideal bioindicator due to its sensitivity to environmental changes, strong site
59 fidelity, high densities, and role in ecosystem processes (Welsh and Droege 2001; Davic and
60 Welsh 2004; Homyack and Haas 2009). These salamanders require cool and moist microhabitats
61 typically found under downed wood, rocks, and leaf litter for respiration and hydration (Petranka
62 2010). These requirements lead to their presence, abundance, and body condition being linked to
63 environmental gradients (e.g. soil temperature, moisture, and pH) and forest structure (Wyman
64 1988; Sugalski and Claussen 1997; McKenny et al. 2006; Homyack et al. 2010). As mid-level
65 consumers, they play an important role in maintaining ecosystem function and stability by
66 regulating nutrient cycling and balancing food webs (Davic and Welsh 2004; Hickerson et al.
67 2017). Given their sensitivity to changes in microhabitat conditions, Eastern Red-backed
68 Salamander populations are particularly vulnerable to disturbances that alter forest structure and
69 microclimates, such as forestry practices (deMaynadier and Hunter Jr. 1995).

70

71 A common forest harvest system in eastern Canada is the sequence of clear-cutting, replanting,
72 and herbicide application. Clear-cutting alters forest structure by removing the majority of tree
73 biomass, including standing dead trees, woody debris, and leaf litter, resulting in a more
74 homogenous landscape than naturally disturbed forests (Franklin et al. 2000). This loss of
75 structural complexity reduces available cover objects and increases exposure of moisture-
76 dependent species like salamanders to drier conditions, increasing desiccation risk (deMaynadier
77 and Hunter Jr. 1995; Tilghman et al. 2012; Ochs et al. 2022). Additionally, canopy removal
78 increases sunlight penetration, warming the forest floor, reducing humidity, and depleting leaf
79 litter—negatively impacting key habitat components for salamanders (Keenan and Kimmins
80 1993; Tilghman et al. 2012).

81 After clear-cut harvesting, many forest blocks are replanted with coniferous species and treated
82 with herbicides, primarily glyphosate-based, to suppress competing vegetation. Herbicide
83 application facilitates the early dominance of coniferous species by reducing the abundance of
84 deciduous and shrub vegetation, accelerating canopy closure (Wagner et al. 2006; Matute 2019).
85 The suppression on deciduous and shrub vegetation enhances the growth and survival of desired
86 tree species (Wagner et al. 2006); it also alters understory composition by reducing shrub
87 abundance and shifting plant communities towards perennials (De Lombaerde et al. 2021; Xiao
88 et al. 2024). These changes likely extend beyond the understory vegetation, potentially affecting
89 other environmental conditions that are critical to various flora and fauna habitats, such as soil
90 temperature, moisture, and pH. Thus, the combined environmental alterations resulting from
91 herbicide application and clear-cutting may lead to cascading, ecosystem-wide impacts on
92 biodiversity and habitat quality (Keenan and Kimmins 1993; deMaynadier and Hunter Jr. 1995;
93 Tilghman et al. 2012; Ochs et al. 2022).

94
95 However, herbicide application may partially offset the impacts of clear-cutting by reducing
96 competition from understory vegetation, accelerating overstory establishment, and promoting
97 earlier canopy closure and downed log accumulation during forest regeneration (Dempster
98 2022). Since closed canopies and downed logs are key components in salamander habitat,
99 providing cool and moist refugia that are especially valuable in harvested forests with limited
100 overstory (Kluber et al. 2009). Previous research has documented salamander populations
101 declining after clear-cutting, followed by gradual recovery as the forest regenerates (Tilghman et
102 al 2012; Ochs et al. 2022). However, there is limited research on the cumulative impact of clear-
103 cutting and herbicide use. The potentially diverging effects of clear-cutting and herbicide use on

104 important salamander habitat variables may lead to complex and interacting effects on
105 salamander populations.

106

107 The overall objective of this study was to examine the impacts of clear-cutting and herbicide use
108 on salamander populations by assessing both environmental factors (canopy cover, soil moisture,
109 temperature, and pH) and salamander-specific metrics across two scales: population-level effects
110 (abundance and reproductive activity) and individual-level effects (body condition). We
111 hypothesized that the removal of the herbaceous layer by glyphosate-based herbicides would
112 exacerbate the effects of canopy cover removal from clear-cutting on salamander habitat post-
113 harvest. We test the predictions that treating a clear-cut forest with glyphosate-based herbicides
114 will (1) alter environmental conditions through reduced canopy cover, reduced soil moisture,
115 increased temperature, and lower pH, (2) lower Eastern Red-backed Salamander abundance, (3)
116 lower body condition and increase presence of injuries (including autotomized tails potentially
117 due to increased predation), and (4) decrease the presence of gravid females and egg masses, and
118 lower the ratio of juveniles to adults within the population.

119

120 **Methods**

121 *Study Area*

122 The study was conducted in and around the Acadia Research Forest (ARF), located
123 approximately 25 km east of Fredericton, New Brunswick (46°00'00"N, 66°20'24"W). The ARF
124 encompasses 9000 ha of coniferous, deciduous, and mixed forests within the Grand Lake and
125 Eastern Lowlands Ecoregions (Swift et al. 2005). Although previous research suggests Eastern
126 Red-backed Salamanders exhibit a preference for deciduous and mixed wood forests over

