

1 Utilizing *Plethodontid* Occupancy to Assess Initial Ecosystem Responses to Invasive Plant
2 Control Treatment in Central Hardwoods

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11 Keywords: salamanders, non-native plants, treatment effects, indicator species

12 Highlights:

- 13 • *Plethodontid* occupancy odds decrease on invasive plant control-treated sites.
- 14 • Large-scale invasive control treatments can negatively impact ecosystem services.
- 15 • Canopy cover is an essential occupancy predictor for *Plethodontid* salamanders.
- 16 • Treatment information needs to be more detailed to identify drivers of change.

17 **Abstract**

18 Invasive plants are a growing concern for land managers, impacting ecosystem resilience
19 and outcompeting native vegetation. To combat this, invasive plant control treatments can assist
20 in reducing the impacts and spread of damaging, non-native plant species. However, intensive
21 treatments completed at large scales have the potential to negatively impact ecosystem services
22 as well. To monitor these impacts, we utilized a well-known indicator in the Central Appalachian
23 region, *Plethodontid* salamanders, to assess impacts of invasive plant control treatments in the
24 Central Hardwood forests. We completed 12 visual samples across 60 sites in West Virginia,
25 USA during Spring and Fall of 2025 (720 sampling occasions) on state lands that received

invasive plant control treatment during the previous summer. We also collected habitat metrics to observe impacts of invasive plant presence on *Plethodontid* salamander occupancy. Using a single-species, single-season occupancy model, we identified important predictors of salamander occupancy across landscapes managed for invasive plants. Salamander occupancy on sites that received invasive plant control treatments decreased by 42.1%, whereas occupancy increased by 6.0% for every 1.0% increase in canopy cover. The inclusion of invasive plant ground cover in the occupancy model was uninformative, which is consistent the inconclusive relationship between adult, terrestrial salamanders and invasive plants in previous studies. Overall, our results support findings of recent studies, including that invasive plant control treatments have unintended, negative impacts on *Plethodontid* salamanders and their associated ecosystem services.

1.1. Introduction

In the eastern US, invasive plants pose a major threat to biodiversity within temperate deciduous forests (Early et al., 2016). Through direct (e.g., competition and altering soil chemistry, soil microbial composition, and erosion control) and indirect (e.g., habitat alteration) effects, invasive plant species have been shown to reduce diversity of native flora and fauna (Leger & Espeland, 2010; Arthur et al. 2012; Malinich et al. 2017; Cipollini & Wagner, 2011; Matte et al., 2022; Webster et al., 2006). Monitoring these impacts in a cost effective and comprehensive way is challenging, due to the effects of invasive plants often being species dependent (van Kleunan et al., 2010; Ni et al., 2021) and their widespread presence (Early et al., 2016). To combat this, many recent studies use indicator species to identify/monitor ecosystem changes (Fleishman & Murphy, 2009). Ideally, indicator species presence (or absence) reflects meaningful environmental changes, is cost efficient to sample, provides highly relevant

information on ecological processes, and has low temporal variability (Fleishman & Murphy, 2009; Siddig et al., 2016a).

Recent studies within eastern forests point to *Plethodontid* salamanders as key indicator species (Welsh & Hodgson, 2013; Siddig et al., 2016a; Siddig et al., 2016b). *Plethodontid* salamanders are a highly abundant, widespread family of salamanders with unique morphological and physiological characteristics that make them exceptional indicators of ecosystem changes. *Plethodontids* are lungless and have permeable skin, which is used for respiration, making them sensitive to changes in temperature, moisture, and pollutants (Wells, 2019). *Plethodontids* also have particular microhabitat requirements, necessitating refugia (e.g., cover objects) that maintain high humidity and moderate temperature. They also require adequate leaf litter to predate and use both terrestrial and aquatic habitats (Riddell et al., 2019; Farallo & Miles, 2016; Welsh & Ollivier, 1998; Cabe et al., 2007). Additionally, *Plethodontids* have low vagility, rarely moving from their microhabitat between years (Cabe et al., 2007; Farallo & Miles, 2016). *Plethodontids* occupying unfavorable conditions will either die, retreat, or evacuate the area (Semlitsch et al., 2008). This makes a lack of *Plethodontid* presence on a particular site within their geographic distribution indicative of unfavorable conditions.

Similar studies also reference *Plethodontid* salamanders (hereafter: “salamanders”) as quality indicator species because of their unique trophic position. Salamanders are predators of detritivorous arthropods and thus regulate multiple ecosystem functions: nutrient cycling, carbon capture, soil-building, and conversion of leaf litter (Laking et al., 2021; Davic & Welsh, 2004; Milanovich & Peterman, 2016). Salamanders are also important prey species, serving as a bridge between invertebrate biomass and protein-rich vertebrate food resources (Best, 2012).

Many studies have examined the effects of invasive species on amphibians, but few have investigated the specific interactions between invasive plants and adult, terrestrial salamanders (Bucciarelli et al., 2014). Invasive plants have known effects on larval stage amphibians, affecting respiratory development and fitness (Maerz et al., 2005; Watling et al. 2011a; Watling et al., 2011b; Stephens et al., 2013). In contrast, invasive plants may serve as refugia in degraded habitats (Nunes et al., 2019; Nagy et al., 2011). For adult terrestrial salamanders, there are potential links between invasive plants, nonnative earthworms, and reduction in leaf litter negatively impacting terrestrial salamanders (Maerz et al., 2009). However, within the same study, Maerz et al. (2009) found no significant reduction in salamanders (*Plethodon cinereus*) with increasing garlic mustard (*Alliaria petiolata*) and Japanese barberry (*Berberis thunbergii*) abundance. Additional studies support this claim, with adult salamanders being minimally or entirely unaffected by invasive plants (Watling et al., 2011b; Utz & Fetsko, 2020; Lehtinen et al., 2022). However, adult salamanders can be indirectly impacted by invasive plant presence, particularly if required habitat conditions are altered (Maerz et al., 2009).

Management strategies that remove invasive plants can alleviate ecosystem biodiversity concerns (Prior et al., 2018; Petri & Ibanez, 2025). This would potentially allow for native plant re-establishment to support native populations of wildlife, benefiting overall biodiversity. However, intensive invasive plant removal can negatively impact salamander populations (Lehtinen et al., 2022). Similarly, silvicultural and forest management practices that alter forest floor habitat can detrimentally impact salamander populations (Gibbs, 1998; Hocking et al., 2013a; Hocking et al., 2013b). This was observed for prescribed fires (O'Donnell et al., 2015; Pilliod et al., 2003), timber harvesting (clear cuts and partial removals) (O'Donnell et al., 2015; Ochs et al., 2022; Leslie et al., 2025), mine land reclamation efforts (Wood & Williams, 2013),

and invasive plant removal (Lehtinen et al., 2022). Many of the negative impacts on salamander populations are contingent on canopy removal, loss of refugia and leaf litter, altered vegetation structure, and drier, warmer soil conditions (Och et al., 2022; O'Donnell et al., 2015; Knapp et al., 2003, Semlitsch et al., 2009; McKenny et al., 2006). Leslie et al. (2025) found that herbicide applications to control unwanted vegetation promoted recovery of salamander populations, suggesting that the recovery of suitable conditions is more essential for salamanders than specific treatment effects.

Lehtinen et al. (2022) examined the effects of invasive plant removal on salamanders, noting the loss of understory vegetative structure as the primary reason for lower Northern ravine salamander (*Plethodon electromorphus*) presence, due to increased predation risk perception (Forester et al., 2019). This effect was most impactful on sites that were heavily invaded by invasive plants, as these sites had greater losses of vegetative structure during treatment (Lehtinen et al., 2022).

In this study, we observed *Plethodontid* salamander occupancy on sites with varying levels of invasive plant presence, with some sites receiving invasive species control treatment. *Plethodontid* salamanders act as indicators of ecosystem functions and biodiversity, and few studies have examined the impacts of invasive plant control treatments on *Plethodontid* occupancy. To further our understanding, we performed visual and cover board surveys of salamander detection and non-detection on treated and untreated sites with varying levels of invasive plant invasion in four hardwood-dominated forests in West Virginia, USA. We expected invasive plant control treatments to be the strongest predictor of salamander occupancy, with various metrics of invasive vegetation abundance and cover as an additional, negative factors. We also anticipated interspecific variation in both the strength of invasive plants impacts and the

responses of salamander species those impacts, which would remain consistent with previous studies (Nunes et al., 2019; Bucciarelli et al., 2014).

2.1 Methods

2.1.1 Study sites

This project was initiated by a large energy corporation that started forest management activities on West Virginia state lands to support Environmental, Social, and Governance (ESG) goals. The team included a consulting forestry firm that initiated forest management plans and invasive plant density, an invasive plant control contractor, and a team from West Virginia University that led the treatment validation work. On the ground management began in March of 2024, and over the next 7 months, 55 state lands (state forests and WMAs) received invasive plant control treatments totaling approximately 12,400 hectares. Treatment areas were selected by state land managers and were surveyed by the consulting forestry company. These areas were mapped into KMZ files and used by treatment crews to perform and record invasive vegetation management, detailing treatment activity using tracts and points in Google Earth. Images were provided with most point data, along with date, time, coordinates, and notes. Images were taken of pre-treatment and post-treatment vegetation. Images were used to verify the invasive species being treated at the listed coordinates and the quality of treatment. Additional information collected during treatment (e.g., herbicide use [L/ha]) was provided within a constant-contact style data management system. Treatment consisted of herbicide use, hacking, girdling, and cut and spray treatments. On all sites, 41% glyphosate in a concentration of approximately 25.1 ml per liter was used for spraying directly on leafy vegetation. Garlon 3A (44.4% concentration) was used directly on cut or girdled stumps.

Study locations were selected from all state lands that received treatment in 2024 and were selected based on two main criteria: travel distance and amount of herbicide used (L/ha). To maximize both efficiency and economics, travel distance was limited to a maximum of 145 km one direction from West Virginia University's Morgantown campus. From the state lands within this distance, we selected sites with the highest amount of herbicide use, which is indicative of invasive intensity. With these criteria in mind, we selected four study WMAs: Burnsville Lake WMA (Napier, Braxton County, WV), Bear Rock Lake (Valley Grove, Ohio County, WV), Castleman Run WMA (Bethany, Ohio County, WV), and Pleasant Creek WMA (Grafton, Taylor County, WV).

These WMAs are all examples of dry-mesic oak, apart from a portion of Castleman Run's plots, which are a mixed mesophytic forest. Common native overstory species included black oak (*Quercus velutina*), white oak (*Quercus alba*), chestnut oak (*Quercus montana*), northern red oak (*Quercus rubra*), as well as pignut hickory (*Carya glabra*), mockernut hickory (*Carya tomentosa*), and shagbark hickory (*Carya ovata*). Other overstory species included yellow-poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), black cherry (*Prunus serotina*), black gum (*Nyssa sylvatica*), and American beech (*Fagus grandifolia*). The native midstory and understory species consisted primarily of serviceberry (*Amelanchier arborea*), staghorn sumac (*Rhus typhina*), American holly (*Ilex opaca*), flowering dogwood (*Cornus florida*), and hop hornbeam (*Ostrya virginiana*). Native ground cover and vine species identified include clearweed (*Pilea pumila*), Christmas fern (*Polystichum acrostichoides*), wood fern (*Dryopteris spp.*), white snakeroot (*Ageratina altissima*), and Virginia creeper (*Parthenocissus quinquefolia*), among others.

