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Factors affecting the growth of a moss species necessary for nesting habitat restoration of the four-toed salamander (*Hemidactylium scutatum*, Temminck and Schlegel 1838)

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***Abstract.*—Habitat loss and degradation is threatening amphibian populations worldwide. The four-toed salamander, *Hemidactylium scutatum*, is a small plethodontid salamander that deposits eggs terrestrially in moss clumps overhanging vernal pools. *Hemidactylium scutatum* has declined across its range, largely due to the loss of wetland habitat necessary for breeding. Constructed ponds and wetlands are common tools used to combat amphibian declines, but they often require several years for natural vegetation communities to establish. As a result, there have been calls to better understand the factors that promote the growth of critical habitat components to refine ex situ cultivation methods and expedite restoration effort. Here we evaluate the factors that influence the growth of *Climacium americanum* moss, a preferred nesting substrate of *H. scutatum*, in a greenhouse setting. We examined the impacts of plant density, soil type, and soil moisture on changes in biomass. Our analysis determined that density has little impact on growth rates while two of the three soil types had a significantly higher change in mass. We determined soil moisture–as a result of soil type–is the most critical component in greenhouse-grown moss, with plants in the 75th quartile of moisture seeing the largest positive change in biomass. Our results show that growing moss in greenhouses for use in constructed wetlands is achievable when proper soil moisture is maintained. Ultimately, this work aids restoration efforts for *H. scutatum* by providing a simple methodology to produce high volumes of nesting habitat and promote population recovery.**

Keywords. amphibian, *Climacium americanum,* conservation, constructed wetlands, greenhouse, soil moisture, vernal pool

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Introduction

Habitat loss is a primary driver of amphibian decline worldwide, interacting with the threats of climate shifts, disease, and human influence to create a global species crisis (Dodd and Smith 2003; Grant et al. 2016; Green et al. 2020; Houlahan et al. 2000). Salamanders (Order Caudata) are particularly threatened with habitat loss and degradation from human activity, as all Caudate families face habitat modification that can lead to loss of local populations (Nowakowski et al. 2017). In the Plethodontidae family–reaching their highest diversities in the eastern United States (Petranka 1998)–timber harvest, agriculture, mining, and urbanization are the primary drivers of habitat degradation, fragmentation, and destruction (Mitchell et al. 1999).

The four-toed salamander, *Hemidactylium scutatum* (Temminck and Schlegel 1838), is the most widely distributed plethodontid salamander in North America, ranging from the Great Lakes region east to Maine and south to the panhandle of Florida (Petranka 1998). However, this wide range is filled with disjunct populations increasingly threatened by habitat degradation and loss. Among the 29 states in which the species resides, 17 have designated it with some level of conservation status (Ferguson and Hamed 2024). Like many plethodontids, the largest threat appears to be habitat degradation and destruction of the forested

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wetlands the species requires for reproduction (Petranka 1998).

Hemidactylium scutatum relies on vernal wetlands in the form of ponds, bogs, or swamps within the hardwood forests it inhabits. These wetlands are critical to the nesting ecology of the species, providing shelter and nest sites during the vulnerable nesting season (Blanchard 1934). Females select nest sites from moss mats and moist cavities just above the waterline in these wetlands so larvae can fall directly into the water upon hatching (Blanchard 1923; Petranka 1998). While eggs can be found in decaying wood and vegetation, moss is the preferred substrate for nesting and essential to breeding wetlands. Females deposit eggs in several moss genera, often utilizing *Sphagnum* sp. where prevalent and *Climacium* sp., *Mnium* sp., and *Thuidium* sp. in the Southeastern United States where *Spaghnum* is less common (Petranka 1998). A lack of preferred moss species reduces nest site availability to a point where the species may decline in portions of its range (Chalmers and Loftin 2006; King and Richter 2022; Mitchell and Gibbons 2010). In southeast Kentucky, where tree moss (*Climacium americanum*) is known to populate *H. scutatum* nest sites, King and Richter (2022) documented a correlation between nesting success and the presence of moss. Nests per wetland, eggs per nest, and eggs per wetland all had a positive correlation to the amount of moss present, indicating how critical proper nesting substrate is to a healthy population.

