

1 An experimental approach to understanding elevation limits in a montane terrestrial salamander,  
2 *Plethodon montanus*

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16 Survival

17

18 **Abstract**

19 Understanding the abiotic and biotic factors that determine the limits to species' range is an  
20 essential goal in ecology, biogeography, evolutionary biology, and conservation biology.  
21 Moreover, predictions of shifts in species' distributions under future changes in climate can be  
22 improved through understanding the spatial variation in survival, growth, and reproduction. A  
23 long-standing hypothesis postulates that, for Northern Hemisphere species, abiotic factors like  
24 temperature limit northern and/or higher elevation extents, while biotic factors like competition  
25 limit the southern and/or lower elevation range edges; though amphibians may not follow this  
26 general trend. Therefore, we combined environmental suitability models and a reciprocal  
27 transplant experiment across an elevational gradient to explore the role of the abiotic  
28 environment on the range limits of a montane salamander (*Plethodon montanus*). We first  
29 determined suitability of the abiotic environment for *P. montanus*, under current (1960 – 2000)  
30 and future (2050) climate scenarios. Second, we collected juveniles from each of three elevations  
31 and transplanted them within mesocosms such that each origin population was represented  
32 within each transplant location and vice-versa. We found that environmental suitability in 2050  
33 decreased throughout the range compared to current predictions, especially at lower elevations.  
34 Additionally, we found that individuals' starting body condition and transplant location were  
35 important predictors of survival, growth, and reproduction condition; importantly, individuals  
36 transplanted to low elevation had lower survival and growth rates compared to those moved to  
37 mid or high elevations. Our study provides experimental support that the abiotic environment  
38 limits the lower elevation distribution of *P. montanus* and, unfortunately, our results also paint a  
39 possible bleak future for this species and likely other montane terrestrial plethodontids. The  
40 abiotic environment, which will become increasingly limited under future changes in climate,  
41 was found to have more influence on survival and growth than population identity.

42

43

## 44 Introduction

45 Fundamentally, a species persists when the numbers of individuals entering the  
46 population (birth and immigration) are at least equal to those leaving (death and emigration) the  
47 population (Gaston 2009). However, the numbers and fitness of individuals across a species'  
48 range vary due to spatial and temporal variation in abiotic (e.g., temperature, precipitation) or  
49 biotic (e.g., predation, food availability) factors. Limits to a species' range often arise because of  
50 lowered resource availability or quality at range edges that can result in diminished condition or  
51 death of individuals (Hutchins 1947; Gaston 2003). For example, in the Southern Appalachians,  
52 warmer and drier conditions at lower elevations physiologically constrains the montane endemic  
53 salamander *Plethodon jordani* to higher elevations, while *P. teyahalee* is excluded from high  
54 elevations by the superior competitor, *P. jordani* (Gifford and Kozak 2012). Understanding how  
55 abiotic and biotic factors result in a population becoming a sink or extirpated is essential in  
56 determining the role of the environment on species' range limits. As such it is both a  
57 fundamental question in ecology, biogeography, and evolutionary biology (Brown 1984; Gaston  
58 2003; Case et al. 2005; Parmesan et al. 2005; Gaston 2009; Lee-Yaw 2016), and also critical for  
59 effective conservation and predictive modeling (Gaston 2003; Hampe and Petit 2005; Gaston  
60 2009; Urban et al. 2016).

61 The North-South Hypothesis is a long-standing macroecological hypothesis (Darwin  
62 1859; MacArthur 1972) which posits that abiotic conditions determine a species' pole-ward or  
63 higher elevation range limit, but biotic conditions determine the equator-ward or lower elevation  
64 range limit (Dobzhansky 1950; MacArthur 1972; Brown et al. 1996; Gaston 2003; Parmesan et  
65 al. 2005; reviewed in Schemske et al. 2009; Hargreaves et al., 2014). For species in the Northern  
66 Hemisphere, this means that northern and/or higher elevation populations should be more  
67 constrained by abiotic factors like temperature, while southern and/or lower elevation  
68 populations should be more constrained by biotic factors like competition. However, several  
69 studies have shown that amphibians may not conform to this general trend (Hairston 1980;  
70 Nishikawa 1985; Gifford and Kozak 2012; Cunningham et al. 2016; Lyons et al. 2016). While  
71 studies examining range limits across different species are not uncommon (Schemske et al.  
72 2009), there are fewer that examine what limits the different portions of a single species' range  
73 (reviewed in Cahill et al. 2014; but see Cunningham et al. 2009).