To make comparisons between treated and untreated sites, we assumed that the initial composition of invasive species (woody and herbaceous) was similar within WMAs, but not between WMAs. While there is a possibility that invasive species compositions differed prior to treatment, we assumed that due to proximity and similar conditions, these compositions are comparable. Target species that received treatment included non-native woody and liana species: kudzu (*Pueraria montana* var. *lobata*), Russian olive (*Elaeagnus angustifolia*), wisteria (*Wisteria sinensis*), paulownia (*Paulownia* spp.), Japanese knotweed (*Fallopia japonica*), Japanese honeysuckle (*Lonicera japonica*), border privet (*Ligustrum obtusifolium*), autumn olive (*Elaeagnus umbellata*), Chinese privet (*Ligustrum sinense*), Japanese Barberry (*Berberis thunbergii*), Amur honeysuckle (*Lonicera maackii*), tree-of-heaven (*Ailanthus altissima*), multiflora rose (*Rosa multiflora*), mile-a-minute (*Persicaria perfoliata*), oriental bittersweet (*Celastrus orbiculatus*), and buckthorn (*Rhamnus cathartica* and *Rhamnus frangula*). Herbaceous species, such as Japanese stilt grass (*Microstegium vimineum*) and garlic mustard (*Alliaria petiolata*), did not receive targeted treatment due to their persistent seed bank and rapid spread that requires additional treatment measures (Pile Knapp et al., 2023).

Pleasant Creek WMA had the highest amount of herbicide use per hectare (312.6 L/ha). Based on the amount of herbicide used and photos of treatment, this site was heavily invaded and experienced a loss of canopy in much of its treatment area. Invasive species in the over and mid story include tree-of-heaven (*Ailanthus altissima*) and autumn olive. Herbaceous, understory invasive species include multiflora rose (*Rosa multiflora*), Japanese stiltgrass (*Microstegium vimineum*), Japanese barberry (*Berberis thunbergii*), Amur honeysuckle (*Lonicera maackii*), oriental lady's thumb (*Persicaria longiseta*), and garlic mustard (*Alliaria petiolata*). Burnsville Lake WMA had an herbicide use amount of 119.8 L/ha, with a high dominance of autumn olive

in the midstory. Other invasive species present at Burnsville Lake WMA included multiflora rose, garlic mustard, oriental lady's thumb, and Japanese stiltgrass. Castleman Rock WMA and Bear Rock Lake had relatively lower herbicide use per acre (82.8 L/ha and 51.3 L/ha, respectively) and similar invasive species composition. These WMAs were primarily invaded by multiflora rose, Japanese barberry, oriental lady's thumb, and privet species (Chinese and border) (*Ligustrum spp.*).

2.1.2 Site Characteristics

We established fifteen 0.02 ha sampling plots throughout each WMAs, totaling 60 sites. Sites included a gradient of various environmental conditions. Sampling plot centers were marked with tape to ensure replication when completing vegetation and soil sampling. GPS points were marked for each plot, at plot center, using the Avenza Maps app (Avenza Systems Inc.). This information was exported into ArcGIS Pro (ver. 3.5.0), where the slope, aspect, and elevation for each site were extracted from the point data. Soil temperature and soil moisture were measured during each salamander sampling occasion and during our vegetation sampling using an OGETFUUR 4-in-1 digital soil tester inserted at a 2 cm depth. We also measured lumen (light) amounts during each diurnal sample. pH was only recorded once per plot, during vegetation sampling. We chose to not use a more intensive soil temperature and moisture measuring process due to the frequency and difficulty of terrain during sampling. Leaf litter depth was collected by measuring five points within our 0.02 ha, by using a ruler to estimate leaf litter depth. The five points included plot center, and then four randomly selected points.

2.1.3 Vegetation Sampling

Understory vegetation sampling was completed in the late summer, before fall senescence. At each site, four 1m² quadrats were used to estimate the understory vegetation and

coarse woody debris cover. Within the quadrat, we identified the vegetation to species, aside from native grass species. Then, we estimated the percent cover of each species and coarse woody debris within the quadrat.

Overstory sampling was conducted by recording species and diameter at breast height (DBH) all woody vegetation with a DBH ≥ 10.16 cm within our 0.02 ha plot. We then recorded species and DBH for all stems between 2.54 cm and 10.16 cm within a 0.009 ha plot, located around the same plot center. Canopy cover (%) was determined by taking a photo at approximately breast height (approx. 1.5m) (Xiong et al., 2019). Then, using ImageJ (Version 1.54p; Schneider et al., 2012) a binary version of the image was created. Canopy cover (%) was determined by dividing the number of pixels representing canopy cover by the total pixel amount.

2.1.4 Salamander Sampling

Salamander sampling was conducted during the mid-spring to mid-fall of 2025, with most of the sampling occurring during mid-Spring to early Summer, and early Fall. This was done to increase likelihood of detection due to favorable temperature and moisture conditions. In compliance with special provisions outlined in the Scientific Collecting Permit granted by the West Virginia Division of Natural Resources, decontamination protocols were conducted during each sample. These protocols are detailed by the Northeastern Partners in Amphibian and Reptile Conservation and include the use of Virkon Aquatic ® 1% solution as a disinfectant for personal gear and equipment to prevent the spread of herpetofaunal diseases (e.g., Ranavirus spp. [RV], Batrachochytrium dendrobatidis [Bd], and B. salamandriovorus [Bsal]) (Bletz et al., 2023).

Sampling across all sites was conducted in a stretch of two to four consecutive days, to increase the probability of similar weather conditions between sites. There were six sampling

occasions conducted during diurnal conditions, and a similar six sampling occasions conducted during nocturnal conditions. These samples alternated, beginning with diurnal sampling in our first week, doing nocturnal sampling during our second, and continuing respectively. This totaled 12 samples collected for each site.

At each site, six 0.61 m x 0.15 m yellow-poplar coverboards were placed within our 0.02 ha plot (Figure 1). Coverboards were placed on both treated and untreated plots, and used to increase the likelihood of salamander detection, even in unfavorable conditions. Coverboards were checked in tandem with the visual sampling at each plot.

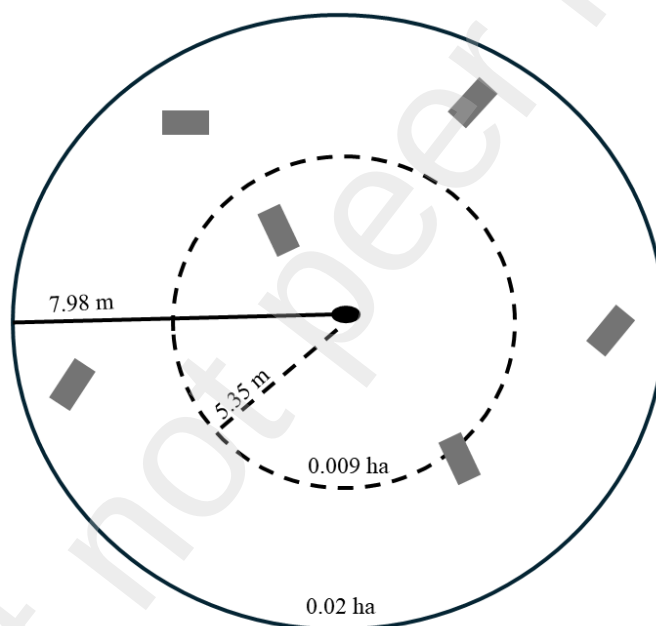


Figure 1: Each site had six 0.61 m x 0.15 m yellow-poplar coverboards placed around a 0.02 ha area from the plot center. Coverboards were placed in microhabitats most suited for salamander detection (e.g., preexisting cover, shade, wet areas). The 0.02 ha plot was also used to measure trees above 10.16 cm DBH. Trees within 2.54 cm to 10.16 DBH class were measured within the 0.009 ha plot.

Along with the coverboards surveys, visual sampling was conducted during each visit. Visual sampling consisted of actively searching for salamanders within the site. This included overturning logs, stones, leaf litter, and other potential covers. Refugia was returned to original placement if moved. During nocturnal sampling, headlamps were used. When located,

salamanders were identified to the species level and recorded whether they were found visually or under a coverboard. Per provisions outlined in the Scientific Collecting Permit, powderless nitrile gloves sprayed with dechlorinated water were used to handle salamanders for identification if necessary.

We detected 4 eastern newts (*Notophthalmus viridescens*) during our sampling occasions. Due to their similar habitat requirements and ecological roles, we included *N. viridescens* detections in our dataset. *N. viridescens* has also been referenced as an indicator species in previous studies, making it functionally similar to *Plethodontid* salamanders (Siddig et al., 2016b, Mossman et al., 2019).

We standardized survey effort by adjusting the amount of time sampled at each site based on the amount of people within the sampling crew. If there was a single sampler, sampling would last ten minutes, and if there were four samplers, they would sample for 2.5 minutes simultaneously. Crew sizes ranged from 1-5 people. We also randomized the order plots sampled to reduce the chance of inducing sampling bias related to the timing of surveys. This was done by grouping sites into clumps based on similar locations and randomizing the order in which those clumps were sampled. Additionally, the order in which WMAs were sampled were also alternated week to week to reduce the likelihood of fatigue at a particular WMA.

2.1.5 Statistical analysis

Before beginning the analysis, we tested all covariates for correlations using Pearson's correlation coefficient. Any correlation value of ≥ 0.65 between a pair of variables resulted in the exclusion of one of the variables (retained variables included in Table 1). For each correlated pair, we excluded variables that showed multiple high correlations, lacked strong support in the literature, or whose effects were adequately represented by a correlated alternative (e.g.,

retaining basal area and excluding trees per hectare). To account for imperfect detection, we used single-season, single-species occupancy modeling in RStudio (ver. 2026.01.0+392, R ver. 4.5.1) using package “unmarked” (ver. 1.5.1) (MacKenzie et al., 2002; Kellner et al., 2023; Fiske & Chandler, 2011). Two fundamental parameters are estimated with this model type; occupancy (ψ), the probability that a species is present at a site, and detection (p), the probability that the species will be detected if present.

We used single-species, single-season occupancy models to account for imperfect species detection and to estimate detection and species-specific occupancy probabilities. Single-season occupancy models assume site-closure, meaning occupancy status and site location and size do not change within the sampling period. We anticipated the potential for harsh conditions in the summer months (e.g., drier soil, hotter soil temperatures), which could cause salamanders to retreat from a site. To address this hypothesis while simultaneously accounting for the closure assumption, we coded ‘Season’ as a site covariate to test for differences in occupancy between ‘Spring’ (May-June 2025) and ‘Fall’ (September-October 2025), excluding two sampling occasions that took place during mid-summer. Single-season occupancy models assume that detection probability is less than one, meaning that species may be present at a site but not be detected. Single-season occupancy models also assume that sampling methods used are suitable for detecting focal taxa when present. We addressed this assumption by conducting repeated diurnal and nocturnal visual surveys and incorporating soil-temperature as an observation-level covariate, accounting for variation in surface activity.

We assumed similar detectability among *Plethodontids* due to their comparable surface activity patterns (Grover, 2006; Sanchez et al., 2020; Sites, Jr., 1978; O’Donnell et al., 2014; Anderson et al., 2025). Therefore, we constrained the detection parameters to be equal across all

species. This allowed us to estimate detection probabilities with adequate precision given limited detections for several species. We estimated the occupancy for our 8 detected species by coding each species as a factor (with 8 levels). Due to multiple species being modeled within the same sites, species-specific occupancy estimates shared site-level covariates. Consequently, we emphasize shared habitat effects and interpret species-specific intercepts as baseline differences rather than independent, site-level responses. All continuous covariates were scaled by using the methods described in Gelman (2008), in which the mean is subtracted by each value and divided by two standard deviations to allow for comparisons between binary and continuous covariates.