Anthropogenic activities such as urban development and timber harvest can destroy entire wetlands, but finer scale habitat loss resulting from moss decline poses a major threat to *H. scutatum* populations (Mitchell and Gibbons 2010; Petranka 1998). Harvest for horticultural purposes, shifts in hydrology, and changes to forest composition all pose a subtle threat to wetland mosses and therefore *H. scutatum* nesting success. In response to both large- and small-scale habitat loss, some land managers are utilizing constructed wetlands to prevent further decline of the species. These constructed wetlands must mimic critical aspects of local hydrology, pool structure, and vegetation to meet the species' life history requirements (Calhoun et al. 2014). However, there is a time lag between the implementation of wetlands and use by *H. scutatum* due to the time needed for moss species to colonize the new habitat (King and Richter 2022). The delay in successful reproduction in constructed wetlands costs valuable time for this at-risk species. To support *H. scutatum* throughout its range, there is a need for methods to head-start moss growth to be utilized in restoration and construction of new wetlands.

Our primary goal for this study was to head-start *Climacium americanum* in a greenhouse setting. We selected *C. americanum* due to its documented correlation with nesting success in *H. scutatum* (Ferguson and Hamed 2024; King and Richter 2022), particularly in the southeastern United States where *Spaghnum* sp. is less common than the northern portions of *H. scutatum*'s range. *Climacium americanum* is rarely sold commercially (Martin 2015), and no apparent literature addresses best practices for cultivation. Our aim was to improve overall understanding of growth conditions for this moss species to utilize in *H. scutatum* habitat construction and restoration. This led to three clear objectives: (1) successfully grow *C. americanum* in a greenhouse setting, (2) develop a repeatable design for habitat conservation practitioners to utilize, and (3) determine components critical to *C. americanum* cultivation. We utilized a simple study design with easily available topsoil mixes and minimal manipulation of greenhouse conditions. The simplicity of the design allowed us to examine components assumed to be critical to growth rates, particularly plant density and soil moisture, and verify what elements to prioritize when cultivating this moss species.

Materials and Methods

Study Species

Climacium, or 'tree moss,' named for its dendroid growth structure, is a singular genus within the family *Climaciaceae* comprising four species. *Climacium americanum* is a large moss approximately 3.8 to 8.3 cm tall, with subterranean rhizomes that grow horizontally with vertical shoots growing into its tree-like shape. Growing patterns of individual plants are long, linked lines, but colonies may also intertwine, making it useful in erosion and flood control. Sporophytes originate from the same tip, with multiple sporophytes per plant. Endemic to the eastern United States, the moss thrives in rich loam soils with high moisture retention; it thrives in shady areas but can tolerate sun exposure if adequate moisture is present (Martin 2015).

Field Collection

We collected *C. americanum* on January 26, 2020, from the Tennessee Valley Authority's South Holston Weir Dam (36.5215°N; –82.1086°W; Sullivan County, Tennessee). Four-toed salamanders have nested at this site for the past 20 years (Hamed and Gentry 2003; Ferguson and Hamed 2024), ensuring the moss we would be cultivating was known to be preferred by the salamander species. To avoid disrupting future four-toed salamander nesting attempts, we collected moss from areas adjacent (<2 m) to nests documented in previous years. We gently lifted moss from the log or soil substrate on which it was growing. Once collected, we placed moss in plastic totes, moistened with water from pools on site, and transported to a greenhouse located at Virginia Tech.

Experimental design

We split samples of *C. americanum* into 36 polystyrene trays (504 x 238 x 60 mm; Handy Pantry; Salt Lake City, UT), washed soil and debris from the moss, and blotted each plug dry. We randomly assigned each sample to one of the four experimental densities: 1,