127 coniferous habitats (Degraaf and Rudis 1990), our preliminary study confirmed their presence
128 across all three forest types in New Brunswick (see Supplementary Materials; Table S1).
129 Therefore, we selected a total of 20 blocks that were at least 3 ha in size and harvested by clear-
130 cutting between 5 and 26 years ago. All harvest blocks were planted with either a single
131 coniferous species or a mix of coniferous species (Balsam Fir (*Abies balsamea*), White Spruce
132 (*Picea glauca*), or Red Spruce (*Picea rubens*)) 1-3 years after harvest. Ten blocks did not receive
133 herbicide application (hereafter untreated), and ten were treated with a glyphosate-based
134 herbicide (hereafter treated). The treated blocks received an application of a glyphosate-based
135 herbicide 5-6 years after harvest applied by helicopter. Limited herbicide use has occurred within
136 the ARF, therefore treated blocks were located on crown land adjacent to the ARF (Figure 1).
137 We qualitatively observed that treated blocks were dominated by planted coniferous species
138 (height proportional to time since harvest) with sparse understory vegetation. In contrast,
139 untreated blocks were generally mixed wood, consisting of naturally regenerating deciduous and
140 coniferous species, along with planted conifers, and ground cover was characterized by some
141 woody debris, minimal leaf litter, and a dense herbaceous layer.
142
143 To serve as controls, we selected 10 unharvested forest stands in the ARF that have no harvest
144 history (Figure 1). These ecological reserve stands serve as reference conditions for the Acadian
145 Forest, providing insight into the expected forest composition and structure of harvested blocks
146 had they not undergone recent forestry practices (Mosseler et al. 2003). The control stands
147 contained a diverse mix of tree species, including boreal species such as Balsam Fir, Jack Pine
148 (*Pinus banksiana*), and White Spruce, as well as temperate species such as Sugar Maple (*Acer*
149 *saccharum*), Yellow Birch (*Betula alleghaniensis*), and Red Spruce. Ground cover of control

150 stands consisted of woody debris, leaf litter, and an herbaceous layer primarily composed of
151 ferns or moss.

152

153 ***Field Sampling***

154 Field surveys for salamanders occurred from July to August 2022. Although detectability
155 is generally higher during nighttime or following rainfall, plethodontid salamanders are
156 commonly detectable during daytime conditions as shown in previous research (O'Donnell and
157 Semlitsch 2015) and our preliminary surveys in NB (Table S1). We therefore conducted all
158 surveys during the day to ensure consistency across sites and accommodate logistical and safety
159 constraints. To minimize potential biases related to weather conditions and time of day, one to
160 three harvested blocks (treated or untreated) or unharvested control stands were randomly
161 selected and surveyed each day. Each block or stand was surveyed once during the study period,
162 with no repeated counts. Within each of the blocks or stands, we established a circular sampling
163 plot with a diameter of 30 m. We established the center of each sampling plot to ensure a
164 minimum 50 m buffer of similar habitat around its perimeter, minimizing potential edge effects
165 (Murcia 1995). We conducted standardized area-constrained searches using circular transects at
166 30 m, 20 m, 10 m, and 0 m from the sampling plot's center (Figure S2). Two researchers
167 searched under cover objects, rocks and logs, within 5 m of each transect and hand-captured
168 salamanders. At the sampling plot's center, we measured soil moisture (Campbell Scientific
169 Hydrosense II Soil-water Sensor CS658), temperature (Master Chef Digital Instant Read
170 Thermometer), and pH (Hanna Instruments Direct Soil pH Measurement Kit HI99121) at depths
171 of approximately 20 cm, 12 cm, and 10 cm, respectively. Additionally, we took a 360° photo
172 using a Ricoh Theta 360 camera to document the canopy cover and ground cover of each survey

173 plot. We estimated canopy cover by analyzing Ricoh Theta 360 images with ImageJ using the
174 digital dot grid method (Goeking 2012).
175
176 Each time a salamander was captured, we identified and recorded the species, weighed the
177 individual using a digital scale (US-Ranger) (± 0.01 g), and measured snout–vent length (SVL)
178 with digital callipers (± 0.1 mm) (i.e., the distance from the snout to the anterior boundary of the
179 cloaca). Species richness was low across plots, ranging from 0 to 3 species (see Supplementary
180 Materials; Table S2). Most plots contained only one species, the Eastern Red-backed
181 Salamander, which was captured in all plots. Given this limited variation, we restricted our
182 analysis to Eastern Red-backed Salamander data. We categorized individuals into two age
183 classes based on SVL: juveniles (≤ 32 mm) and adults (> 32 mm) (Mazerolle et al. 2021). Male
184 Eastern Red-backed Salamanders were identified by the observation of testes using the candling
185 method described by Gillette and Peterson (2001), and females were identified through the
186 absence of testes and/or observation of eggs. We noted if females were gravid, recorded any
187 injuries, including cuts, lesions, and tail autotomy. All salamanders were immediately released at
188 the location of capture after processing. Sampling followed protocols to prevent disease spread
189 as outlined by the Canadian Herpetofauna Health Working Group (2017) and that were approved
190 by the Mount Allison University Animal Care Committee—ACC # 103181, as well research was
191 conducted with authorization from The Department of Natural Resources and Energy
192 Development, Government of New Brunswick under Scientific Permit No. SP22—002.
193

194 ***Data Analysis***

195 All statistical tests were conducted in R version v 4.2.2 (R Core Team 2022). Before
196 analyses, we examined the data to ensure the absence of unexplainable outliers or collinearity
197 between predictor variables. The significance level (α) for all models was set at 0.05. For each
198 model, we assessed the assumptions of normality of residuals and homogeneity of variance by
199 examining a histogram and a normal probability plot (Q-Q plot) of the residuals, as well as a
200 visual representation of the residuals plotted against the fitted values. Data are presented as mean
201 \pm standard error (SE) in the text unless otherwise specified.

202

203 Environmental Factors

204 We compared environmental factors among forest treatments (control, treated, and untreated) to
205 evaluate our predictions regarding the impact of forest harvest practices on salamander habitat.
206 First, using the '*glm*' function from the '*stats*' R package (R Core Team 2022) we performed two
207 generalized linear models (GLMs). These models examined the influence of forest treatment (a
208 categorical variable including control, untreated, and treated levels) and years since harvest (a
209 continuous variable ranging from 5 to 26 years) on canopy cover (%) and soil moisture (%).
210 Since canopy cover and soil moisture are expressed as percentages ranging from 0 to 100, we
211 converted the data to proportions and used a binomial distribution for analysis (McCullagh and
212 Nelder 1989). Second, we used the '*lm*' function from the '*stats*' R package (R Core Team 2022)
213 to carry out linear models (LM) assessing the effect of forest treatment and years since harvest
214 on soil temperature ($^{\circ}\text{C}$) and soil pH.