Table 1
Covariates retained after testing for correlated variables to be used in the analyses of occupancy and detection of *Plethodontid* salamanders on West Virginia WMAs that received invasive plant control treatments. Any pair with a correlation value ≥ 0.65 resulted in the exclusion of one of the variables.

Variable	Model Parameter	Description	Source
Season	ψ	Seasonal grouping of Sampling occasions 1-6 (Spring) and 7-10 (Fall)	Individual survey
Slope	ψ	Rate of change of elevation for a site (degrees)	Treatment KMZ in ArcGIS
Aspect	ψ	Compass direction that downhill slope of a site faces (degrees)	Treatment KMZ in ArcGIS
Treatment	ψ	Indicator of presence or absence of invasive plant control treatment	Treatment KMZ in ArcGIS
Canopy Cover	ψ	Percent canopy cover, measured from binary pixel percentage (ImageJ)	Vegetation survey
Soil pH	ψ	Measure of hydrogen ion concentration in the soil at the site center	Vegetation survey
Average Soil Temperature (D)	ψ	Average soil temperature ($^{\circ}\text{C}$) readings	Individual survey
Coarse Woody Debris Percentage	ψ	Mean percent cover of coarse woody debris across 4 quadrats at a site	Vegetation survey
Average DBH (0.02)	ψ	Average diameter at breast height (cm) within the 0.02 ha plot at each site	Vegetation survey
Sum BA/ha (0.02)	ψ	Sum of the estimated basal area per hectare within the 0.02 ha plot at each site	Vegetation survey
Average DBH (0.009)	ψ	Average diameter at breast height (cm) within the 0.009 ha plot at each site	Vegetation survey
Sum BA/ha (0.009)	ψ	Sum of the estimated basal area per hectare within the 0.009 ha plot at each site	Vegetation survey
Ground Cover Richness	ψ	Count of different species (native and invasive) within 4 quadrats within a site	Vegetation survey
Invasive Ground Cover Richness	ψ	Count of different species (invasive) within 4 quadrats within a site	Vegetation survey
Invasive Ground Cover	ψ	Average percentage ground cover of invasive plant species (woody and herbaceous)	Vegetation survey
Soil Temperature	p	Soil temperature at time of sampling ($^{\circ}\text{C}$)	Individual survey
Soil Moisture	p	Soil moisture at the time of sampling (%)	Individual survey
Precipitation	p	Amount of rainfall within 24 hours prior to sampling (cm)	Individual survey
Lumen	p	Perceived power of visible light measured from forest floor at the time of sampling	Individual survey

Table 2

Reduced set of covariates used in the analyses of occupancy (ψ) and detection (p) of *Plethodontid* salamanders on West Virginia WMAs that received invasive plant control treatments. We reduced our covariate set to target our research objectives (identifying impacts of invasive plant control treatment and invasive ground cover), as well as addressing results in previous literature. Season was included to accommodate the closure assumption of single-season occupancy models. Canopy cover was retained due to the well-established importance of canopy cover for *Plethodontid* habitat, especially regarding silvicultural management. Canopy cover, while not correlated with soil moisture and refugia availability (% CWD) in our dataset, is associated with increased soil moisture and refugia in previous studies. Soil temperature was retained as the most practical detection covariate because of recent data suggesting variation in species detectability patterns across soil moisture and precipitation gradients.

Variable	Model Parameter	Description	Source	Citation
Canopy cover	ψ	Percent canopy cover, measured from binary pixel percentage (ImageJ)	Vegetation survey	O'Donnell et al., 2014; Ochs et al. 2022; Semlitsch et al., 2009; Tilghman et al., 2012; Connette & Semlitsch, 2013; O'Donnell et al., 2015
Invasive ground cover	ψ	Average percent ground cover of invasive plant species (woody and herbaceous)	Vegetation survey	Lehtinen et al., 2022
Season	ψ	Seasonal grouping of Sampling occasions 1-6 (Spring) and 7-10 (Fall)	Individual survey	
Treatment	ψ	Indicator of presence or absence of invasive plant control treatment	KMZ files from Treatment crew	Lehtinen et al., 2022
Soil temperature	p	Soil temperature at time of sampling (°C)	Individual survey	Lehtinen et al., 2026

We limited the number of parameters of our global model to 13 parameters, including the 8 intercepts representing the 8 different species to avoid overfitting the data while still allowing for interspecific variation in occupancy. With 60 sites and 12 sampling occasions, we constrained our set of covariates to a small set of effects supported by previous literature and our hypotheses (canopy cover, invasive ground cover, season, and treatment) (O'Donnell et al., 2014; Ochs et al., 2022; Semlitsch et al., 2009; Tilghman et al., 2012; Connette & Semlitsch, 2013; O'Donnell et al., 2015; Lehtinen et al., 2022; Lehtinen et al., 2026), while including species-specific intercepts to model interspecific heterogeneity in baseline occupancy (Table 2).

We also reduced the detection model to only include soil temperature to reduce complexity, as it was the most supported of the detection parameters in the literature (Shoo et al., 2011). We first developed an initial global model based on prior knowledge of salamander habitat conditions (Farallo & Miles, 2016) and compared this with a model that included 'season' as an additional variable to determine the validity of its inclusion in future models. Based on the model comparison results, season was retained as a variable to explain occupancy (a factor, with two levels) and included into the final global model.

The final global model included soil temperature as a detection covariate and species-specific intercepts and the full set of supported site-level covariates (season, canopy cover, treatment, and invasive ground cover) as occupancy covariates. We also included three biologically relevant interaction models (canopy cover x treatment, canopy cover x season, and treatment x season) to observe any occupancy differences that could be explained by habitat or season. Post-hoc, we added two models to infer the importance of covariates included in all a priori models, one excluding soil temperatures as a detection covariate, and one excluding canopy cover as an occupancy covariate.

We ranked models based on Akaike's Information Criterion values adjusted for small sample size (AICc; Akaike 1973, Anderson et al., 1998) and the difference between a candidate model and the top model in the set ($\Delta AICc$). We also used Akaike weights (ω_i) to determine the weight of evidence in favor of each model in the set. We considered models with $\Delta AICc \leq 2$ as having substantial support. We did not perform model averaging because of our focus being on inference, not prediction. Competing models also differed primarily by inclusion of uninformative covariates. Using suggestions outlined in Arnold (2010), we determined whether additional parameters meaningfully improved fit relative to added complexity. Models

containing parameters with confidence intervals overlapping zero that did not reduce AICc by ≥ 2 were acknowledged to include uninformative parameters and were discarded. With multiple models within $\Delta\text{AICc} \leq 2$, we prioritized biological relevance and parsimony in model selection, particularly to evaluate relationships outlined in our hypotheses. We retained the most parsimonious model that included covariates with statistical significance and clear ecological justification.

3.1 Results

3.1.1 Descriptive Summary

During spring to fall of 2025, we performed 720 visual encounter surveys at 60 sites (≈ 120 person hours [720 site sampling occasions, 10 minutes each]). Surveys included portions of the northern panhandle and central West Virginia. Each site was surveyed 12 times, 6 times diurnally and 6 times nocturnally each. We encountered salamanders on 39 of the 60 sites, yielding a naïve occupancy of 0.65. Nineteen of the 39 sites had ≥ 2 salamander detections, and 13 sites had ≥ 2 species detected. We detected the following species with respective counts: *Plethodon cinereus* (116), *Plethodon glutinosus* (25), *Eurycea bislineata* (6), *Notophthalmus viridescens* (3), *Desmognathus ochropheaus* (4), *Plethodon electromorphus* (2), *Eurycea longicauda* (2), and *Desmognathus fuscus* (1).

Across all sites, percent canopy cover averaged $67.44\% \pm 2.53$ SE (range = 0% - 87.97%). Percent invasive ground cover averaged $56.34\% \pm 4.83$ SE, suggesting high average invasion intensity. Twenty-four of the 60 sites did not receive invasive plant control treatment ('Untreated'), and the other 36 received invasive plant control treatment to some degree (e.g., hacking/cutting, herbicide application). Sampling occasions 7 and 8 were omitted from the final analysis to establish a distinct 'Season' factor, as they were within the period in which we

hypothesize salamanders may have been emigrating out of sites. Sampling occasions 1-6 took place from mid-May 2025 to late June 2025 and were labeled as ‘Spring’ sampling occasions. Occasions 9-12 were categorized as ‘Fall’ sampling occasions, taking place during late September 2025 to late October 2025. The exclusion of sampling occasions 7 and 8 resulted in the exclusion of 6 salamander detections, bringing the total number of salamander detections used in our occupancy modelling to 154, excluding 4 *Plethodon glutinosus*, 1 *Notophthalmus viridescens*, and 1 *Eurycea longicauda*.

3.1.2 Occupancy Model Results

Our initial model selection procedure supported the inclusion of season as a factor to explain changes in occupancy between spring and fall. The seasonal model had lower AIC_c ($\Delta\text{AIC}_c = 6.25$) and received 95.8% of model weight relative to the model without season included. Season was a significant predictor of occupancy ($\beta = -1.07 \pm 0.41$ SE, 85% CI: [-1.65 to -0.48]), suggesting lower odds of salamander occupancy in fall sampling occasions compared to spring sampling occasions. Both models retained temperature as a detection covariate, demonstrating that occupancy varied between seasons independent of soil temperature.

Model selection supported a model that also included canopy cover as an essential predictor of salamander occupancy ($\beta = 1.33 \pm 0.47$ SE, 85% CI: [0.47 to 1.84]), with increased probability of occupancy at sites with greater percent canopy coverage. Removing canopy cover reduced model support ($\Delta\text{AIC} = 4.84$). Treatment effects with reduced salamander occupancy odds on treated sites ($\beta \approx -0.546 \pm 0.37$ SE, 85% CI: [-1.07 to -0.02]).

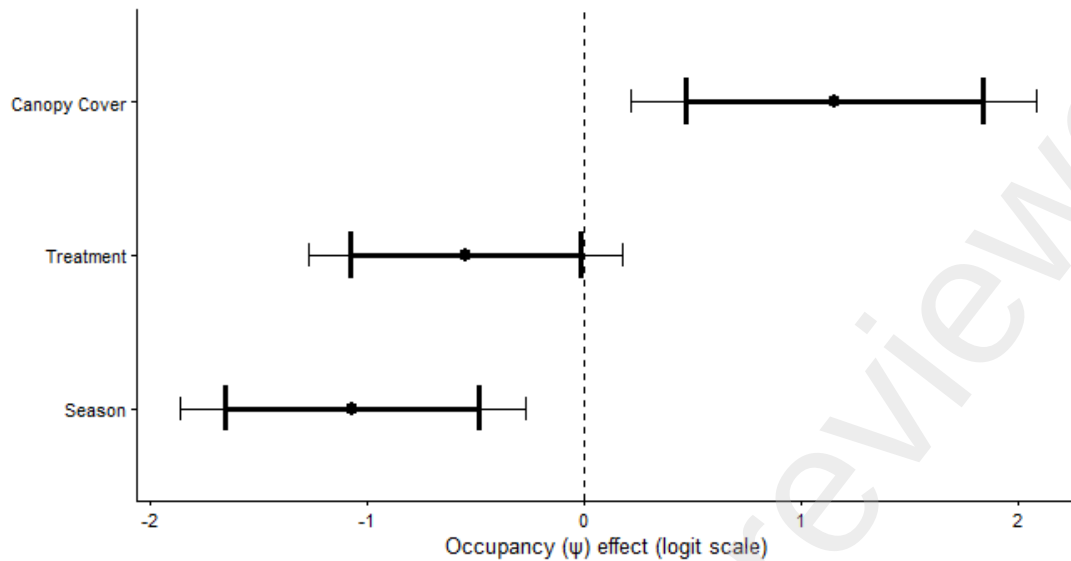


Figure 2: Covariate effects on salamander occupancy (ψ) throughout WMAs in West Virginia, USA. All covariates included are present in the top-ranked model. Covariate effect estimates on salamander occupancy (logit scale) are represented by points. 85% confidence intervals and 95% intervals for each covariate estimate are represented by thick and thin bars, respectively.