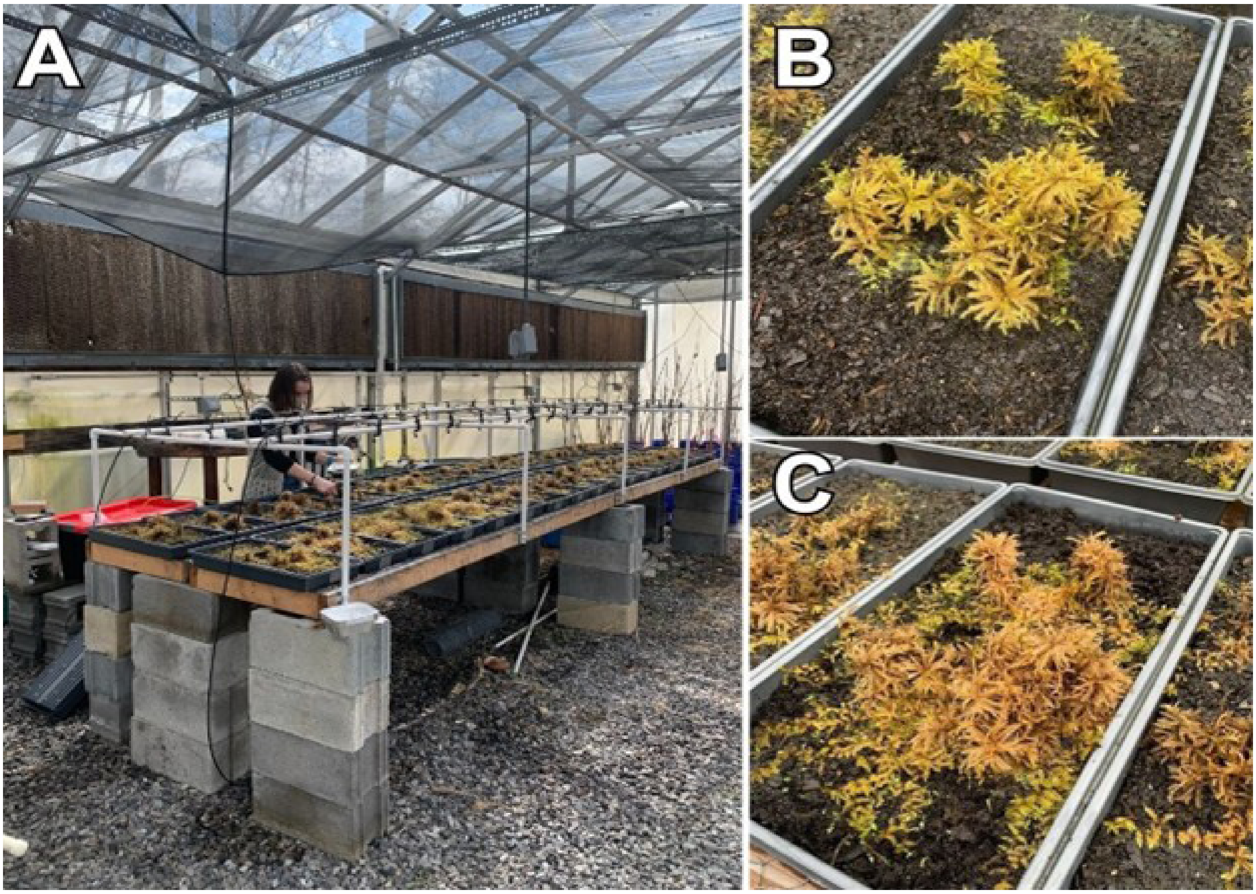

Figure 1. **A)** shows the greenhouse setup with the two randomly selected groups in each row. **B)** shows a single tray setup with 2, 1, 8 and 4 plug density in each position, moving clockwise from the top left, at the start of the growth period. **C)** shows the tray nearing the end of the growth period.

2, 4, or 8 individual moss plugs. To determine initial weights of each set of plus, we used a JSR–150 Digital Scale (HBI Technologies; Phoenix, AZ) to weigh each to the nearest 0.1 g. We then assigned each tray to one of three soil types–Pro-Mix HP Mycorrhizae (PT Growers and Consumers, Quakertown, PA), Miracle Gro Raised Bed Soil (Marysville, OH), or Scotts Premium Topsoil (Marysville, OH) and added four sets of moss plugs to each. Pro-Mix is a porous soil, while Miracle Gro and Scotts are designed to retain moisture. These soil types were selected based on the recommendations of horticultural extension faculty at Virginia Tech, as they are some of the most common greenhouse soils and allowed us to examine the effects of retained moisture.