215

216 Initially, the interaction between forest treatment and years since harvest was included in both
217 GLMs and LMs. The significance of the interaction was evaluated based on the model output
218 obtained from the ‘*anova*’ function of the ‘*stats*’ R package using the χ^2 -test statistic for GLMs
219 and the *F*-test statistic for LMs. If not significant, we removed the interaction and re-ran the
220 model to allow for the interpretation of main effects (Gelman and Hill 2007). For models where
221 forest treatment had a significant main effect, we generated contrasts for each comparison (three
222 comparisons total) using the ‘*emmeans*’ function from the ‘*emmeans*’ R package (Lenth 2022). *P*
223 values generated for comparisons between forest treatments were corrected using a Tukey’s HSD
224 multiplicity adjustment (Lenth 2022).

225

226 Abundance

227 We tested for differences in the relative abundance (i.e., the number of salamanders
228 within our standardized survey area) of Eastern Red-backed Salamanders by performing a GLM
229 with a Poisson distribution (McCullagh and Nelder 1989) using the same approach as describe
230 for our analysis of environmental factors. The model included the fixed effects of forest
231 treatment and years since harvest. We used the same approach to test interactions ($z = -1.45$, $p =$
232 0.15 , not significant), then re-ran the model with the interaction removed to allow interpretation
233 of the main effects (Gelman and Hill 2007). We performed post-hoc comparisons between forest
234 treatments using the same approach as previously described.

235

236 Body condition

237 We used the scaled mass index (SMI), derived from a standardized major axis (SMA)-adjusted
238 ordinary least squares (OLS) regression of log-transformed body mass on log-transformed snout-

239 vent length (SVL), as an index of body condition for adult Eastern Red-backed Salamanders
240 (Schulte-Hostedde et al. 2005; Peig and Green 2009). SMA regression was used to account for
241 allometric scaling, providing a scaling exponent that adjusts mass to a standardized SVL, making
242 body condition estimates more size-independent (Peig and Green 2009). Since body condition
243 serves as an indicator of energy reserves, particularly fat stores, higher SMI values indicate better
244 condition (high mass relative to length) while lower values indicate poorer conditions. A similar,
245 but slightly different approach, is to calculate SMI with a robust regression model to better
246 account for outliers in the data (Maronna et al. 2019). Thus, we compared using OLS and robust
247 regression estimators to assess which method best described the mass-SVL relationship using our
248 data. We found that the OLS regression estimator met standard assumptions (independent and
249 normally distributed residuals) and provided a better fit than the robust regression based on
250 visual assessments, residual diagnostics, and RMSE and AIC values (see Supplementary
251 Materials, Figure S2 and Table S3). As estimating SMI using robust regression did not improve
252 model performance for our data, we selected to use the SMA-adjusted OLS regression to
253 calculate our SMI (i.e., the body condition) of salamanders (as described by Peig and Green
254 2009).

255

256 To test for differences in body condition between forest treatments, we used a linear mixed-
257 effects model (LMM) with the *lmer* function in the *lmerTest* R package (Kuznetsova et al.
258 2017). The model included forest treatment, years since harvest, and sex (a categorical variable
259 including females and males) as fixed effects, and plot identity as a random effect. We used the
260 same approach to test interactions ($F_{1, 101} = 1.50, p = 0.22$, not significant) and perform multiple

261 comparisons as described previously. Due to the low numbers of instances of injury and tail
262 autonomy observed, we report counts rather than performing statistical analyses.

263

264 Reproductive Activity

265 To analyze the effects of forest treatment and years since harvest on the proportion of
266 juvenile Eastern Red-backed Salamanders relative to the total number of individuals observed,
267 we performed a GLM with a binomial distribution (McCullagh and Nelder 1989). This metric
268 serves as a proxy for demographic structure, providing insight into juvenile recruitment and
269 potential population dynamics under different forest management conditions (Homyack and
270 Haas 2009). While it does not directly measure reproductive output, it captures potential
271 variation in juvenile survival and recruitment. The model included forest treatment and years
272 since harvest as fixed factors. We used the same approach for testing interactions ($\chi^2_{1, 15} = 0.46, p$
273 $= 0.50$, not significant) and for comparisons between treatment levels as described previously.
274 Due to the low number of gravid females and egg masses observed during the study, we report
275 counts rather than performing statistical analysis.

276

277 **Results**

278 *Forest Environmental Factors*

279 Canopy cover increased significantly with years since harvest ($\chi^2_1 = 169.47, p < 0.01$),
280 and varied among forest treatments ($\chi^2_2 = 326.90, p < 0.01$). Control plots had the highest
281 average canopy cover percentage ($77.5 \pm 2.28\%$), followed by treated blocks ($10.7 \pm 1.08\%$) and
282 untreated blocks ($7.61 \pm 0.78\%$) (Figure 2a). Post-hoc contrasts confirmed that canopy cover was

283 significantly greater in control plots compared to both treatment types ($p < 0.01$ for both) and
284 was also greater in treated than untreated blocks ($p < 0.01$) (Table 1a).

285

286 We observed a significant interaction between years since harvest and forest treatment regarding
287 soil temperature ($F_{1, 25} = 6.23, p = 0.02$). Visual assessment suggested that soil temperature
288 remained relatively constant across years since harvest in untreated blocks, but declined with
289 increasing years since harvest in treated blocks (Figure 2b). Summary statistics suggest that
290 control stands had lower soil temperatures ($14.5 \pm 0.36^{\circ}\text{C}$) compared to untreated ($16.1 \pm$
291 0.39°C) and treated ($16.0 \pm 0.61^{\circ}\text{C}$) blocks.

292

293 There was also a significant interaction between years since harvest and forest treatment
294 regarding soil moisture ($\chi^2_1 = 25.57, p < 0.01$). Based on visual assessment, soil moisture
295 declined with years since harvest in untreated blocks, while remaining relatively stable in control
296 and treated blocks (Figure 2c). Summary statistics indicate that on average, soil moisture was
297 higher in control stands ($30.6 \pm 4.16\%$) than in untreated ($21.3 \pm 4.61\%$) and treated ($14.8 \pm$
298 2.03%) blocks.

299

300 In contrast, soil pH did not differ significantly with years since harvest ($F_{1, 26} = 3.59, p = 0.07$)
301 nor among forest treatments ($F_{2, 26} = 1.79, p = 0.19$; Table 1b; Figure 2d). Although estimated
302 marginal means indicated that soil pH was lowest in control stands, intermediate in treated
303 blocks, and highest in untreated blocks, post-hoc comparisons revealed no significant differences
304 among treatments (all $p > 0.05$; Table 1b).