Invasive Ground Cover ($\beta \approx -0.06 \pm 0.38$ SE, 85% CI: [-0.60 to 0.49]) was uninformative. Our top model's -2loglikelihood value (720.37) was still preferred to that of the -2loglikelihood value of the global model, which includes invasive ground cover (720.35) (Table 3). Therefore, we cannot conclude a relationship between invasive ground cover and salamander occupancy odds from our data. None of the interaction terms modeled (canopy cover*treatment, canopy cover*season, treatment*season) outperformed additive models. Additionally, including interaction terms caused substantial variance inflation due to the additional parameters.

Table 3

Complete model set results for *Plethodontid* salamander occupancy (ψ) throughout WMAs in West Virginia, USA. Header 'Model' represents the model evaluated. 'AICc' indicates the values produced from the Akaike's Information Criterion adjusted for small sample size. Δ AICc represents Delta AICc and indicates difference between a model and a top-ranked model. w represents model weight. K indicates the number of parameters included in each model.

Model	AICc	Δ AICc	-2loglik	w	K
ψ (~0 + Species + Season + Canopy Cover + Treatment), p (Soil Temperature)	746.37	0.00	720.37	0.250	13
ψ (~0 + Species + Season + Canopy Cover), p (Soil Temperature)	746.61	0.24	722.61	0.221	12
ψ (~0 + Species + Season + Canopy Cover x Treatment), p (Soil Temperature)	747.26	0.89	719.26	0.160	14
ψ (~0 + Species + Season + Treatment x Season), p (Soil Temperature)	747.49	1.12	719.49	0.143	14
ψ (~0 + Species + Season + Canopy Cover x Season), p (Soil Temperature)	748.03	1.65	720.03	0.109	14
ψ (~0 + Species + Season + Canopy Cover + Treatment + Invasive Ground Cover), p (Soil Temperature)	748.35	1.98	720.35	0.093	14
ψ (~0 + Species + Season + Treatment), p (Soil Temperature)	751.22	4.84	727.22	0.022	12
ψ (~0 + Species + Season + Canopy Cover + Treatment + Invasive Ground Cover), p (.)	789.84	43.47	763.84	0.000	13

The inclusion of species-specific intercepts accounted for substantial heterogeneity in baseline occupancy estimates among salamanders. Species occupancy intercepts ranged from -6.35 to -1.37 (on the logit scale) respectively (Figure 2). Baseline occupancy probability varied among species, ranging from $\psi = 0.003$ (85% CI: 0.000 to 0.023) for species including *Desmognathus fuscus*, *Eurycea longicauda*, and *Desmognathus ochrophaeus* to $\psi = 0.323$ (85% CI: 0.099 to 0.675) for *Plethodon cinereus* (Table 4). Species identity explained more variance than any individual habitat occupancy covariate. The inclusion of species intercepts increased parameter count but prevented the confounding of habitat effects with intrinsic species rarity differences and improved habitat covariate interpretability.

Table 4

Occupancy (Ψ) Probability Estimates for each salamander species detected throughout WMAs in West Virginia, USA. 'Species' represents the scientific species name of the salamander species in which we are estimating occupancy probability for. ' Ψ Probability Estimate' is the logit-scale species intercept from the top-ranked model transformed to a probability estimate. '85% CI' and '95% CI' represent the logit-scale 85% confidence interval and 95% confidence interval of occupancy estimates transformed to probability estimates.

Species	Ψ Probability Estimate	85% CI	95% CI
<i>Plethodon cinereus</i>	0.323	0.099-0.675	0.061-0.779
<i>Plethodon glutinosus</i>	0.055	0.013-0.199	0.008-0.296
<i>Eurycea bislineata</i>	0.021	0.005-0.088	0.003-0.144
<i>Notophthalmus viridescens</i>	0.010	0.002-0.049	0.001-0.085
<i>Plethodon electromorphus</i>	0.007	0.001-0.036	0.001-0.065
<i>Desmognathus fuscus</i>	0.003	0.000-0.023	0.000-0.047
<i>Eurycea longicauda</i>	0.003	0.000-0.023	0.000-0.047
<i>Desmognathus ochrophaeus</i>	0.003	0.000-0.023	0.000-0.047

Soil temperature as a detection covariate greatly improved model fit ($\Delta AIC = 41.47$). Soil temperature has strong support as a predictor of salamander detection ($\beta = -1.70 \pm 0.27$ SE, 85% CI: [-2.08 to -1.30]), indicating that higher soil temperatures decrease the odds of detecting salamanders even if they occupy a site. At mean soil temperature (16.3°C), detection probability given that a site was occupied increased to 0.16 ($\beta = 0.16 \pm 0.02$ SE, 85% CI: [0.12 to 0.19]). Detection estimates were modeled as shared across species, as *Plethodontids* respond similarly to conditions that impact detectability (Sanchez et al., 2020; Anderson et al., 2025).

4.1 Discussion

We modeled salamander occupancy using site and detection covariates from hardwood forests in West Virginia that underwent invasive plant control treatments. Habitat structure, treatment, and species-specific variation accounted for much of occupancy variability. Naïve detection across all sites was low (0.02), but when modeled explicitly, detection probability conditional on occupancy was higher (0.16) at mean temperature (16.3°C). We recommend conducting similar sampling efforts, potentially using Before and After Impact frameworks

(BAI) or monitoring recovery patterns multiple years post-treatment. Collectively, our results suggest that *Plethodontid* occupancy is structured primarily by intrinsic interspecific differences, forest canopy structure, and treatment impacts, while invasive ground cover effects were uninformative. This suggests that while treatment impacts may negatively reduce salamander occupancy odds, the retention of canopy during treatment efforts may help mitigate negative impacts for *Plethodontid* salamanders and their related ecosystem services.

4.1.1 Detectability

Soil temperature as a detection covariate was an important predictor in our model, with model fit drastically declining without it ($\Delta AIC = 41.47$). Soil temperature has an established effect on salamander detectability, with many previous studies referencing the detectability of salamanders declining at higher soil temperatures (Sanchez et al., 2020; Anderson et al., 2025). As soils warm, salamanders burrow beneath the surface of the soil to maintain moderate temperatures and support respiration. Periods of desiccation occur when soils are too hot or dry to support salamander's respiration through skin and their temperature regulation. In our study, when soil temperature was at or below its mean (16.3°C), salamanders were moderately detectable given that the site was occupied (0.16), across both treated and untreated sites.

Accounting for the effect of soil temperature at each site during each sampling occasion was highly important in determining occupancy effects, so the impacts of soil temperature were not incorrectly attributed to an occupancy covariate. Additionally, soil temperature's importance as a detection covariate was consistent across all models, suggesting that it is robust and independent of occupancy covariate effects. The precipitation and temperature patterns of 2025 included record high temperatures, and drought periods in spring and late summer (West

Virginia Department of Agriculture [WVDA], 2025). These conditions could have created microhabitat soil temperatures that were the primary determinant of detection.

In future studies observing salamander occupancy at large spatial scales, incorporating soil temperature's impact on detectability is highly important. To perform productive, informative samples in an energy and cost-efficient manner, soil temperature impacts should be considered in study design. Sampling during moderate temperatures (at or near 16.3°) increases detection probability. Incorporating observation-level soil temperature into future *Plethodontid* occupancy modeling and study design is imperative, as not accounting for soil temperature at the time of observation may attribute variance to occupancy components, rather than variation in detectability.

4.1.2 Occupancy

Of the three site-level covariates that we included in our occupancy modeling, canopy cover had the highest explanatory power of salamander occupancy. Canopy cover, however, came second in predictive power when compared to including species-specific occupancy intercepts. Separate occupancy intercepts attributed inherent species occupancy differences to variation in our model that would otherwise be inaccurately attributed to a site-level covariate. Occupancy covariate slopes (canopy cover, invasive ground cover, treatment) were modeled as shared across species, although variation was higher in species with infrequent detections. Due to species rarity differences observed in our data, as seen in *Desmognathus spp.* and *Eurycea spp.*, these species may be less suitable to use as stand-alone indicator species for the purpose monitoring large-scale ecosystem changes. These species have been referenced in previous studies as indicator species (Barrett & Price, 2014; Southerland et al., 2004), but for central Appalachian hardwood forests, they may be too sparsely distributed or reliant on adjacent

aquatic habitats to provide data for adequate conclusions without the inclusion of other species of *Plethodontidae*.

Canopy cover at the site level was also an important predictor of occupancy. Occupancy odds increased 3.8-fold (280%) with one standard deviation increase of percent canopy cover. Canopy cover has known moisture retention and microclimate buffering capacity (Ochs et al., 2022), which creates ideal habitat for *Plethodontids*. Areas with sufficient canopy cover may retain moderate temperatures and higher soil moisture throughout summer months, decreasing the likelihood of a desiccation event. It is well-documented that substantial alteration of forest structure can be detrimental to salamander populations (Gibbs, 1998; Hocking et al., 2013). Loss of canopy could reduce a site's ability to mediate soil temperatures as temperature extremes increase during summer months, potentially causing salamanders to die, retreat, or evacuate (Semlitsch et al., 2008). Our results suggest that areas with low canopy cover are less likely to be occupied by *Plethodontids*, which is consistent with previous studies.

Season was included in occupancy covariates to accommodate occupancy changes between Spring to Fall 2025. Relative to species and canopy effects, season was a minor predictor of occupancy. Differences in occupancy between the seasons could represent phenological differences or indicate decreased occupancy in areas post-desiccation period (Summer 2025). Summer 2025 had a long period of drought in the Central Appalachian region, with the WVDA stating that by September 23, 2025, 94% of West Virginia was experiencing moderate (D1) to extreme (D3) drought conditions (WVDA, 2025). Additionally, July 2025 was the hottest July on record for the state of West Virginia. Due to these conditions, a change in occupancy between Spring 2025 and Fall 2025 may represent the emigration of salamanders from sites that do not adequately buffer against intense moisture and temperature conditions.

While these sites may have been able to accommodate salamander habitat requirements throughout Fall 2024-Spring 2025, the intensive summer conditions may have resulted in the loss of salamander occupancy, whether through mortality or emigration. It is worth noting that this result is not conclusive and may be due to inherent phenological variation in salamander occupancy. However, salamanders have reported low vagility and little documentation of phenological variation in habitat occupancy (Farello & Miles, 2016; Cabe et al., 2007).