After each tray received its designated moss samples, we randomly placed it into one of two groups and assigned a position on the greenhouse table. The two groups–random position and random distribution of initial density–were done to reduce any bias from table position in growth if one end of the table received more sunlight or a temperature difference. We planted the moss on January 26, 2020–the same day as the moss was collected–and let it grow for 473 days until May 13, 2021. After the growth period was completed, we carefully harvested moss from each tray and followed our initial procedure to remove soil debris by hand, wash any remaining soil from the moss, blot it dry, and weigh each moss plug to the nearest 0.1 g.

To ensure moss trays remained moist during the experiment, we used an automatic misting system (Ultimate Misting System–Jungle Hobbies; Essex, ON, Canada). The misting system used reverse osmosis water (TDS <5 ppm) filtered from a Reverse Osmosis Filter (Jungle Hobbies; Essex, ON, Canada). We programmed the misting system to water each tray for 60 seconds every hour during daylight hours and modified timers to account for changing photoperiods. To determine the amount of water released during each 60–second period, we used a 250 mL beaker (Pyrex–Thermo Fisher Scientific; Waltham, MA), placed it directly under each misting nozzle, and poured water from the beaker into a 100 mL graduated cylinder (Pyrex–Thermo Fisher Scientific; Waltham, MA). Each one-minute misting cycle released 180 mL of water.

However, due to potential inconsistencies in the system applying the desired amount of water to each tray consistently, we chose not to directly manipulate soil moisture and instead examined how much water each soil type could absorb. Immediately after the misting system had watered the trays, we used a stainless-steel scoop to remove soil from the center of the tray directly between the four sets of moss plugs. We placed soil in

Table 1. Summary of initial mass, moisture levels and final mass across experimental growing conditions. Values reported are medians. The range within each treatment group is provided in parentheses.

	Pro-Mix	**Miracle Gro**	**Scotts**
Initial Mass			
Density 1	1.19 (0.37-2.58)	1.46 (0.30-5.11)	1.67 (0.66-3.14)
Density 2	1.16 (0.36-6.28)	1.10 (0.34-2.60)	1.23 (0.56-2.31)
Density 4	0.90 (0.28-2.61)	0.96 (0.52-2.41)	1.10 (0.57-2.62)
Density 8	1.08 (0.70-2.75)	1.14 (0.57-2.21)	1.09 (0.21-1.59)
Moisture			
Density 1	85.42 (82.97-87.4)	72.19 (62.21-77.45)	70.96 (63.73-76.75)
Density 2	85.42 (82.97-87.4)	72.19 (62.21-77.45)	70.96 (63.73-76.75)
Density 4	85.42 (82.97-87.4)	72.19 (62.21-77.45)	70.96 (63.73-76.75)
Density 8	85.42 (82.97-87.4)	72.19 (62.21-77.45)	70.96 (63.73-76.75)
Final Mass			
Density 1	1.50 (0.50-7.58)	3.82 (0.52-13.46)	4.17 (0.59-11.43)
Density 2	1.60 (0.54-3.45)	1.65 (0.44-12.22)	2.88 (0.40-6.04)
Density 4	1.30 (0.39-3.73)	1.61 (0.78-12.49)	1.69 (0.40-5.06)
Density 8	1.28 (0.73-2.58)	2.21 (0.59-5.21)	1.88 (0.47-5.47)

Table 2. Comparison of GLMM models to predict the final mass of moss cultures under different experimental growing conditions. Predictors included initial mass, plug density, soil type, and moisture level. All models included tray (i.e., location within the greenhouse) as a random effect. Reported statistics include the number of parameters in each model (*K*), AIC corrected for small sample size (*AICc*), difference in *AICc* values (*ΔAICc*), and model weights (w_i). Competing models are ordered by descending level of support.