306 *Salamander Population Structure*

307 Within our 30 m² sample plots, we captured a total of 183 Eastern Red-backed Salamanders in
308 the control stands, 10 in the untreated blocks, and 42 in the treated blocks. Abundance of Eastern
309 Red-backed Salamanders increased significantly with years since harvest ($\chi^2_1 = 14.60, p < 0.01$)
310 (Table 2a). Based on comparisons across sites, salamander abundance was predicted to increase
311 by 9.4% per year, corresponding to an approximate 2.45-fold increase over 10 years within the
312 26-year post-harvest range sampled. Additionally, Eastern Red-backed Salamander abundance
313 differed significantly among forest treatments ($\chi^2_2 = 205.46, p < 0.01$) (Table 2a). Average
314 salamander abundance was highest in control stands, followed by treated blocks, and lowest in
315 untreated blocks (Figure 3; Table 2b).

316

317 *Salamander Body Condition*

318 Eastern Red-backed Salamander body condition, quantified using a SMI (Peig and Green
319 2009), was significantly and negatively related to years since harvest (Table 3a). Body condition
320 was lower in the control stands (0.74 ± 0.05 g) than in untreated (1.26 ± 0.14 g) and treated (1.24
321 ± 0.15 g) blocks, but did not differ between treated and untreated blocks or between sexes (Table
322 3b; Figure 4). Body condition of Eastern Red-backed Salamanders was approximately 0.5 g
323 higher in the treated and untreated blocks than the control stands (Table 3b). During our study,
324 we identified 11 Eastern Red-backed Salamander individuals with missing or regenerating tails:
325 10 in the control stands and one in the untreated blocks. Among these, nine were female and two
326 were male. No Eastern Red-backed Salamanders with additional injuries, such as cuts or lesions,
327 were observed.

328

329 *Salamander Reproductive Activity*

330 We observed six gravid Eastern Red-backed Salamander females during the surveys: five
331 in control stands and one in treated clear-cut blocks. Additionally, we observed 10 females
332 guarding eggs in control stands, but none in harvested blocks. The proportion of juveniles within
333 a survey was not related to years since harvest, and did not differ significantly among forest
334 treatments (Table 4).

335

336 **Discussion**

337 Herbicide application following clear-cutting altered key abiotic conditions of
338 salamander habitat, which significantly influenced salamander abundance in regenerating stands.
339 Contrary to our prediction that herbicide would exacerbate the negative effects of canopy
340 removal on Eastern Red-backed Salamanders, treated clear-cut blocks instead exhibited more
341 favourable conditions than untreated blocks. These differences were associated with greater
342 canopy cover and higher abundance of salamanders in treated blocks. While the impacts of clear-
343 cutting on salamander populations are well documented (e.g. DeMaynadier and Hunter 1995,
344 Tilghman et al. 2012; Ochs et al. 2022), our study adds new insight into how herbicide
345 application interacts with canopy removal to shape post-harvest habitat.

346

347 We identified significant interactions between forest treatment and years since harvest, indicating
348 that the effects of canopy removal on soil temperature and moisture differ depending on whether
349 a clear-cut forest was treated with herbicide (Figure 2). Treated blocks showed a decreasing
350 trend in soil temperature and a slight increase in soil moisture, gradually approaching the cooler
351 and wetter conditions observed in control stands (Table 2). In contrast, untreated blocks

352 maintained consistently warmer soil temperatures and a negative trend in soil moisture over time,
353 diverging from control conditions (Table 2). The findings for untreated blocks align with
354 previous research showing that clear-cutting elevates soil temperature due to increased solar
355 radiation and initially increases soil moisture as reduced tree root respiration limits water uptake
356 (Keenan and Kimmins 1993). Though herbicide-treated blocks exhibit a return of herbaceous
357 species to pre-herbicide levels within 3-5 years, abundance remains lower than in similarly aged
358 untreated blocks for at least 10 years after application (Xiao et al. 2024). These long-term shifts
359 in understory composition may contribute to the observed differences in microclimate
360 conditions. Together, these findings suggest that herbicide-induced acceleration of canopy
361 closure may help mitigate post-harvest abiotic changes, promoting a faster return to habitat
362 conditions favourable for salamanders.

363
364 In contrast to soil temperature and moisture, we found no significant differences in soil pH
365 among forest treatments. Short-term effects of clear-cutting (0-3 years post-harvest) typically
366 lead to soil acidification (Johnson et al. 1991). Therefore, shifts in soil pH that may impact
367 salamander populations are likely more evident in early seral blocks (approximately 0-5 years)
368 compared to control stands, considering the progression of forest development. However, our
369 study did not include harvest blocks within this early seral range, limiting our ability to assess
370 these changes directly. Additionally, glyphosate strongly binds to soil particles and has a
371 relatively short half-life in soil, 45-60 days (Feng et al. 1990), suggesting minimal long-term
372 impact on soil pH and other chemical properties within the timescale of our study. While pH
373 remained consistent across forest treatments, the changes observed in other abiotic factors, such
374 as temperature and moisture, reflect how herbicide application can influence salamander habitat

375 quality. Nonetheless, our study highlights the resilience of Eastern Red-backed Salamander
376 populations, demonstrating their ability to withstand the challenging post-harvest and herbicide-
377 exposed period.

378
379 This resilience was also reflected in salamander body condition. Contrary to our prediction that
380 Eastern Red-backed Salamander body condition would be highest in unharvested (control)
381 stands, we observed the opposite trend: body condition was lower in control stands than in both
382 treated and untreated harvest blocks, where it remained similar. This finding contrasts with
383 Welsh et al. (2008), who reported higher body condition in the Siskiyou Mountains salamander
384 (*Plethodon stormi*) in mature versus young forests. However, our results align with those of
385 Gade et al. (2023), where Eastern Red-backed Salamander body condition was lower in mature
386 forests than in early successional stands. The disparity between these findings may be explained
387 by differences in the competitive regimes under which each population exists, which may impact
388 their relative fitness. Body condition, an indicator of fat reserves, reflects density-dependent
389 processes such as foraging success and energy expenditure in response to competition and
390 predation pressures (Homyack et al. 2011). Lower body condition in high-density populations, as
391 observed in the control stands, may indicate resource limitation on a per individual basis due to
392 higher salamander abundance or reduced food availability, both of which can increase
393 intraspecific competition (Getz 1996). Meanwhile, the similar body condition observed in treated
394 and untreated blocks suggests that energy availability or competition may be comparable
395 between salamanders in both environments, despite differences in overall abundance. The link
396 between forest management and salamander body condition likely involves multiple indirect
397 pathways, requiring further investigation, particularly regarding the differences in inter- and
398 intra-specific interactions across various management practices.