Treatment effects on salamander occupancy in our data are negative, and statistically significant at an 85% confidence interval. This suggests that sites treated for invasive plant control, odds of salamander occupancy decreased. The potential impact of treatment as a covariate could be due to herbicide application, vegetation structure changes, or both. Notably, there is limited research on the impact of herbicides on adult *Plethodontids*. However, Gertzog et al. (2011) found that *P. cinereus* will behaviorally avoid herbicides at 10-100% of the herbicide's full concentration. Additionally, the intensity of treatment varied, with some sites losing most or all vegetation structure, and some losing only minor understory vegetation. Our results suggest that invasive plant control treatments, through various mechanisms encompassed by categorical 'Treatment', decrease odds of salamander occupancy, which is consistent with previous findings (Lehtinen et al., 2022).

As suggested by Lehtinen et al. (2022), treatment impacts on occupancy may be due to increased perceived predation risk. Salamanders may perceive predation risk to be higher in sites with less vegetation structure, prompting emigration (Forester et al., 2019). Lehtinen et al. argued that this is a more feasible explanation than other factors (herbicide, arboreal foraging, and human physical trampling). Notably, soil moisture and temperature did not differ significantly between treated and untreated sites in Lehtinen et al.'s study. In our study, due to the high

intensity of invasion on sites, soil conditions were likely altered from treatment. The findings of our study suggest that invasive plant control treatments can reduce salamander occupancy odds one year post treatment, suggesting microhabitat degradation and alteration of crucial ecosystem services.

We found no evidence to suggest that percent invasive plant species ground cover explains salamander occupancy. Our results, therefore, cannot provide clarity to the limited data available on adult terrestrial salamander interactions with invasive plants. Aside from documented harmful impacts to larval stage amphibians, there is little evidence to support the claim from this study that invasive plants negatively affect adult salamanders. The microclimate conditions created by sites dominated by invasives are potentially similar enough to native microclimate conditions to support similar occupancy odds of *Plethodontid* salamanders. Our data further supports the hypothesis that complex vegetative structure is a more reliable predictor of salamander occupancy than the species composition.

4.1.3 Management Implications

Our results suggest that due to invasive plant control treatment negatively impacting *Plethodontid* occupancy, retention of canopy cover is crucial to retaining quality habitat for *Plethodontids* and their ecosystem services. This is supported by previous studies, acknowledging the importance of retaining a percentage of canopy cover post timber harvest (Ochs et al., 2022). Without adequate canopy to buffer temperatures, microhabitats may be more susceptible to desiccation events. This is increasingly important with projected extreme temperatures in summer and fall seasons, as well as projected moisture extremes in the Appalachian region (Butler et al., 2015). As these temperatures rise, canopy cover will likely be the first line of defense against desiccation risk. Previous studies suggest 50-60% retention of

canopy in order to mitigate losses to *Plethodontid* populations (Ross et al., 2000; Knapp et al., 2003; Semlitsch et al., 2009). However, in highly invaded landscapes, this may be impractical. A similar alternative may be to retain or provide supplementary refugia for *Plethodontids* to utilize during harsh conditions. Additionally, seasonality of invasive plant control treatment may allow for vegetative recovery in the understory to provide cover prior to harsh temperature conditions. Performing invasive plant control treatment, particularly hack-and-spray efforts, in fall or winter may act as a buffer by allowing for vegetation growth before intense summer conditions. Coupling hack-and-spray treatments with immediately planting native seedlings may provide effective invasive plant control treatment while restoring salamander habitat, as originally suggested in Lehtinen et al. (2022).

Our results were inconclusive regarding the impacts of invasive plant ground cover on salamander occupancy. While there are potential negative effects of invasive vegetation in native landscapes, such as altering soil conditions and forest regeneration (Early et al., 2016), we could not draw a conclusion of an association with adult *Plethodontid* salamanders, and by proxy its related ecosystem services. This is important to consider when weighing the costs and benefits of performing invasive plant control treatments. If retaining ecosystem services is the main target of treatments, the treatments themselves have the potential to be more damaging to ecosystem function than the invasion itself. However, this is with the assumption that our current understanding of invasive plant's impact on ecosystem services is thorough and accurate and that we are observing only immediate impacts. Observing the long-term impacts and recovery of *Plethodontids* on treated sites would provide a better understanding on the trade-offs of invasive plant control treatments. Additionally, *Plethodontid* salamander occupancy may not be indicative

of all ecosystem services and species. Species that are dependent on native vegetation may experience benefits from invasive plant control treatments.

The inclusion of species-specific intercepts highlights the role of *Plethodontid* species as indicators of ecosystem changes. For the purposes of large-scale, hardwood forest monitoring in central Appalachia, *Plethodon cinereus* is well-supported in our dataset as a quality indicator. Stream salamander species (genuses *Desmognathus* and *Eurycea*), due to sparse distribution and reliance on stream habitats, may be difficult to use as a stand-alone, large-scale indicator for ecosystem changes in central Appalachian hardwood forests. However, this is primarily due to *Plethodon cinereus*' role as an abundant generalist in contrast to less-abundant stream salamanders. Acknowledging inherent interspecific differences in distribution and utilizing all *Plethodontid* species as indicators can simplify sampling efforts at state-wide, multi-year scales.

Future studies should continue investigations into the relationship between *Plethodontid* salamanders and treatment effects, as well as *Plethodontid* salamanders and invasive plants. To gain a better understanding of the impacts of invasive plant control treatment, Before and After impact (BAI) frameworks would isolate the impacts of canopy loss directly. Additionally, being able to account for details such as species treated per site, herbicide amount applied per site, target vs. broad herbicide application, and similar metrics may provide a more thorough understanding of impacts on occupancy. Continuing to monitor occupancy across multiple years may also inform better understandings of ecosystem and *Plethodontid* recovery post-treatment. Predicting recovery time for *Plethodontids* may help inform management practices and planning when attempting to remove invasive plant species. As forests regenerate post-treatment, new vegetation growth can allow more ample refugia and temperature buffers to create conditions that are once again suitable for *Plethodontid* occupancy.

While our results do not convey a conclusive impact of invasive plants on salamander occupancy, continued exploration of relationships between invasive plants and *Plethodontids* is worthwhile, particularly as they become more established within forest landscapes. Understanding how they may impact *Plethodontid* habitat use, breeding, predation, detectability, and climate change adaptability are all important relationships that remain widely undescribed.

The growing emergence of biodiversity credit markets alongside traditional carbon offset programs further supports the importance of identifying reliable biological indicators of ecosystem conditions. Unlike carbon credits, which focus on a single aspect of a complex ecosystem, biodiversity credits incorporate metrics of ecological integrity and functional resilience (Wunder et al., 2025). *Plethodontid* salamanders are uniquely positioned to serve as this role in central Appalachian hardwood forests. *Plethodontids* require stable microclimates and thus reflect influences on and from canopy structure, soil conditions, detrital dynamics, and invertebrate prey availability (Welsh & Hodgson, 2013; Siddig et al., 2016b). Their occupancy reflects broader ecosystem processes including nutrient cycling, litter decomposition, and trophic regulation. Because our results demonstrate strong canopy-mediated occupancy patterns and substantial interspecific heterogeneity, *Plethodontid* responses may provide an early-warning system for microclimatic degradation or recovery following invasive species control efforts. Incorporating occupancy monitoring of *Plethodontids* into restoration frameworks can improve our ability to detect how invasive plant control treatments alter microclimate structure, habitat quality, and ecosystem stability, by revealing how treatment intensity and timing impact ecosystem recovery trajectories over time.

Acknowledgements

I wanted to thank the West Virginia state agencies that assisted in this project, including the WV Division of Natural Resources and the WV Division of Forestry. I also want to thank Isabelle Uganski for being the best fieldwork and research partner. I couldn't have made it through without you, and I hope that I have helped you half as much as you helped me.

Literature Cited

- Akaike, H. (1973). "Information Theory and an Extension of the Maximum Likelihood Principle." In Proceeding of the Second International Symposium on Information Theory, edited by B. N. Petrov and F. Csaki, 267–281. Budapest: Akademiai.
- Anderson, C. N., Pierson, T. W., Barrett, K., & Bodinof Jachowski, C. M. (2025). A comparison of detection probabilities for the patch-nosed salamander (*Urspelierpes brucei*) using six survey methods. *Wildlife Society Bulletin*, 49(1), e1562. <https://doi.org/10.1002/wsb.1562>
- Anderson, D. R., Burnham, K. P., & White, G. C. (1998). Comparison of Akaike information criterion and consistent Akaike information criterion for model selection and statistical inference from capture–recapture studies. *Journal of Applied Statistics*, 25(2), 263–282. <https://doi.org/10.1080/02664769823250>
- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*, 74, 1175–1178. <https://doi.org/10.1111/j.1937-2817.2010.tb01236.x>
- Arthur, M. A., Bray, S. R., Kuchle, C. R., & McEwan, R. W. (2012). The influence of the invasive shrub *Lonicera maackii* on leaf decomposition and microbial community

668 dynamics. *Plant Ecology*, 213(10), 1571–1582. <https://doi.org/10.1007/s11258-012->
669 0112-7

670 Avenza Systems Inc. (2025). *Avenza Maps*® (5.5, 262.custom). <https://www.avenzamaps.com/>

671 Barrett, K., & Price, S. J. (2014). Urbanization and stream salamanders: A review, conservation
672 options, and research needs. *Freshwater Science*, 33(3), 927–940.
673 <https://doi.org/10.1086/677556>

674 Best, M. (2012). Ecological role of the salamander *Ensatina eschscholtzii*: direct impacts on the
675 arthro-pod assemblage and indirect influence on the carbon cycle in mixed hardwood-
676 conifer forest in Northwestern California. Thesis. Humboldt State University, Arcata,
677 California, USA.

678 Bletz, M., Julian, J., Kirchgessner, M., Drasher, J., Henry, P., Jewell, S., Meier, P., Michell, K.,
679 Olori, J., Oxenrider, K., Ravesi, M., & Smith, S. (2023). Disinfection protocols for
680 herpetofaunal pathogens. *Herpetological Review*, 54, 200–203.