Model	***K***	***AICc***	***ΔAICc***	w_i
final mass ~ initial mass + soil + moisture	7	271.24	0.00	0.91
final mass ~ initial mass + soil + moisture + density	10	277.36	6.11	0.04
final mass ~ initial mass + soil	6	279.87	8.62	0.01
final mass ~ initial mass	4	279.89	8.64	0.01
final mass ~ initial mass + moisture	5	280.64	9.40	0.01
final mass ~ initial mass X moisture	6	280.79	9.55	0.01
final mass ~ initial mass + soil + density	9	285.54	14.30	0.00
final mass ~ initial mass + density	7	285.55	14.31	0.00
final mass ~ initial mass X soil	8	286.03	14.78	0.00
final mass ~ initial mass X density	10	290.80	19.56	0.00
final mass ~ moisture	4	333.88	62.64	0.00
final mass ~ soil	5	334.47	63.22	0.00
final mass ~ density	6	334.90	63.66	0.00

473 mL aluminum pans with plastic lids (Stock Your Home; New York, NY). To determine initial mass, we weighed the pan prior to adding soil and then again after adding soil, calculating the difference. We placed pans without lids in an Isotemp 737F drying oven (Fisher Scientific; Waltham, MA) for 24 hours at 105° C and then weighed each container again with and without soil. We calculated percent soil moisture values from the difference [wet weight – dry weight)/wet weight]. Based on the 25th and 75th quartiles, we split samples into low and high moisture groups for statistical analysis.

Statistical Analyses

We fit generalized linear mixed models (GLMMs) to the final mass of moss after 67 weeks of growth. We explored the effects of initial mass, soil type, soil moisture, and plug density on final mass. In all models, initial mass and final mass were log–transformed to account for heteroskedasticity, and tray ID was included as a random effect (random intercepts). We first fit models with single predictors of final mass and then used a stepwise selection procedure to increase model complexity. For models with more than one predictor, we compared models with and without interactions between predictors. Models were ranked using AICc and AIC weights (Akaike 1974). Our approach minimizes overfitting and reduces the chance of erroneous inferences that arise due to covariance between predictors. For the best supported model, confidence intervals and p-values for parameter effect sizes were computed using a Wald t-distribution approximation. All analyses were performed in R (R Core Team 2022) using the *lme4* package (Bates et al. 2015). Model comparison and evaluation were conducted using the packages *multcomp* and *AICcmodavg* (Hothorn et al. 2008; Mazerolle 2023).

Results

At the conclusion of the growth period, 119 (82.6%) of 144 moss samples showed a positive change in mass, while 25 (17.3%) showed a negative change. No specific variable showed a particular correlation with the samples that declined in mass throughout the growth period. The largest increase was 46.86 g, with the largest decrease being 7.98 g. 49 (34.0%) remained within 1 g of their initial mass. As anticipated, initial mass was positively correlated with final mass (beta = 0.80, 95% CI [0.63, 0.98], $t = 9.02$, $p < .001$).

Our models (Table 2) indicated that soil type and soil moisture had the strongest interaction with final mass, both showing weights of w_i = 0.01 when added to the explanatory power of initial mass (Table 2). Miracle Gro yielded larger plants than Pro-Mix (beta = 0.98, 95% CI [0.52, 1.44], t = 4.20, p < .001), as did Scotts (beta = 0.94, 95% CI [0.47, 1.41], t = 3.97, p < .001), but we found no significant difference between Miracle Gro and Scotts (Tukey's, p = 0.98). Trays with higher soil moisture had greater final mass (beta = 3.22, 95% CI [1.11, 5.32], t = 3.02, p = 0.003). Independent of soil type, plants in the 75% quartile of moisture had a larger positive change in mass, while trays on the lower end of soil moisture yielded smaller plants (Figure 2).

The model showing the additive effects of initial mass, soil moisture, and soil type had the strongest weight, w_i = 0.91 (Table 2). The added effect of density reduced the power of the model, reflected in the low weight density had as a single predictor. The slight differences caused by density (Figure 3) did not have any significance in our analysis. The full model's total explanatory power is substantial (conditional R^2 = 0.52), and the part related to the fixed effects (marginal R^2) is 0.41.