74 Understanding the mechanisms responsible for range limits is also of concern for  
75 conservation biologists given the current rate of global climate change (Loarie et al. 2009). Mean  
76 global temperatures have increased by 0.6°C over the last century and are expected to increase 2  
77 – 4°C more by 2100 (IPCC 2014). As a response to contemporary changes in climate,  
78 amphibians have shown shifts in breeding phenology (Beebee 1995; Reading 1998; Gibbs and  
79 Breisch 2001; Chadwick et al. 2006; Green 2016), geographic range limits (Pounds et al. 1999;  
80 Seimon et al. 2007), and body size (Reading 2007; Caruso et al. 2014). Environmental suitability  
81 models predict 50-100% reduction in suitable climate space for Southern Appalachians  
82 salamanders (Milanovich et al. 2010) – a major amphibian hotspot (Rissler and Smith 2010).  
83 Although potentially suitable future habitat may exist, many species lack the ability to disperse  
84 through the intervening lower suitability habitat in the face of climate change (Bernardo and

85 Spotila 2006, Gifford and Kozak 2012; Lyons et al. 2016). Therefore, as global climates continue  
86 to shift, predicting species' persistence will require an understanding of the relationship between  
87 climate and population vital rates (e.g., survival; Buckley et al. 2010; Urban et al. 2016) as well  
88 as decoupling local adaptation and plastic responses to climate (Parmesan 2006; Merilä and  
89 Hendry 2014; Urban et al. 2014).

90 Improvement to predictions of shifts in species' distributions under future changes in  
91 climate can be accomplished through understanding how survival, growth, and reproduction vary  
92 spatially. Therefore, we combine environmental suitability models and a reciprocal transplant  
93 experiment across an elevational gradient to explore the role of the abiotic environment on the  
94 range limits of a montane salamander (*Plethodon montanus*). Using environmental suitability  
95 models we explore the variation in current and future suitability of the abiotic environment and  
96 compare models to identify how future ranges will be affected by changes in climate. Moreover,  
97 we used a reciprocal transplant experiment to investigate the role of origin population (i.e.,  
98 where individuals were captured) and transplant location (i.e., where individuals were raised) on  
99 three relevant population responses: survival, growth, and maturation, to test the hypothesis that  
100 abiotic conditions limit the warmer range edge (i.e., lower elevations) of montane salamanders.  
101 Therefore, we asked the following questions, 1) how does environmental suitability vary across  
102 the current range of *P. montanus*, and how will suitability change (e.g., among elevations) under  
103 a future climate scenario? and 2) How do the origin location, transplant location, and initial body  
104 condition of individuals influence survival, growth rate, and maturation? Thus, if abiotic  
105 conditions limit the lower, warmer range edge, we expected to find lowest growth, survival, and  
106 maturation at the lower elevation sites and highest growth, survival, and maturation at the higher  
107 elevation sites. Moreover, if montane salamanders do best at their origin population we would  
108 expect to find increased survival, growth, and maturation for individuals at those locations  
109 compared to individuals transplanted to a non-origin location.

110

## 111 **Methods**

### 112 *Environmental Suitability Models*

113 We created predictive Ecological Niche Models (ENMs) for *P. montanus*, under current  
114 (1960 – 2000) and future (2050) climate scenarios, using program Maxent version 3.3.3k  
115 (Phillips et al. 2006). We obtained 262 unique high accuracy (at least four decimal points; ~11 m  
116 resolution) geographic coordinates (latitude and longitude) using GBIF (<http://www.gbif.org/>) on  
117 17 March 2016. We used the 11 bioclimatic variables that Rissler and Apodaca (2007) and  
118 Milanovich et al. (2010) used in distribution models of other plethodontid species (30 sec  
119 resolution; Hijmans et al. 2005) clipped to North America. We bootstrapped our ENMs by using  
120 75% of the data for training and 25% of the data to test the models with 100 replicates. We used  
121 area under the curve (AUC) of the receiver operating characteristic (ROC) plots to evaluate  
122 model fit (i.e., values closer to 1 indicate a better fit; Swets 1988; Elith 2002), and determined if  
123 our current ENM models performed better than 262 random points with 999 replicates (Raes and  
124 ter Steege 2007). We used the default settings in Maxent for all other parameters and projected

125 our current ENM model onto a future climate scenario (Hadley GEM2-ES model; RCP4.5  
126 greenhouse gas scenario; 30 second resolution; Hijmans et al. 2005). For brevity, we report the  
127 average and standard deviation AUC, and data from the average and standard deviation of  
128 current and future ENM of bootstrapped models.