681 Bucciarelli, G. M., Blaustein, A. R., Garcia, T. S., & Kats, L. B. (2014). Invasion complexities:
682 The diverse impacts of nonnative species on amphibians. *Ichthyology & Herpetology*,
683 2014(4), 611–632. <https://doi.org/10.1643/OT-14-014>

684 Butler, P. R., Iverson, L. R., Thompson III, F. R., Brandt, L. A., Handler, S. D., Janowiak, M. K.,
685 Shannon, P. D., Swanston, C., Karriker, K., Bartig, J., Connolly, S., Dijak, W. D., Bearer,
686 S., Blatt, S. L., Brandon, A., Byers, E., Coon, C., Culbreth, T., Daly, J., Dorsey, W., Ede,
687 D., Euler, C., Gillies, N., Hix, D. M., Johnson, C., Lyte, L., Matthews, S., McCarthy, D.,
688 Minney, D., Murphy, D., O’Dea, C., Orwan, R., Peters, M., Prasad, A., Randall, C.,
689 Reed, J., Sandeno, C., Schuler, T., Sneddon, L., Stanley, B., Steele, A., Stout, S., Swaty,

- R., Teets, J., Tomon, I., Vanderhorst, J., Whatley, J., and N. Zegre. (2015). Central Appalachians forest ecosystem vulnerability assessment and synthesis: a report from the central Appalachians climate change response framework project. *General Technical Report NRS-146*. U.S. Department of Agriculture Forest Service, Newtown Square, Pennsylvania, USA. <https://doi.org/10.2737/NRS-GTR-146>
- Cabe, P. R., Page, R. B., Hanlon, T. J., Aldrich, M. E., Connors, L., & Marsh, D. M. (2007). Fine-scale population differentiation and gene flow in a terrestrial salamander (*Plethodon cinereus*). *Heredity*, 98(1), 53–60. <https://doi.org/10.1038/sj.hdy.6800905>
- Carter, S., Mills, C., Hao, Z., Mott, R., Hauser, C. E., White, M., Sharples, J., Taylor, J., & Moore, J. L. (2024). Spatial prioritization for widespread invasive species control: Trade-offs between current impact and future spread. *Ecological Applications*, 34(5), e2982. <https://doi.org/10.1002/eap.2982>
- Cipollini, K., & Wagner, K. (2011). Allelopathic effects of invasive species (*Alliaria petiolata*, *Lonicera maackii*, *Ranunculus ficaria*) in the Midwestern United States. *Allelopathy Journal*, 29, 63–76.
- Connette, G. M., & Semlitsch, R. D. (2013). Context-dependent movement behavior of woodland salamanders. *Zoology*, 116(6), 325–330. <https://doi.org/10.1016/j.zool.2013.08.004>
- Davic, R. D., & Welsh, H. H. (2004). On the ecological role of salamanders. *Annual Review of Ecology, Evolution, and Systematics*, 35, 405–434. <https://doi.org/10.1146/annurev.ecolsys.35.112202.130116>

711 Early, R., Bradley, B., Dukes, J. S., Lawler, J. J., Olden, J. D., Blumenthal, D. M., Gonzalez, P.,
712 Grosholz, E. D., Ibañez, I., Miller, L. P., Sorte, C. J., & Tatem, A. J. (2016). Global
713 threats from invasive alien species in the twenty-first century. *Nature Communications*, 7,
714 12485. <https://doi.org/10.1038/ncomms12485>

715 Esri Inc. (2025). ArcGIS Pro (Version 3.5.0). Redlands, CA: Esri Inc..

716 Farallo, V. & Miles, D. (2016). The Importance of Microhabitat: A Comparison of Two
717 Microendemic Species of Plethodon to the Widespread *P. cinereus*. *Copeia*, 2016, 67-77.
718 <https://doi.org/10.1643/CE-14-219>.

719 Fleishman, E., & Murphy, D. D. (2009). A realistic assessment of the indicator potential of
720 butterflies and other charismatic taxonomic groups. *Conservation biology : the journal of*
721 *the Society for Conservation Biology*, 23(5), 1109–1116. [https://doi.org/10.1111/j.1523-](https://doi.org/10.1111/j.1523-1739.2009.01246.x)
722 [1739.2009.01246.x](https://doi.org/10.1111/j.1523-1739.2009.01246.x)

723 Forester, J.D., Forester, D.C., & Matkowski, J.M. (2019). Making the best of a bad situation:
724 differential predator avoidance in a diminutive woodland salamander. *Animal*
725 *Behaviour*, 148, 169-181. <https://doi.org/10.1016/j.anbehav.2018.12.009>

726 Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics*
727 *in medicine*, 27(15), 2865-2873. <https://doi.org/10.1002/sim.3107>

728 Gertzog, B.J., Kaplan, L.J., Nichols, D., Smith, G.R. & Rettig, J.E. (2011). Avoidance of three
729 herbicide formulations by eastern red-backed salamanders (*Plethodon*
730 *cinereus*). *Herpetological Conservation and Biology*, 6(2), 237-241.
731 <https://doi.org/10.1655/0733-1347-38.1.74>

732 Gibbs, J.P. (1998). Distribution of woodland amphibians along a forest fragmentation
733 gradient. *Landscape Ecology*, 13, 263–268. <https://doi.org/10.1023/A:1008056424692>

734 Grover, M.C. (2006). Comparative effectiveness of nighttime visual encounter surveys and cover
 735 object searches in detecting salamanders. *Herpetological Conservation and Biology*, 1(2),
 736 93-99.

737 Hocking, D. J., Babbitt, K. J., & Yamasaki, M. (2013). Comparison of silvicultural and natural
 738 disturbance effects on terrestrial salamanders in northern hardwood forests. *Biological*
 739 *Conservation*, 167, 194-202. <https://doi.org/10.1016/j.biocon.2013.08.006>

740 Hocking, D. J., Connette, G. M., Conner, C. A., Scheffers, B. R., Pittman, S. E., Peterman, W.
 741 E., & Semlitsch, R. D. (2013). Effects of experimental forest management on a terrestrial,
 742 woodland salamander in Missouri. *Forest Ecology and Management*, 287, 32-39.
 743 <https://doi.org/10.1016/j.foreco.2012.09.013>

744 Fiske, I., & Chandler, R. (2011). unmarked: An R Package for Fitting Hierarchical Models of
 745 Wildlife Occurrence and Abundance. *Journal of Statistical Software*, 43(10), 1–23.
 746 <https://doi.org/10.18637/jss.v043.i10>

747 Kellner, K.F., Smith, A.D., Royle, J.A., Kery, M., Belant J.L., & Chandler, R.B. (2023). The
 748 unmarked R package: Twelve years of advances in occurrence and abundance modelling
 749 in ecology. *Methods in Ecology and Evolution*, 14(6), 1408-1415.
 750 <https://doi.org/10.1111/2041-210X.14123>

751 Knapp, S. M., Haas, C. A., Harpole, D. N., & Kirkpatrick, R. L. (2003). Initial effects of
 752 clearcutting and alternative silvicultural practices on terrestrial salamander
 753 abundance. *Conservation Biology*, 17(3), 752-762. [https://doi.org/10.1046/j.1523-](https://doi.org/10.1046/j.1523-1739.2003.02061.x)
 754 [1739.2003.02061.x](https://doi.org/10.1046/j.1523-1739.2003.02061.x)

755 Laking, A. E., Li, Z., Goossens, E., Miñarro, M., Beukema, W., Lens, L., Bonte, D., Verheyen,
 756 K., Pasmans, F., & Martel, A. (2021). Salamander loss alters litter decomposition

757 dynamics. *The Science of the total environment*, 776, 145994.

758 <https://doi.org/10.1016/j.scitotenv.2021.145994>

759 Leger, E. A., & Espeland, E. K. (2010). Coevolution between native and invasive plant

760 competitors: implications for invasive species management. *Evolutionary*

761 *applications*, 3(2), 169–178. <https://doi.org/10.1111/j.1752-4571.2009.00105.x>

762 Lehtinen, R. M., Hartman, H., Marlowe, B., & Rojas, A. (2022). Evidence for negative impacts

763 on terrestrial salamanders following invasive plant removal. *Journal of*

764 *Herpetology*, 56(1), 92-98. <https://doi.org/10.1670/21-018>

765 Lehtinen, R. M., Calhoun, D. D., Gabriel, J. W., & Edgington, H. A. (2026). Long-Term

766 Surveillance of a Woodland Salamander Community with a Review of Long-Term Field

767 Studies in Plethodontids. *Animals*, 16(3), 487. <https://doi.org/10.3390/ani16030487>

768 Leslie, S. E., Edge, C. B., & Riley, J. L. (2025). Herbicide application improves plethodontid

769 salamander habitat conditions in regenerating clear-cut forests. *Canadian Journal of*

770 *Forest Research*, 55, 1-12. <https://doi.org/10.1139/cjfr-2024-0294>

771 MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Andrew Royle, J., & Langtimm,

772 C. A. (2002). Estimating site occupancy rates when detection probabilities are less than

773 one. *Ecology*, 83(8), 2248-2255. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)

774 [9658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)

775 Maerz, J. C., Brown, C. J., Chapin, C. T., & Blossey, B. (2005). Can secondary compounds of an

776 invasive plant affect larval amphibians?. *Functional Ecology*, 19(6), 970-975.

777 <https://doi.org/10.1111/j.1365-2435.2005.01054.x>

778 Maerz, J. C., Nuzzo, V. A., & Blossey, B. (2009). Declines in woodland salamander abundance

779 associated with non-native earthworm and plant invasions. *Conservation biology : the*

780 *journal of the Society for Conservation Biology*, 23(4), 975–981.
781 <https://doi.org/10.1111/j.1523-1739.2009.01167.x>

782 Malinich, E., Lynn-Bell, N., & Kourtev, P. S. (2017). The effect of the invasive *Elaeagnus*
783 *umbellata* on soil microbial communities depends on proximity of soils to plants.
784 *Ecosphere*, 8(5):e01827. <https://doi.org/10.1002/ecs2.1827>

785 Matte, R., Boivin, M., & Lavoie, C. (2022). Japanese knotweed increases soil erosion on
786 riverbanks. *River Research and Applications*, 38(3), 561-572.
787 <https://doi.org/10.1002/rra.3918>

788 McKenny, H., Keeton, W., & Donovan, T. (2006). Effects of structural complexity enhancement
789 on eastern red-backed salamander (*Plethodon cinereus*) populations in northern hardwood
790 forests. *Forest Ecology and Management*, 230, 186-196.
791 <https://doi.org/10.1016/j.foreco.2006.04.034>.

792 Milanovich, J. R., & Peterman, W. E. (2016). Revisiting Burton and Likens (1975): Nutrient
793 Standing Stock and Biomass of a Terrestrial Salamander in the Midwestern United
794 States. *Copeia*, 104(1). <https://doi.org/10.1643/OT-14-180>

795 Mossman, A., Lambert, M. R., Ashton, M. S., Wickle, J., & Duguid, M. C. (2019). Two
796 salamander species respond differently to timber harvests in a managed New England
797 forest. *PeerJ*, 7, e7604. <https://doi.org/10.7717/peerj.7604>

798 Nagy, C., Aschen, S., Christie, R., & Weckel, M. (2011). Japanese stilt grass (*Microstegium*
799 *vimineum*), a nonnative invasive grass, provides alternative habitat for native frogs in a
800 suburban forest. *Urban Habitats*, 6, 1-10.

801 Ni, M., Deane, D.C., Li, S., Wu, Y., Sui, X., Xu, H., Chu, C., He, F. & Fang, S. (2021). Invasion
802 success and impacts depend on different characteristics in non-native plants. *Diversity*
803 *and Distributions*, 27(7), 1194-1207. <https://doi.org/10.1111/ddi.13267>

804 Nunes, A. L., Fill, J. M., Davies, S. J., Louw, M., Rebelo, A. D., Thorp, C. J., Vimercati, G., &
805 Measey, J. (2019). A global meta-analysis of the ecological impacts of alien species on
806 native amphibians. *Proceedings. Biological sciences*, 286(1897), 20182528.
807 <https://doi.org/10.1098/rspb.2018.2528>

808 Ochs, A. E., Saunders, M. R., & Swihart, R. K. (2022). Response of terrestrial salamanders to the
809 decade following timber harvest in hardwood forests. *Forest Ecology and*
810 *Management*, 511, 120159. <https://doi.org/10.1016/j.foreco.2022.120159>

811 O'Donnell, K.M., Thompson III, F.R. & Semlitsch, R.D. (2014). Predicting variation in
812 microhabitat utilization of terrestrial salamanders. *Herpetologica*, 70(3), pp.259-265.
813 <https://doi.org/10.1655/HERPETOLOGICA-D-13-00036>

814 O'Donnell, K. M., Thompson III, F. R., & Semlitsch, R. D. (2015). Prescribed fire and timber
815 harvest effects on terrestrial salamander abundance, detectability, and microhabitat
816 use. *The Journal of Wildlife Management*, 79(5), 766-775.
817 <https://doi.org/10.1002/jwmg.884>

818 Petri, L., & Ibáñez, I. (2025). Successful Recovery of Native Plants Post-Invasive Removal in
819 Forest Understories is Driven by Native Community Features. *Ecological Applications*,
820 35(2): e70012. <https://doi.org/10.1002/eap.70012>

821 Pile Knapp, L., Coyle, D., Dey, D., Fraser, J., Hutchinson, T., Jenkins, M., Kern, C., Knapp, B.,
822 Maddox, D., Pinchot Wilson, C., & Wang, G. (2023). Invasive plant management in

823 eastern North American Forests: A systematic review. *Forest Ecology and Management*,
824 550(2023), 121517. <https://doi.org/121517.10.1016/j.foreco.2023.121517>.