Discussion

To inform best practices in *Hemidactylium scutatum* habitat construction and restoration, our objectives for this study were to (1) successfully grow *C. americanum* in a greenhouse setting, (2) develop a repeatable design for habitat conservation practitioners to utilize, and (3) determine components critical to *C. americanum* cultivation. Our results indicate that we achieved our first and second objectives, as the majority of moss samples increased in mass in our project design. Through our explanatory model, we were able to achieve our third objective and determine critical growth factors.

Soil type and moisture absorption proved to be the key components to a high growth rate. Moss is generally known to prefer moist environments–including the ponds and bogs preferred by *H. scutatum*–and our results confirm this is true for *C. americanum.* The interaction between soil type and moisture absorption is explained by characteristics of the brands themselves. Miracle Gro Raised Bed Soil and Scotts Premium Topsoil were designed to retain moisture and include organic materials designed to promote growth, while Pro-Mix HP Mycorrhizae is a high porosity formula to promote water drainage and support plants more sensitive to overwatering. Despite our hard-bottomed trays preventing drainage from the soil, moisture values showed Pro-Mix, on average, will not readily absorb enough water to promote moss growth (Figure 2). This outcome was anticipated based on the marketed traits of each soil type; however, with the prevalence of the three soil types in the horticultural industry, it is important to highlight the relationship between moisture, soil, and moss. While moisture is the underlying component, our results highlight the importance of selecting a soil mix that is designed to retain moisture when cultivating *C. americanum*. Even if water is not a limiting resource, a porous soil will prevent the necessary moisture from reaching the plant.

In contrast, the density of moss plugs showed no significant interaction on final mass. Figure 3 shows the sets with 1 and 2 plugs having a higher final mass–on average–than 4 or 8, but our models indicate this did not have a large enough effect to influence final mass significantly (Table 2). If moss samples were left to grow longer, it is possible overcrowding would have a negative effect among higher densities, but our analysis did not support this during our growth period of 473 days. Among the components assessed in our study, prioritizing soil moisture based on soil type appears to be the most critical factor.

To our knowledge, no prior studies have demonstrated successful growing conditions for *C. americanum*. By conducting this project with soil mixtures and supplies common in the horticultural industry, others can easily replicate these conditions to provide proper nesting substrate for *H. scutatum* when constructing or restoring wetland habitats. The next natural step following our study would be manipulating temperature, sunlight, and moisture directly in order to identify the most successful conditions to efficiently head-start *C. americanum* on a large scale. Additionally, we recommend future investigation of transplanting practices and colonization rates at wetland sites to maximize efficient use of greenhouse-cultivated moss in applied environments.

The results of this study have notable broader implications for *H. scutatum* and its habitat management. Identifying factors that limit population growth is crucial for species recovery. Nest–site availability is a critical factor in population health, often resulting in species declines as quality sites decrease in availability (Jimenez-Franco et al. 2018; Mainwaring et al. 2017; Scheele et al. 2012). Because females are known to select wetlands with higher amounts of moss (Wahl et al. 2008), the destruction of moss like *C. americanum* poses a severe threat to *H. scutatum* populations (Mitchell and Gibbons 2010; Petranka 1998). As observed by King and Richter (2022), moss presence is directly correlated with breeding success in *H. scutatum*. By increasing our knowledge on propagation of vegetative nesting substrate, we hope to reduce nest-site limitations on this species.

Habitat restoration is a critical conservation tool that often allows land managers to support multiple species in one concerted effort (Brodman et al. 2006; Pechman et al. 2001; Sexton et al. 1998). Our study addresses a critical part of constructing healthy wetlands and enables restoration managers to create habitats with more suitable nesting sites. If the growth conditions presented in our study are successfully replicated and implemented to support wetland restoration and construction, populations of *H. scutatum* facing declines could see recovery as available nesting sites increase. Anthropogenic