399

400 Although salamander abundance and body condition varied among forest treatments, we
401 observed no significant differences in reproductive activity, measured by the proportion of
402 juveniles, number of gravid females, and egg masses. While our dataset was sufficient to assess
403 the proportion of juveniles in the population, the low number of gravid females and egg masses
404 constrained the strength of our inferences for these indicators. To improve detection of gravid
405 females and egg masses, future studies could increase sampling frequency during the
406 reproductive season and target periods following recent rainfall when salamander surface activity
407 is highest (O'Donnell and Semlitsch 2015). While previous research has reported a higher
408 proportion of juvenile Eastern Red-backed Salamanders in unharvested stands compared to
409 harvested blocks (Homyack and Haas 2009), we found no evidence that these differences were
410 reflected in reproductive activity in our study.

411

412 Unsurprisingly, control stands, which serve as reference stands for mature Acadian Forest, had
413 highest canopy cover, soil moisture, and lowest soil temperatures than harvested blocks. These
414 conditions are optimal for salamanders (Wyman 1988; Petranka 2010) and likely explain our
415 finding of higher Eastern Red-backed Salamander abundance in control stands compared to
416 harvested blocks, regardless of whether they were treated with an herbicide. While our results
417 support this pattern, we caution that variation in cover object availability was not accounted for
418 in our sampling design, which may have an influence on salamander detectability across plots
419 and confounded abundance estimates (O'Donnell and Semlitsch 2015). Differences in cover
420 availability could influence salamander estimates across all forest treatments. Nonetheless, our
421 findings align with Homyack and Haas (2009), who reported significantly lower salamander

422 abundance in harvested forests where the canopy has been removed compared to unharvested
423 stands.

424

425 Historical forest management practices in the Acadian Forests of New Brunswick have increased
426 the amount of conifer and decreased the amount of deciduous and mixed forests (Noseworthy
427 and Beckley 2020). The increase in planting of conifer trees has led to increased use of
428 glyphosate-based herbicides, up to 30 % of forested lands in some watershed have been treated
429 over the last 10 years (Edge et al. 2023). Changes in forest composition could have significant
430 ecological implications, particularly for forest-dependant species like the Eastern Red-backed
431 Salamander. Our findings indicate that while herbicide-treated clear-cut blocks support higher
432 salamander abundance compared to untreated ones, their recovery to levels comparable to
433 unharvested control stands within the typical harvest rotation length (40-60 years) for crown land
434 in New Brunswick remains uncertain (Frego et al. 2014). Given that older Acadian Forests serve
435 as critical refuges for salamander and other forest interior species, prioritizing the protection of
436 these stands is essential for maintaining biodiversity in managed forest landscapes.

437

438 As the regeneration cycle advances beyond the scope of this study (26 years post-harvest), the
439 environments of harvested forests continue to change. While our results demonstrate that
440 herbicide application may enhance salamander habitat conditions and support higher abundance
441 during forest regeneration, longer-term consequences for salamander populations and habitat
442 quality remain uncertain and are in need of further study. This study offers a foundational step
443 toward understanding how post-harvest silvicultural practices interacts with forest harvesting to
444 influence forest floor microhabitats and forest specialist species. However, the short-term and

445 single-season design of this work limits the strength of our conclusions for generalization. Future
446 studies incorporating long-term, repeated sampling and continuous environmental monitoring
447 across successional and climatic gradients are needed to fully understand the ecological
448 consequences of forest management practices. Integrating these insights into forestry planning
449 will support the development of more adaptive and ecologically informed strategies that balance
450 timber production with sustaining biodiversity and ecological integrity.

451

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457

458 **Article Information**

459 ***Data availability***

460 The data and R code for this study are available from Open Source Framework (OSF), which can
461 be found at the following link:

462 https://osf.io/5hc6s/?view_only=8a428e3052a94760a295ffedb1bfbd31

463

464 **Author Information**

465 ***Author ORCIDS***

466 SEL: 0009-0008-0442-8801; CBE: 0000-0002-4713-0035; JLR: 0000-0001-7691-6910

467 ***Author contributions***

468 Conceptualization: SEL, CBE, JLR. Data curation: SEL, JLR. Formal analysis: SEL, JLR.
469 Funding Acquisition: CBE, JLR. Methodology: SEL, CBE, JLR. Project administration: SEL,
470 CBE, JLR. Supervision: CBE, JLR. Visualization: SEL, JLR. Writing – original draft: SEL.
471 Writing – review & editing: SEL, CBE, JLR.

472

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474

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479

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607 **Tables**

608 **Table 1.** Post-hoc pairwise comparisons testing for differences among the forest treatments
 609 (control, untreated clear-cut, and treated clear-cut) for **(A)** canopy cover (%) and **(B)** soil pH.
 610 Canopy cover was analyzed using a generalized linear model (GLM), while soil pH was
 611 analyzed using a linear model (LM). Since interactions were not significant in initial models,
 612 main effects could be interpreted directly (Figure 2). We present estimates (β) and their
 613 corresponding standard error (SE) on the response scale, test statistics (z -ratios for GLM or t -
 614 ratios for LM), and corrected p -values (p_{corr}) for multiple comparisons. Bolded values indicate
 615 significance.