825 Pilliod, D. S., Bury, R. B., Hyde, E. J., Pearl, C. A., & Corn, P. S. (2003). Fire and amphibians in
826 North America. *Forest ecology and management*, 178(1-2), 163-181.
827 [https://doi.org/10.1016/S0378-1127\(03\)00060-4](https://doi.org/10.1016/S0378-1127(03)00060-4)

828 Posit team (2025). RStudio: Integrated Development Environment for R.
829 Posit Software, PBC, Boston, MA. URL <http://www.posit.co/>.

830 Prior, K. M., Adams, D. C., Klepzig, K. D., & Hulcr, J. (2018). When does invasive species
831 removal lead to ecological recovery? Implications for management success. *Biological*
832 *Invasions*, 20(2), 267-283. <https://doi.org/10.1007/s10530-017-1542-x>

833 R Core Team (2025). R: A Language and Environment for Statistical Computing_. R Foundation
834 for Statistical Computing, Vienna, Austria. <<https://www.R-project.org/>>.

835 Riddell, E. A., Roback, E. Y., Wells, C. E., Zamudio, K. R., & Sears, M. W. (2019). Thermal
836 cues drive plasticity of desiccation resistance in montane salamanders with implications
837 for climate change. *Nature Communications*, 10(1), 4091.
838 <https://doi.org/10.1038/s41467-019-11990-4>

839 Ross, B., Fredericksen, T., Ross, E., Hoffman, W., Morrison, M.L., Beyea, J., Lester, M.B.,
840 Johnson, B.N. & Fredericksen, N.J. (2000). Relative abundance and species richness of
841 herpetofauna in forest stands in Pennsylvania. *Forest Science*, 46(1), 139-146.
842 <https://doi.org/10.1093/forestscience/46.1.139>

843 Sanchez, K., Grayson, K.L., Sutherland, C., Thompson, L.M. & Hernandez-Pacheco, R. (2020).
844 Environmental drivers of surface activity in a population of the eastern red-backed

845 salamander (*Plethodon cinereus*). *Herpetological Conservation and Biology*, 15(3), 642–
846 651. <http://www.herpconbio.org/>

847 Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of
848 image analysis. *Nature Methods*, 9(7), 671–675. <https://doi.org/10.1038/nmeth.2089>

849 Semlitsch, R. D., Conner, C. A., Hocking, D. J., Rittenhouse, T. A., & Harper, E. B. (2008).
850 Effects of timber harvesting on pond-breeding amphibian persistence: testing the
851 evacuation hypothesis. *Ecological Applications*, 18(2), 283-289.
852 <https://doi.org/10.1890/07-0853.1>

853 Semlitsch, R.D., Todd, B.D., Blomquist, S.M., Calhoun, A.J., Gibbons, J.W., Gibbs, J.P.,
854 Graeter, G.J., Harper, E.B., Hocking, D.J., Hunter Jr, M.L. & Patrick, D.A. (2009).
855 Effects of timber harvest on amphibian populations: Understanding Mechanisms from
856 Forest Experiments. *BioScience*, 59(10), 853-862.
857 <https://doi.org/10.1525/bio.2009.59.10.7>

858 Shoo, L.P., Olson, D.H., McMenamin, S.K., Murray, K.A., Van Sluys, M., Donnelly, M.A.,
859 Stratford, D., Terhivuo, J., Merino-Viteri, A., Herbert, S.M. & Bishop, P.J. (2011).
860 Engineering a future for amphibians under climate change. *Journal of applied*
861 *ecology*, 48(2), 487-492. <https://doi.org/10.1111/j.1365-2664.2010.01942.x>

862 Siddig, A.A., Ellison, A., Ochs, A., Villar-Leeman, C., & Lau, M. (2016). How do ecologists
863 select and use indicator species to monitor ecological change? Insights from 14 years of
864 publication in Ecological Indicators. *Ecological Indicators*, 60, 223-230.
865 <https://doi.org/10.1016/j.ecolind.2015.06.036>.

866 Siddig, A.A., Ellison, A., & Mathewson, B. (2016). Assessing the impacts of the decline of
 867 *Tsuga canadensis* stands on two amphibian species in a New England forest. *Ecosphere*,
 868 7(11), e01574. <https://doi.org/10.1002/ecs2.1574>.

869 Siddig, A.A., Ellison, A., & Jackson, S. (2015). Calibrating abundance indices with population
 870 size estimators of red back salamanders (*Plethodon cinereus*) in a New England forest.
 871 *PeerJ*, 3, e952. <https://doi.org/10.7717/peerj.952>

872 Sites Jr, J.W. (1978). The foraging strategy of the dusky salamander, *Desmognathus fuscus*
 873 (Amphibia, Urodela, Plethodontidae): an empirical approach to predation theory. *Journal*
 874 *of Herpetology*, 12(3), 373-383. <https://doi.org/10.2307/1563619>.

875 Southerland, M., Jung, R., Baxter, D., Chellman, I., Mercurio, G., & Volstad, J. (2004). Stream
 876 salamanders as indicators of stream quality in Maryland, USA. *Applied Herpetology*,
 877 2(1), 23-46. <https://doi.org/10.1163/1570754041231596>.

878 Stephens, J. P., Berven, K. A., & Tiegs, S. D. (2013). Anthropogenic changes to leaf litter input
 879 affect the fitness of a larval amphibian. *Freshwater Biology*, 58(8), 1631-1646.
 880 <https://doi.org/10.1111/fwb.12155>

881 Tilghman, J.M., Ramee, S.W. & Marsh, D.M. (2012). Meta-analysis of the effects of canopy
 882 removal on terrestrial salamander populations in North America. *Biological*
 883 *Conservation*, 152, 1-9. <http://dx.doi.org/10.1016/j.biocon.2012.03.030>

884 Utz, R. & Fetsko, M. (2020). Exploratory Survey of Salamanders in Pennsylvanian Forests with
 885 Dense Understories of *Berberis thunbergii* (Japanese Barberry), an Invasive Shrub.
 886 *Northeastern Naturalist*, 27(2), 299. <https://doi.org/10.1656/045.027.0211>.

887 van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between
 888 invasive and non-invasive plant species. *Ecology letters*, 13(2), 235–245.
 889 <https://doi.org/10.1111/j.1461-0248.2009.01418.x>
 890 Watling, J., Hickman, C., & Orrock, J. (2011). Invasive shrub alters native amphibian
 891 communities. *Biological Conservation*, 144(11), 2597-2601.
 892 <https://doi.org/10.1016/j.biocon.2011.07.005>.
 893 Watling, J., Hickman, C., & Orrock, J. (2011). Predators and invasive plants affect performance
 894 of amphibian larvae. *Oikos*, 120(5), 735-739. [https://doi.org/10.1111/j.1600-](https://doi.org/10.1111/j.1600-0706.2010.19255.x)
 895 [0706.2010.19255.x](https://doi.org/10.1111/j.1600-0706.2010.19255.x).
 896 Webster, C., Jenkins, M., & Jose, S. (2006). Woody Invaders and the Challenges They Pose to
 897 Forest Ecosystems in the Eastern United States. *Journal of Forestry*, 104(7), 366-374.
 898 <https://doi.org/10.1093/jof/104.7.366>.
 899 Wells, K. D. (2019). *The ecology and behavior of amphibians*. University of Chicago press.
 900 <https://press.uchicago.edu/ucp/books/book/chicago/E/bo5298950.html>
 901 Welsh Jr., H.H., & Ollivier, L.M. (1998). Stream Amphibians as Indicators of Ecosystem Stress:
 902 A Case Study from California's Redwoods. *Ecological Applications*, 8(4), 1118-1132.
 903 [https://doi.org/10.1890/1051-0761\(1998\)008\[1118:SAAIOE\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1998)008[1118:SAAIOE]2.0.CO;2)
 904 Welsh Jr., H. H., & Hodgson, G. R. (2013). Woodland salamanders as metrics of forest
 905 ecosystem recovery: a case study from California's redwoods. *Ecosphere*, 4(5), 59. [http://](http://doi.org/10.1890/ES12-00400.1)
 906 doi.org/10.1890/ES12-00400.1
 907 West Virginia Department of Agriculture. (September 18, 2025). *WVDA issues guidance for*
 908 *farmers amid ongoing drought conditions*. [https://agriculture.wv.gov/wvda-issues-](https://agriculture.wv.gov/wvda-issues-guidance-for-farmers-amid-ongoing-drought-conditions/)
 909 [guidance-for-farmers-amid-ongoing-drought-conditions/](https://agriculture.wv.gov/wvda-issues-guidance-for-farmers-amid-ongoing-drought-conditions/)

- 910 Wood, P. B., & Williams, J. M. (2013). Terrestrial salamander abundance on reclaimed
911 mountaintop removal mines. *Wildlife Society Bulletin*, 37(4), 815-823.
912 <https://doi.org/10.1002/wsb.319>
- 913 Wunder, S., Fraccaroli, C., Bull, J.W., Dutta, T., Eyres, A., Evans, M.C., Thorsen, B.J., Jones,
914 J.P., Maron, M., Muys, B. & Pacheco, A. (2025). Biodiversity credits: an overview of the
915 current state, future opportunities, and potential pitfalls. *Business Strategy and the*
916 *Environment*, 34(7), 8470-8499. <https://doi.org/10.1002/bse.70018>
- 917 Xiong, Y., West, C. P., Brown, C. P., & Green, P. E. (2019). Digital image analysis of old world
918 bluestem cover to estimate canopy development. *Agronomy journal*, 111(3), 1247-1253.
919 <https://doi.org/10.2134/agronj2018.08.0502>

Appendix A: Summary of Site Characteristics

Summary data of site-specific covariates collected on WMAs in West Virginia, USA. Covariates included represent covariates included in the final model set. 'Site' represents each unique site name. 'TPD' stands for 'total Plethodontid detections', or the total count of salamanders detected at that site across all sampling occasions. 'Treatment' represents whether site coordinates were located within treatment boundaries provided by crews that performed invasive plant control treatment on WMAs. 'Canopy Cover' represents the estimated percentage of a fixed area of ground covered by vertical projection of tree and tree canopy. 'Invasive Ground Cover' is the estimated percentage of coverage of forest floor by invasive plant species. Invasive Ground Cover can exceed 100% if multiple invasive plants overlap coverage. Abbreviations for WMAs are as follows: 'BL' is Burnsville Lake WMA, 'BR' is Bear Rock Lake WMA, 'CR' is Castleman Run WMA, and 'PC' is Pleasant Creek WMA.