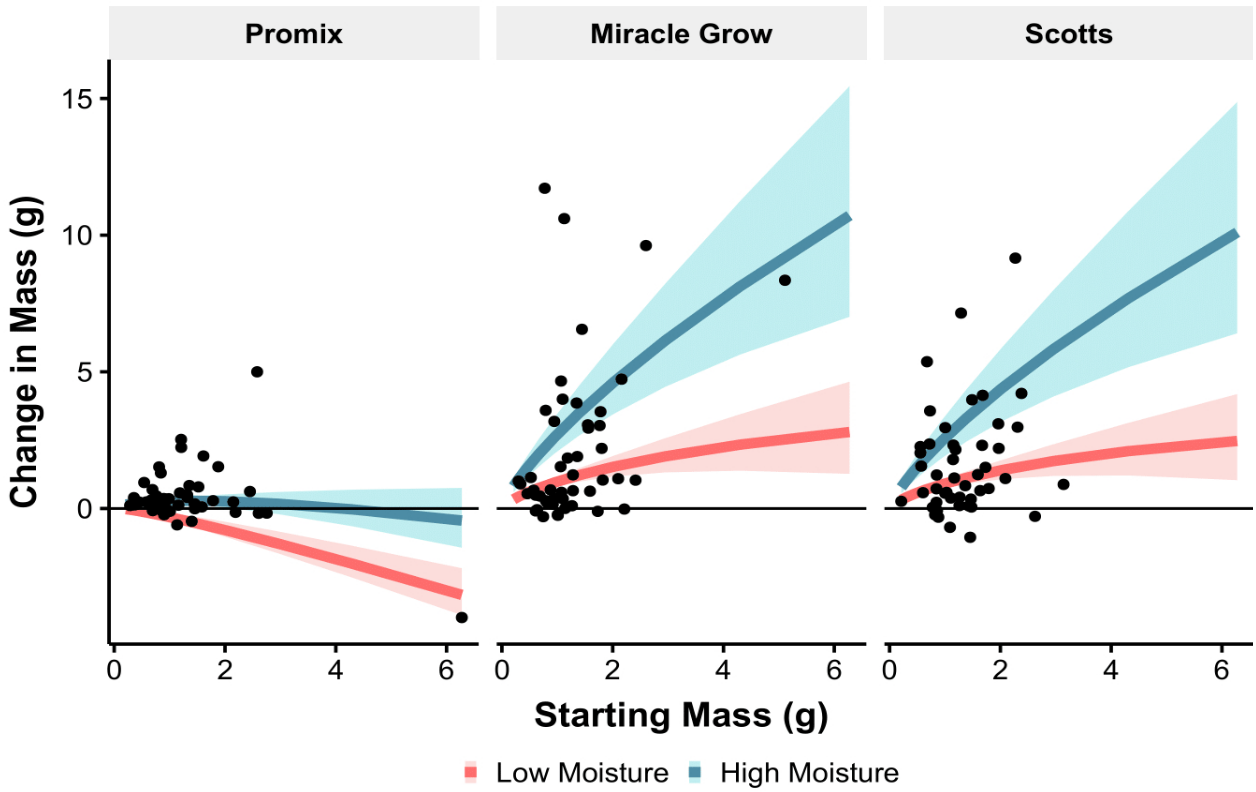

Figure 2. Predicted change in mass for *C. americanum* grown in **a)** Pro-Mix, **b)** Miracle Gro, and **c)** Scotts, given starting mass and moisture level, with black points representing recorded change in mass for each sample. The low and high moisture levels correspond to 25% and 75% quartiles of the range of moisture levels observed.