129

### 130 *Reciprocal Transplant Experiment*

131 From 6 June – 1 October 2015, we conducted this transplant experiment in Pisgah  
132 National Forest, in which we collected salamanders who originated from low (~1,000 m;  
133 82.4258°W, 36.0328°N), mid (~1,250 m; 82.1417°W, 36.1372°N), and high (~1,450 m;  
134 82.0917°W, 36.0928°N) elevations and reciprocally transplanted them to the same low, mid, and  
135 high elevation sites. Thus, each origin population was represented within each transplant location  
136 and vice-versa. Average annual temperatures varied predictably among these three elevations;  
137 the low site was the warmest (10.79°C), followed by the mid (9.59°C) and high elevation sites  
138 (8.78°C), whereas annual precipitation was lowest at the mid elevation site (1346.76mm) and  
139 higher and the low (1463.81mm) and high (1394.13mm) elevation sites (PRISM 2017). We  
140 established two replicate sites within each transplant elevation, with each replicate site  
141 containing 18 mesocosms (36 per elevation) for a total of 108 mesocosms. Replicate sites were  
142 chosen based on proximity to established mark-recapture sites, were approximately 200 – 400 m  
143 apart, and were on northwestern facing slopes with similar canopy coverage. Each mesocosm  
144 consisted of a single 53 x 43 x 30 cm polyethylene tub (Cunningham et al. 2009) that had the  
145 same number and size of holes drilled along the bottom and side for drainage. We filled each  
146 mesocosm with a layer of approximately 10 cm of soil, then a layer of approximately 2 cm of  
147 leaf litter (each gathered from the respective transplant site) and one 30 x 15 x 5 cm untreated  
148 pine cover board. The soil and leaf litter were collected and homogenized, separately, prior to  
149 adding equal amounts to each mesocosm in order to maintain consistency among mesocosms  
150 within each experimental site.

151 After establishing the mesocosms, we collected 36 juvenile salamanders that ranged from  
152 30 – 45 mm SVL from each origin population. This size class was chosen because it represented  
153 the range of animals that could potentially reach reproductive maturity by the end of the  
154 experiment (N.M.C. *unpublished data*). Because the sex of juvenile salamanders is currently  
155 impossible to determine without dissection, we assumed a 1:1 sex ratio, which is consistent with  
156 museum specimens (N.M.C. *unpublished data*). Animals were kept in a cooler, maintained  
157 between 15 – 20°C, for approximately 36 hours before the start of the experiment. Immediately  
158 before beginning the experiment, we measured the snout-to-vent length (tip of the snout to  
159 posterior margin of the vent; SVL), tail length, and weighed each animal. All measurements  
160 were taken while the animal was secured in a new plastic bag to ensure consistent measurements  
161 and reduce probability of disease transmission from potentially contaminated equipment. We  
162 randomly assigned animals to a transplant elevation (low, mid, and high) and replicate site within  
163 transplant location (1 or 2). After adding a single salamander to each mesocosm, the mesocosm  
164 was covered with window screen and secured by both zip ties and waterproof caulk to prevent  
165 animal escape. Because we could not logistically collect all animals on a single day, the start date

166 of the experiment varied from 6 June 2015 – 16 June 2015, and the end date of the experiment  
167 varied from 29 September 2015 – 1 October 2015 (106 – 115 days). At the end of the  
168 experiment, we thoroughly searched the leaf litter and soil of all mesocosms; salamanders were  
169 assumed dead if not found.

170 All animals were measured, euthanized (20% liquid Benzocaine), and dissected to  
171 determine sex and assess reproductive maturity. For males with pigmented testes, we assessed  
172 reproductive maturity by removing both testes and photographing them using a Leica M165C  
173 stereo microscope. All photos were taken on the same day, under identical lighting conditions,  
174 and using the same field of view. We used Leica Application Suite version 4.1 (Wetzlar,  
175 Germany) to determine the average area of both testes and ImageJ version 1.49 (Schneider et al.  
176 2012) to determine mean pigmentation; we standardized testes area and pigmentation by the  
177 SVL at the end of the experiment, and we took the inverse of the mean standardized brightness  
178 of testes, such that darker testes would be scored as a higher number than lighter testes. Males  
179 with unpigmented testes were scored as 0 for standardized area and the inverse of mean testis  
180 brightness. Because testis area and inverse of pigmentation were correlated (0.65;  $t_{22}=4.027$ ;  $P <$   
181 0.001), we used testis pigmentation (scaled and centered) for further analyses. Although we  
182 designed our experiment to assess reproductive maturity for both sexes, no females were found  
183 with mature follicles; therefore, we did not assess female reproductive condition any further.