<i>Response Variable & Contrasts</i>	β	SE	<i>Test Statistic</i>	p_{corr}
(A) Canopy cover				
<i>z</i> -ratio				
Control vs. Untreated	41.81	8.95	17.44	< 0.01
Control vs. Treated	28.83	6.55	14.80	< 0.01
Untreated vs. Treated	0.69	0.08	-3.32	< 0.01
(B) Soil pH				
<i>t</i> -ratio				
Control vs. Untreated	-0.45	0.74	-0.62	0.81
Control vs. Treated	-1.35	0.78	-1.72	0.22
Untreated vs. Treated	-0.90	0.45	-1.99	0.14

616

617

618 **Table 2. (A)** Outcomes of the generalized linear model (GLM) that examined the effect of forest
 619 treatment and year since clear-cut on Eastern Red-backed Salamander abundance. I present
 620 estimates (β) and their corresponding standard error (SE) on the latent scale, z -values, and p -
 621 values (p). **(B)** Post-hoc pairwise comparisons among the effect of forest treatment (control,
 622 untreated clear-cut, and treated clear-cut) on Eastern Red-backed Salamander abundance. We
 623 present estimates (β) and their corresponding standard error (SE) on the response scale, t -ratios,
 624 and p -values (p_{corr}) corrected for multiple comparisons. Bolded values indicate significance.

Eastern Red-backed Salamander Abundance				
(A) Model Output				
<i>Fixed effects</i>	β	SE	z -value	p
Intercept (Control)	2.91	0.07	39.32	< 0.01
Forest treatment (Untreated)	-4.10	0.52	-7.96	< 0.01
Forest treatment (Treated)	-3.10	0.52	-6.02	< 0.01
Years since harvest	0.09	0.02	3.64	< 0.01
(B) Post-hoc Multiple Comparisons				
<i>Forest treatment Contrasts</i>	β	SE	z -ratio	p_{corr}
Control vs. Untreated	60.37	31.10	7.96	< 0.01
Control vs. Treated	22.21	11.44	6.02	< 0.01
Untreated vs. Treated	0.37	0.12	-3.10	< 0.01

625

626 **Table 3. (A)** Outcomes of the linear mixed effects model (LMM) that examined the effect of
 627 forest treatment, year since clear-cut, and sex on Eastern Red-backed Salamander body condition
 628 (g). We present estimates (β) and their corresponding standard error (SE) on the latent scale, t -
 629 values, and p -values (p). For random effects, we present the variance (σ^2) and standard error
 630 (SE). **(B)** Post-hoc pairwise comparisons among the effect of forest treatment (control, untreated
 631 clear-cut, and treated clear-cut) on Eastern Red-backed Salamander body condition (g). We
 632 present estimates (β) and their corresponding standard error (SE) on the response scale, t -ratios,
 633 and p -values (p_{corr}) corrected for multiple comparisons. Bolded values indicate significance.

Eastern Red-backed Salamander Body Condition				
(A) Model Output				
<i>Fixed effects</i>	β	SE	t -value	p
Intercept (Control, Female)	0.87	0.02	39.22	< 0.01
Sex (Male)	-0.02	0.03	-0.78	0.44
Years since harvest	-0.02	0.01	-2.32	0.02
Forest treatment (Untreated)	0.52	0.19	2.74	< 0.01
Forest treatment (Treated)	0.50	0.20	2.48	0.01
<i>Random effects</i>	σ^2	SE		
Plot ID	0.00	0.00		
Residuals	0.03	0.16		
(B) Post-hoc Multiple Comparisons				
<i>Forest treatment Contrasts</i>	β	SE	t -ratio	p_{corr}
Control vs. Untreated	-0.52	0.19	-2.73	0.02
Control vs. Treated	-0.50	0.20	-2.47	0.04
Untreated vs. Treated	-0.02	0.07	0.28	0.96

634

635 **Table 4. (A)** Outcomes of a generalized linear model that examined the effect of forest treatment
 636 and year since clear-cut on the proportion of Eastern Red-backed Salamander that were juveniles
 637 during surveys. We present estimates (β) and their corresponding standard error (SE) on the
 638 latent scale, z -values, and p -values (p). **(B)** Pairwise comparisons among the effect of forest
 639 treatment (control, untreated clear-cut, and treated clear-cut) on the proportion of juveniles found
 640 during surveys. We present estimates (β) and their corresponding standard error (SE) on the
 641 response scale, t -ratios, and p -values (p_{corr}) corrected for multiple comparisons. Bolded values
 642 indicate significance.

Eastern Red-backed Salamander Juvenile Proportion				
(A) Model Output				
<i>Fixed effects</i>	β	SE	z -value	p
Intercept (Control)	-0.89	0.14	-6.51	< 0.01
Forest treatment (Untreated)	0.33	1.71	0.19	0.85
Forest treatment (Treated)	1.49	2.48	0.60	0.55
Years since harvest	-0.10	0.12	-0.79	0.43
(B) Post-hoc Multiple Comparisons				
<i>Forest treatment Contrasts</i>	β	SE	t -ratio	p_{corr}
Control vs. Untreated	0.72	1.23	-0.19	0.98
Control vs. Treated	0.23	0.56	-0.60	0.82
Untreated vs. Treated	0.31	0.40	-0.92	0.63

643

644 **Figure Captions**

645

646 **Figure 1.** Map showing the locations of the study survey sites within the Acadia Research
647 Forest, New Brunswick, Canada. The grey circles indicate control stands, the blue squares
648 indicate untreated harvest blocks, and the green triangles indicate treated harvest blocks. Figure
649 was created using ArcGIS Pro version 3.3.0 and assembled from the following data sources:
650 *North American Atlas – Political Boundaries* (Commission for Environmental Cooperation
651 [CEC], 2022); *Acadia Research Forest Boundary* shapefile (Natural Resources Canada); and
652 *Global Oceans and Seas*, version 1 (Flanders Marine Institute [VLIZ], 2021)

653

654 **Figure 2.** Plots depicting **(a)** a significant difference of canopy cover among forest treatments,
655 **(b)** a significant interaction between years since harvest and forest treatment for soil temperature
656 ($^{\circ}\text{C}$) and **(c)** soil moisture (%), and **(d)** no significant difference in soil pH among forest
657 treatments. Dashed blue lines represent untreated clear-cut blocks and solid green lines show
658 treated clear-cut forest treatments. Points represent raw data. Dotted grey lines represent the
659 mean value in the control stands. For the boxplots, the box itself represents the interquartile
660 range of the data (IQR) and the lower and upper limits of the box are the first and third quartile,
661 respectively. The bottom/top whiskers that extend from the box are represent the minimum and
662 maximum values of the data that are not considered outliers (1.5 times the IQR).