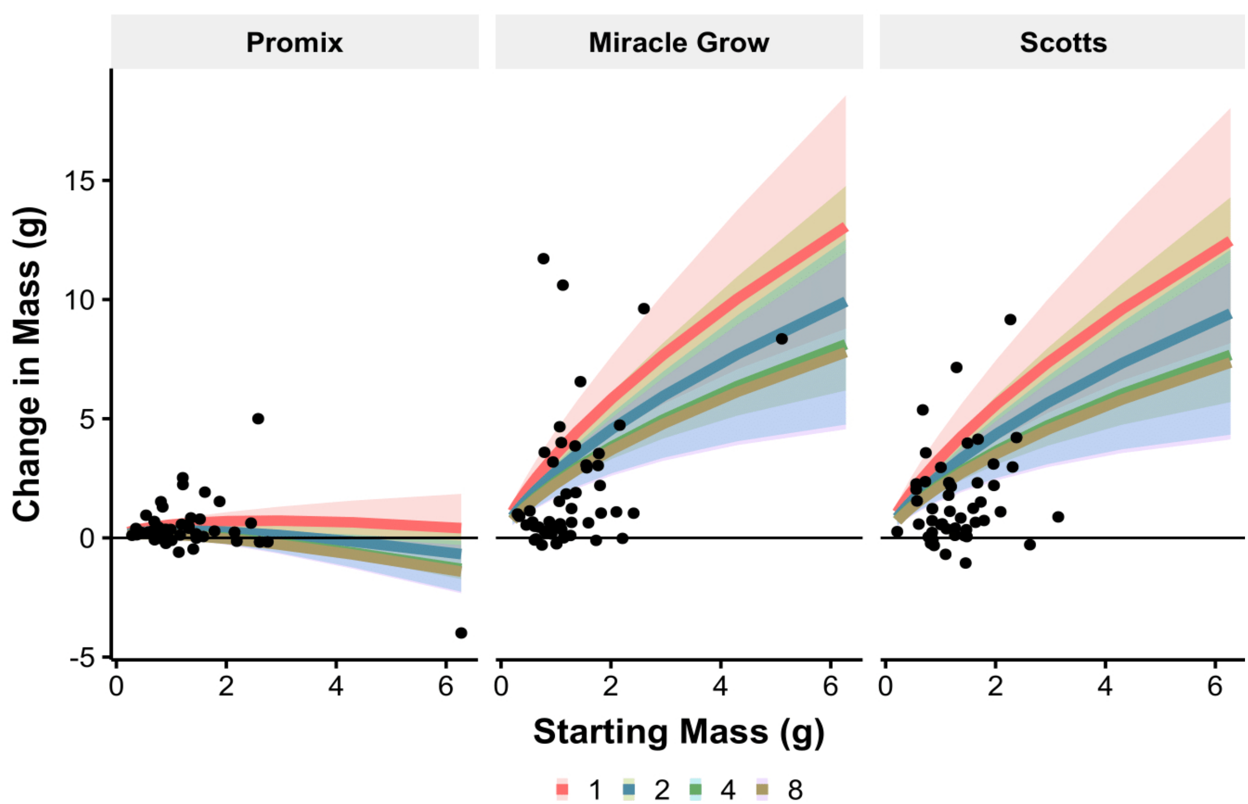

Figure 3. Predicted change in mass for *C. americanum* grown in **a)** Pro-Mix, **b)** Miracle Gro, and **c)** Scotts, given starting mass and density, with black points representing recorded change in mass for each sample. For all predictions, the moisture level is fixed at the 75% quartile of the range of observed levels.

development continues to threaten wetlands, making the ability to construct habitat elsewhere critical. In addition to supporting *H. scutatum*, wetlands with healthy *C. americanum* and other mosses provide habitat for many other species facing the threat of habitat loss. Vegetative cover often acts as a baseline for the broader ecosystem, and by restoring it, managers can better support ecosystem health in degraded areas.

Habitat loss is one of the largest threats for species to overcome worldwide, particularly among amphibians (Dodd and Smith 2003; Houlahan et al. 2000; Stuart 2004). Our study will inform restoration in the face of habitat loss and allow *H. scutatum* to combat this pressing threat. As amphibian populations continue to decline in the eastern U.S. and worldwide, our understanding of every habitat element is critical to achieving the best conservation outcomes for at–risk species.

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

KH conceived, designed, and performed the experiments. MH assisted with performing experiments and led in writing the manuscript, with support from EF. GB analyzed the data and prepared figures and tables. All authors assisted with writing of the manuscript, and all authors approved the final draft.

Data Availability

The raw data and code used to perform the analysis can be provided upon request.

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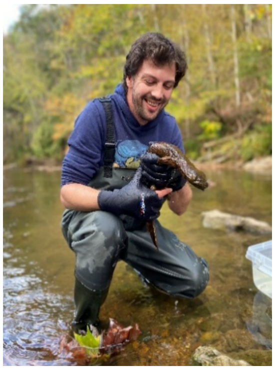

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