Site	TPD	Treatment	Canopy Cover (%)	Invasive Ground Cover (%)
BL01	0	Y	58.9	113
BL02	0	N	80.1	60.8
BL03	1	Y	62.3	39.5
BL04	1	Y	54.8	109.3
BL05	0	Y	67.8	70.3
BL06	1	Y	50.3	23.7
BL07	1	Y	61.9	80.8
BL08	1	N	82.7	22
BL09	0	Y	82.9	22.3
BL10	0	N	80.6	114
BL11	1	N	67.9	82
BL12	1	N	79.1	117.5
BL13	0	N	82.9	121.8
BL14	1	N	82.4	24
BL15	1	N	76.9	54.2
BR01	6	N	81.6	135.7
BR02	16	N	79.9	48.3
BR03	0	Y	62.4	50.3
BR04	1	Y	80.6	47
BR05	0	Y	72	27.7
BR06	0	Y	61.9	18.5
BR07	0	Y	80.5	9.7
BR08	0	Y	30.4	80.3
BR09	0	Y	43.3	87
BR10	0	Y	48.4	53
BR11	5	Y	82.1	27.5
BR12	7	Y	77.5	27.83
BR13	1	Y	23.4	142
BR14	11	N	79.9	54
BR15	7	N	79.6	84.3
CR01	0	Y	84.5	59.9
CR02	1	Y	51.9	63.5
CR03	0	Y	0	24

CR04	9	N	79.4	30.5
CR05	2	N	74.7	7.5
CR06	1	Y	67.5	125.5
CR07	6	Y	77.7	107.5
CR08	1	Y	78.7	18.3
CR09	4	N	80.2	77
CR10	8	N	86.5	47.3
CR11	9	Y	69.7	21
CR12	5	N	68.2	66.3
CR13	5	N	82.8	96.7
CR14	0	N	0	0
CR15	9	N	77.5	23
PC01	1	N	51.9	61
PC02	4	Y	84.2	38.5
PC03	0	N	67.8	16.3
PC04	12	Y	76.	52
PC05	1	Y	68.3	72
PC06	0	Y	68.2	19
PC07	0	Y	72.1	39.5
PC08	1	Y	51.5	121
PC09	1	Y	20.5	30
PC10	0	Y	78.3	18
PC11	5	Y	72.3	57
PC12	1	N	78.2	11.3
PC13	0	N	54.2	23
PC14	5	Y	87.9	0
PC15	0	Y	79.8	49.3

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Appendix B: Detection History of Plethodontid Salamanders

Detection history of salamander sampling on WMAs in West Virginia, USA. 'Sampling Occasion' represents the sample number for each site, as sampling occasions may have been performed across multiple days to survey all sites. 'Date' is the day which that sampling occasion took place, formatted (mm/dd/yyyy). 'Site' indicates the unique site where a salamander was detected, including WMA specific abbreviations ('BL' is Burnsville Lake WMA, 'BR' is Bear Rock Lake WMA, 'CR' is Castleman Run WMA, and 'PC' is Pleasant Creek WMA) and the site number (1-15). 'Species' is the scientific name of the species detected. 'Number Detected' indicates whether multiple of the same species were detected at the site during that specific sampling occasion. *Sampling occasion 7 was not listed because there were no detections across all sites for Sampling occasion 7. Sampling occasion 8 was included in this appendix but detections for this occasion were not included in modelling as discussed in 2.1.5.

Sampling Occasion	Date	Site	Species	Number Detected
1	05/13/2025	PC11	<i>Plethodon cinereus</i>	2
1	05/13/2025	PC14	<i>Plethodon cinereus</i>	1
1	05/13/2025	PC2	<i>Plethodon cinereus</i>	1
1	05/13/2025	PC4	<i>Plethodon cinereus</i>	4
1	05/13/2025	PC4	<i>Desmognathus fuscus</i>	1
1	05/13/2025	PC8	<i>Plethodon cinereus</i>	1
1	05/14/2025	BL14	<i>Eurycea longicauda</i>	1
1	05/14/2025	BL3	<i>Plethodon glutinosus</i>	1
1	05/14/2025	BL7	<i>Notophthalmus viridescens</i>	1
1	05/16/2025	CR10	<i>Plethodon cinereus</i>	3
1	05/16/2025	CR12	<i>Plethodon cinereus</i>	1
1	05/16/2025	CR15	<i>Plethodon cinereus</i>	1
1	05/16/2025	CR4	<i>Plethodon cinereus</i>	1
1	05/16/2025	CR5	<i>Plethodon cinereus</i>	1
1	05/16/2025	CR9	<i>Plethodon cinereus</i>	2

2	05/20/2025	BR12	<i>Plethodon cinereus</i>	1
2	05/20/2025	BR13	<i>Notophthalmus viridescens</i>	1
2	05/20/2025	BR14	<i>Plethodon cinereus</i>	3
2	05/20/2025	BR14	<i>Plethodon glutinosus</i>	2
2	05/20/2025	BR15	<i>Plethodon glutinosus</i>	2
2	05/20/2025	BR2	<i>Plethodon cinereus</i>	2
2	05/21/2025	PC14	<i>Plethodon cinereus</i>	1
2	05/21/2025	PC2	<i>Plethodon glutinosus</i>	1
2	05/22/2025	CR10	<i>Plethodon cinereus</i>	2
2	05/22/2025	CR12	<i>Plethodon cinereus</i>	2
2	05/22/2025	CR15	<i>Plethodon cinereus</i>	1
2	05/22/2025	CR4	<i>Plethodon cinereus</i>	1
2	05/22/2025	CR4	<i>Plethodon glutinosus</i>	1
2	05/22/2025	CR6	<i>Plethodon cinereus</i>	1
2	05/22/2025	CR7	<i>Plethodon cinereus</i>	4
2	05/28/2025	BR1	<i>Plethodon glutinosus</i>	1
2	05/28/2025	BR12	<i>Plethodon cinereus</i>	1
2	05/28/2025	BR2	<i>Plethodon cinereus</i>	1
2	05/28/2025	BR4	<i>Plethodon cinereus</i>	1
3	06/09/2025	BR1	<i>Plethodon glutinosus</i>	1

3	06/09/2025	BR11	<i>Plethodon glutinosus</i>	1
3	06/09/2025	BR12	<i>Plethodon cinereus</i>	1
3	06/09/2025	BR12	<i>Plethodon glutinosus</i>	2
3	06/09/2025	BR14	<i>Plethodon glutinosus</i>	1
3	06/09/2025	BR14	<i>Plethodon cinereus</i>	2
3	06/09/2025	BR15	<i>Plethodon cinereus</i>	2
3	06/09/2025	BR2	<i>Plethodon cinereus</i>	2
3	06/09/2025	CR10	<i>Plethodon cinereus</i>	1
3	06/09/2025	CR13	<i>Plethodon cinereus</i>	1
3	06/09/2025	CR15	<i>Plethodon cinereus</i>	2
3	06/09/2025	CR4	<i>Plethodon cinereus</i>	1
3	06/09/2025	CR5	<i>Plethodon glutinosus</i>	1
4	06/16/2025	PC4	<i>Desmognathus ochropheaus</i>	3
4	06/17/2025	BL6	<i>Eurycea bislineata</i>	1
4	06/23/2025	CR11	<i>Plethodon cinereus</i>	1
4	06/23/2025	CR4	<i>Plethodon cinereus</i>	1
5	06/24/2025	BR12	<i>Plethodon glutinosus</i>	1
5	06/25/2025	BL11	<i>Eurycea bislineata</i>	1
5	06/25/2025	BL4	<i>Eurycea bislineata</i>	1
5	06/25/2025	BL8	<i>Eurycea bislineata</i>	1

6	06/29/2025	PC4	<i>Eurycea bislineata</i>	1
6	06/29/2025	PC4	<i>Desmognathus ochropheus</i>	1
6	07/01/2025	BR2	<i>Plethodon cinereus</i>	2
6	07/02/2025	CR11	<i>Plethodon cinereus</i>	1
6	07/02/2025	CR12	<i>Plethodon glutinosus</i>	1
6	07/02/2025	CR9	<i>Plethodon cinereus</i>	1
8*	07/14/2025	BR14	<i>Plethodon glutinosus</i>	2
8*	07/15/2025	BR15	<i>Plethodon glutinosus</i>	1
8*	07/21/2025	BR12	<i>Plethodon glutinosus</i>	1
8*	07/22/2025	BL9	<i>Notophthalmus viridescens</i>	1
8*	07/23/2025	CR11	<i>Eurycea longicauda</i>	1
9	09/15/2025	BR15	<i>Plethodon glutinosus</i>	1
9	09/15/2025	BR2	<i>Plethodon glutinosus</i>	1
9	09/15/2025	CR2	<i>Plethodon cinereus</i>	1
10	10/09/2025	BL15	<i>Eurycea bislineata</i>	1
10	10/09/2025	PC12	<i>Plethodon cinereus</i>	1
10	10/09/2025	PC14	<i>Plethodon cinereus</i>	1
10	10/09/2025	PC4	<i>Plethodon electromorphus</i>	1
10	10/09/2025	PC9	<i>Plethodon cinereus</i>	1
10	10/10/2025	BR1	<i>Plethodon cinereus</i>	1

10	10/10/2025	BR15	<i>Notophthalmus viridescens</i>	1
10	10/10/2025	BR2	<i>Plethodon cinereus</i>	2
10	10/10/2025	CR10	<i>Plethodon cinereus</i>	1
10	10/10/2025	CR11	<i>Plethodon cinereus</i>	2
10	10/10/2025	CR13	<i>Plethodon cinereus</i>	1
11	10/11/2025	BR1	<i>Plethodon cinereus</i>	1
11	10/11/2025	BR11	<i>Plethodon cinereus</i>	4
11	10/11/2025	BR12	<i>Plethodon cinereus</i>	1
11	10/11/2025	BR14	<i>Plethodon glutinosus</i>	1
11	10/11/2025	BR15	<i>Plethodon cinereus</i>	1
11	10/11/2025	BR2	<i>Plethodon cinereus</i>	3
11	10/13/2025	CR11	<i>Plethodon cinereus</i>	1
11	10/13/2025	CR12	<i>Plethodon cinereus</i>	1
11	10/13/2025	CR13	<i>Plethodon cinereus</i>	3
11	10/13/2025	CR15	<i>Plethodon cinereus</i>	3
11	10/13/2025	CR4	<i>Plethodon cinereus</i>	2
11	10/13/2025	CR7	<i>Plethodon cinereus</i>	1
11	10/13/2025	CR8	<i>Plethodon cinereus</i>	1
11	10/13/2025	CR9	<i>Plethodon cinereus</i>	1
11	10/14/2025	PC11	<i>Plethodon cinereus</i>	1

11	10/14/2025	PC2	<i>Plethodon cinereus</i>	1
11	10/14/2025	PC5	<i>Plethodon cinereus</i>	1
12	10/19/2025	PC1	<i>Plethodon cinereus</i>	1
12	10/19/2025	PC11	<i>Plethodon cinereus</i>	2
12	10/19/2025	PC14	<i>Plethodon cinereus</i>	2
12	10/19/2025	PC2	<i>Plethodon cinereus</i>	1
12	10/20/2025	BL12	<i>Plethodon electromorphus</i>	1
12	10/21/2025	BR1	<i>Plethodon cinereus</i>	2
12	10/21/2025	BR14	<i>Plethodon cinereus</i>	2
12	10/21/2025	BR2	<i>Plethodon cinereus</i>	3
12	10/21/2025	CR10	<i>Plethodon cinereus</i>	1
12	10/21/2025	CR11	<i>Plethodon cinereus</i>	4
12	10/21/2025	CR15	<i>Plethodon cinereus</i>	1
12	10/21/2025	CR4	<i>Plethodon cinereus</i>	2
12	10/21/2025	CR7	<i>Plethodon cinereus</i>	1