663

664

665 **Figure 3.** Salamander abundance in control (grey fill), untreated clear-cut (blue fill), and treated
666 clear-cut (green fill) forest treatments. Median values are represented by the thick horizontal line
667 inside the boxes. Raw data are represented by points. The box itself represents the interquartile
668 range of the data (IQR) and the lower and upper limits of the box are the first and third quartile,
669 respectively. The bottom/ top whiskers that extend from the box are represent the minimum and
670 maximum values of the data that are not considered outliers (1.5 times the IQR). Significant
671 comparisons between forest treatments are shown using a bar connecting them and an asterisks.
672 (*).

673

674 **Figure 4.** Salamander body condition in control (grey fill), untreated clear-cut (blue fill), and
675 treated clear-cut (green fill) forest treatments. Median values are represented by the thick
676 horizontal line inside the boxes. Raw data are represented by points. The box itself represents the
677 interquartile range of the data (IQR) and the lower and upper limits of the box are the first and
678 third quartile, respectively. The bottom/ top whiskers that extend from the box are represent the
679 minimum and maximum values of the data that are not considered outliers (1.5 times the IQR).
680 Significant comparisons between forest treatments are shown using a bar connecting them and an
681 asterisks (*).

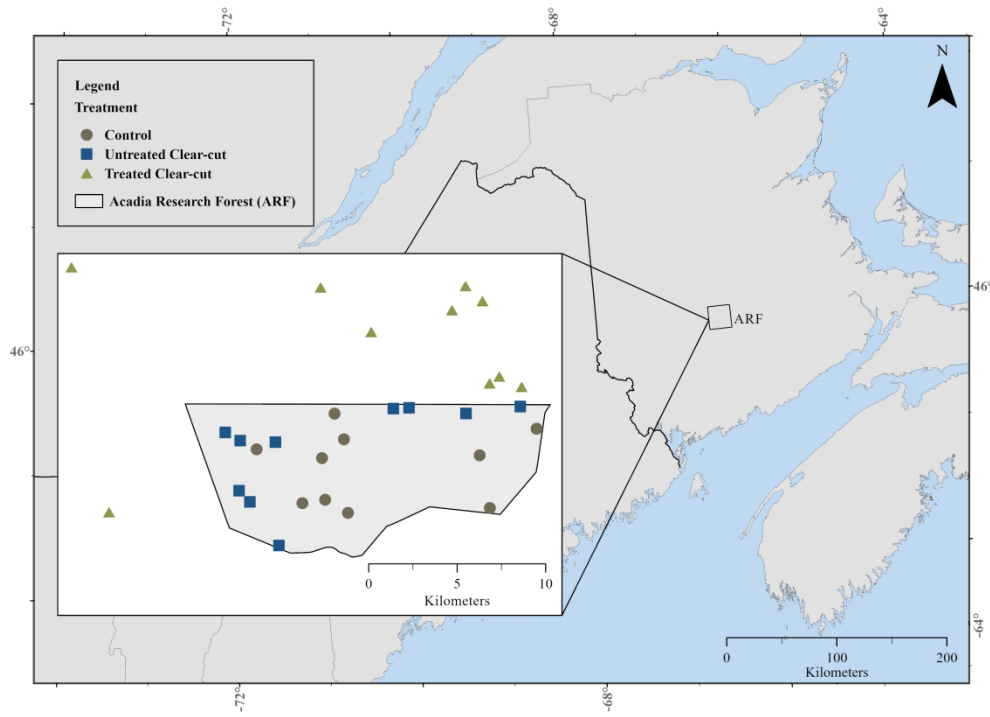
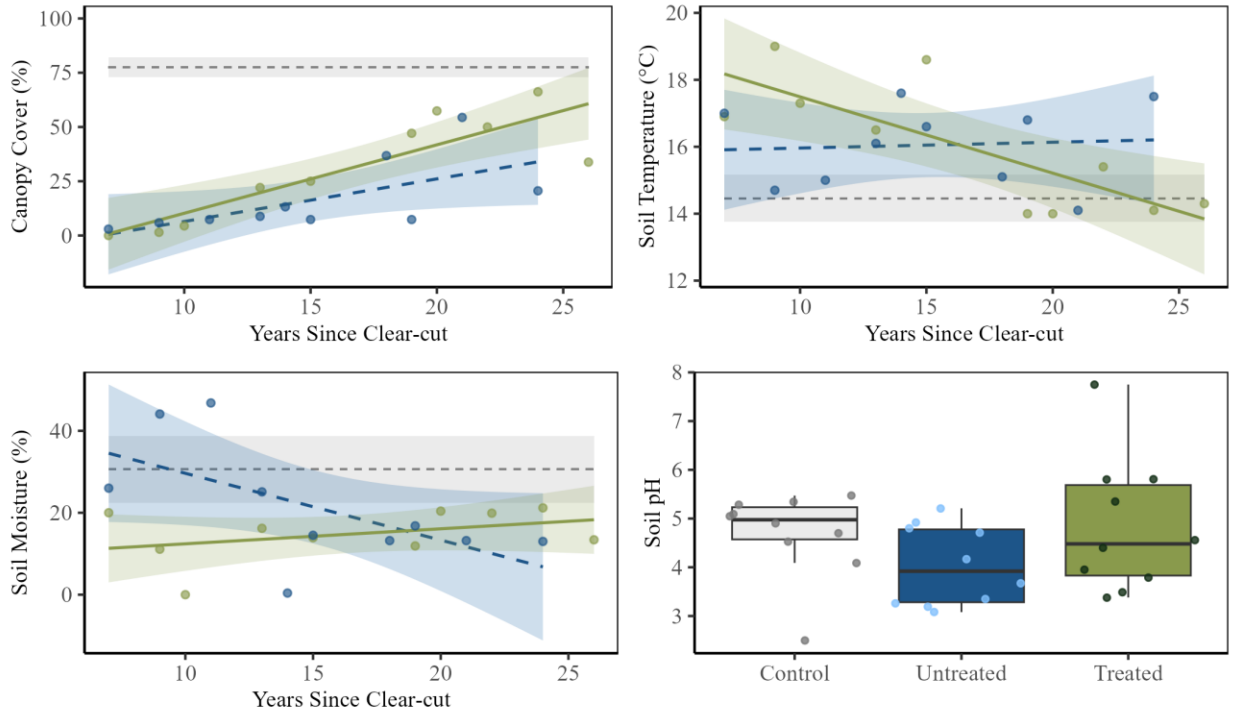
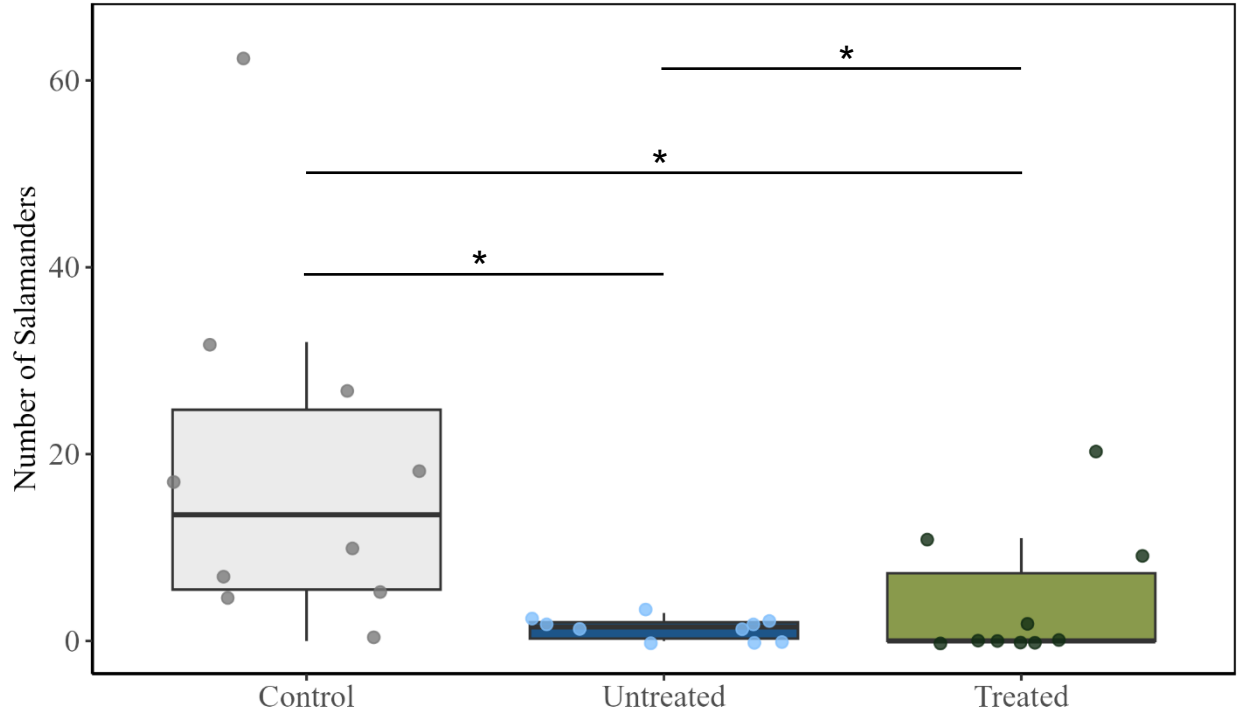