#### 184 *Analyses*

185 To determine if survival varied among origin, transplant, or initial body condition, we  
186 used a generalized linear mixed effect model with a binomial error distribution; our model  
187 contained two random intercepts, transplant location and replicate nested within transplant  
188 location. Similarly, we used linear mixed effects models, with the same random intercepts as  
189 above, to determine if growth rates (i.e., rate of change in SVL or mass) varied. To estimate body  
190 condition, we regressed log transformed mass against the total length (i.e., SVL + tail length) for  
191 all individuals (both beginning and end of the experiment) and extracted the residuals from the  
192 linear model; hereafter, we will refer to this as body condition index (BCI). A positive BCI  
193 indicates individuals with a greater mass for a given SVL, while a negative BCI indicates  
194 individuals with a lesser mass for a given SVL (e.g., Reading 2007; Băncilă et al. 2010). For  
195 both SVL and mass rates of change, we standardized these measures by first dividing them by  
196 the animal's starting SVL and then dividing by the number of days that the animal was in the  
197 experiment. Lastly, we used a linear model, because of our smaller sample size, to determine if  
198 maturation (measured as testes pigmentation) varied among origin location, transplant location,  
199 or initial body condition. For our four response variables, we compared all 18 models using  
200 combinations of our three fixed effects (origin population, transplant location, and initial body  
201 condition) as well as interactions. Interactions were only included when the additive components  
202 of the interaction were present in the model. We were not able to fit the three-way interaction  
203 model for survival; therefore, it was not included. We fit all models using maximum likelihood  
204 and selected the best model based on lowest Akaike's Information Criteria corrected for small  
205 sample size (AICc; Hurvich and Tsai 1989). We determined significance of model parameters of  
206 the top model using a likelihood ratio test. However, when competing models were within 2

207 AICc points of the top model (i.e., those that with “substantial support”; Burnham and Anderson  
208 2002), we determined an average of model parameters, and the significance of parameters was  
209 determined as those with 95% confidence intervals that did not overlap zero; for brevity, we  
210 show visualizations for only significant results. For linear models (i.e., responses of SVL/mass  
211 change and male maturation), we graphically assessed models to ensure they met the  
212 assumptions of homoscedasticity and normality of residuals. All statistical analyses were  
213 performed in Program R version 3.3.1 (R Core Team 2016); we used the *dismo* package  
214 (Hijmans et al. 2016) to simulate random ENM models, the *lme4* package (Bates et al. 2015) for  
215 analyzing mixed effects models, the *Hmisc* package (Harrell Jr. et al. 2015) to determine  
216 binomial confidence intervals of apparent survival, and the *MuMIn* package (Barton 2016) to  
217 compare models by AICc, estimate average model parameters, and determine predictions from  
218 the model sets.

219

## 220 **Results**

### 221 *ENM Modeling*

222 Our ENM model provided an excellent fit (AUC = 0.992; SD = 0.001) to the locality data  
223 and was better than random (rAUC = 0.580 – 0.690). Within the current range of *P. montanus*,  
224 we found that the mean environmental suitability was 0.430 (SD = 0.044). Additionally, the  
225 occurrence data used to train and test our model had a mean ENM suitability of 0.518 (SD =  
226 0.077). As expected, environmental suitability in 2050 decreased throughout the range (Fig. 1;  
227 Supplemental Fig 1), averaging 0.056 (SD = 0.034), while mean predicted ENM suitability was  
228 0.112 (SD = 0.097) for the occurrence data used to train and test our models. Moreover, we  
229 found that the change in mean environmental suitability showed a linear or logistic trend  
230 associated with elevation while the difference in current and future suitability showed a quadratic  
231 or no relationship with both latitude and longitude (Fig. 1). Lastly, while current mean ENM  
232 suitability was similar for our focal sites (low = 0.570 [SD = 0.011]; mid = 0.564 [SD = 0.007];  
233 high = 0.572 [SD = 0.009]), predicted ENM suitability for 2050 is depreciated, especially at  
234 lower elevations (low = 0.075 [SD = 0.063]; mid = 0.065 [SD = 0.054]; high = 0.202 [SD =  
235 0.112]).