Fig 1

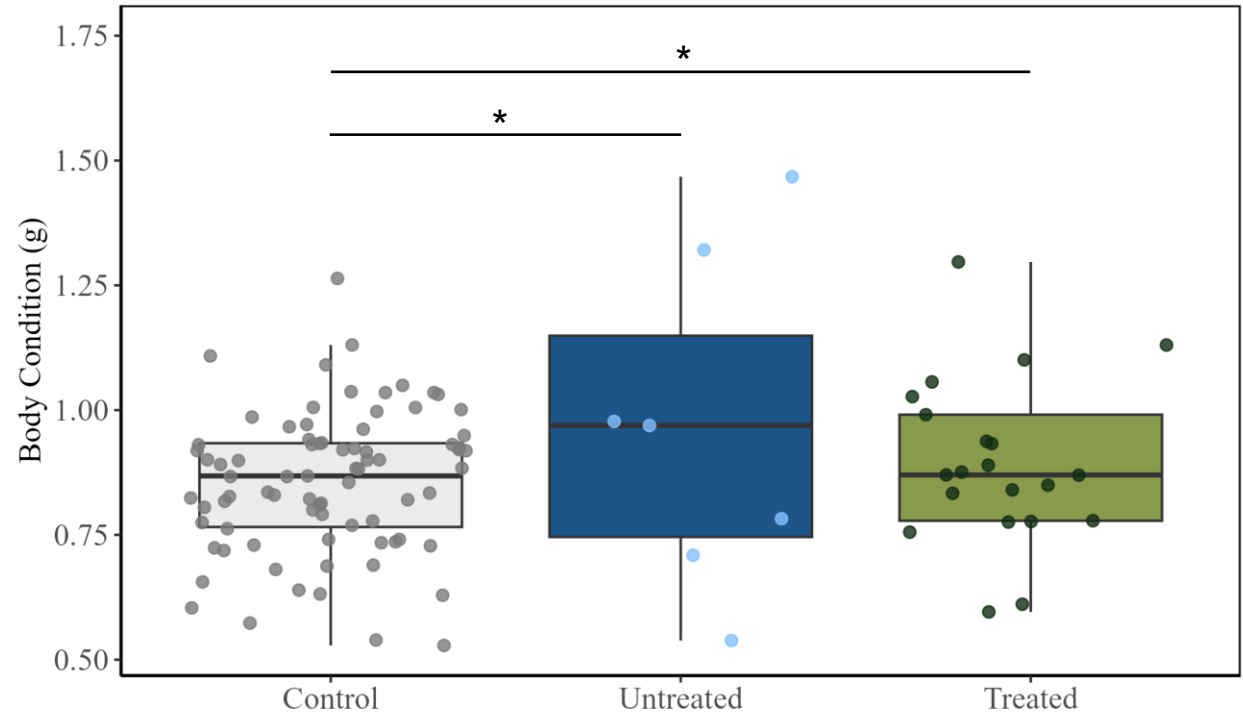
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