236

### 237 *Reciprocal Transplant*

238 We recovered 70 of the 108 salamanders at the end of the experiment (apparent survival  
239 = 65%; 95% CI = 55 – 73%). Apparent survival was lowest for individuals originating from  
240 higher elevations (56%; 95% CI = 40 – 71%) with increasing survival for animals from mid  
241 (64%; 95% CI = 48 – 78%) and low elevations (75%; 95% CI = 59 – 86%); however, apparent  
242 survival was highest for animals transplanted to higher and mid (72%; 95% CI = 56 – 84%)  
243 elevations compared to low elevation (50%; 95% CI = 34 – 66%). Individuals at the start of the  
244 experiment were generally smaller (mean SVL = 38.17 mm; 95% CI = 37.26 – 39.08 mm; mean  
245 Mass = 0.998 g; 95% CI = 0.933 – 1.062 g) but had a higher BCI (0.07; 95% CI = 0.03 – 0.11)  
246 compared to the end of the experiment (mean SVL = 42.64; 95% CI = 41.87 – 43.42 mm; mean

247 Mass = 1.059; 95% CI = 1.002 – 1.115 g; mean BCI = -0.11; 95% CI = -0.13 – -0.08).  
248 Additionally, at the start of the experiment, SVL and mass were similar among origin  
249 populations and among origin populations and transplant locations. However, individuals  
250 transplanted to the low elevation gained less SVL and had more negative change in mass  
251 compared to those transplanted to mid and high elevations (Supplemental Figs. 2, 3). Regardless  
252 of origin population and transplant elevation individuals exhibited a negative change in BCI  
253 through the duration of the experiment (Supplemental Fig. 4). Lastly, most of the males (23/24;  
254 96%) showed some degree of pigmentation and increase in size of their testes; the only male that  
255 did not show pigmented testes originated from, and was transplanted to, the low elevation site.

256 The most parsimonious predictors of survival were a set of five models containing the  
257 parameters of starting BCI, transplant location, origin population and the interaction between  
258 transplant locations and starting BCI (Table 1; Supplemental Table 1). The probability of  
259 survival was greatest for animals that started with a higher BCI, which is not unexpected.  
260 Interestingly, those salamanders with higher BCI who originated from low elevations and those  
261 that were transplanted to mid or high elevations had higher survival than other treatments (Fig.  
262 2). For SVL, our top models included parameters of transplant location and starting BCI (Table  
263 1; Supplemental Table 2). Animals that started off with a lower BCI had more positive rates of  
264 growth (SVL change), and this relationship was greatest for animals transplanted to mid  
265 elevations but lower for animals transplanted to high and low elevations (Fig. 3a). Though our  
266 model selection for mass change included more parameters, results were similar to the change in  
267 SVL (Table 1; Supplemental Table 3); animals that began the experiment with a lower BCI and  
268 were transplanted to mid and high elevations had a more positive rate of mass change (Fig. 3b).  
269 Lastly, we found that starting BCI significantly predicted ( $\chi^2_1 = 8.713$ ;  $P < 0.001$ ) maturation in  
270 males (Supplemental Table 4); males that started the experiment with a more positive BCI had  
271 darker testes (Fig. 4) and was not dependent on the environment or origin population.

272

## 273 Discussion

274 Understanding how survival, growth, and reproduction vary spatially, leading to limits to  
275 species' distributions, can inform population models and improve predictions of species' range  
276 distributions under future changes in climate. Therefore, we determined the effect of origin  
277 population, transplant location, and initial BCI on juvenile salamander survival, growth, and  
278 reproductive condition. We found that individuals transplanted to mid and high elevations  
279 typically had higher survival and higher growth (SVL and mass) rates, while individuals that  
280 originated from low elevations had higher overall survival, irrespective of their transplant  
281 location (Figs. 2 – 4). Lastly, salamander body condition at the beginning of the summer is an  
282 important driver of survival, growth, and maturation; juveniles with a more positive BCI were  
283 more likely to survive, but had slower growth rates, and males had larger, darker testes (Figs. 2 –  
284 4) at the end of the experiment.

285



286 *ENM Models and predicting future changes in suitability of sites and consequences to*  
287 *salamanders*

288 Our current ENM models showed high and similar levels of suitability across our three  
289 transplant sites; however, ENM suitability for *P. montanus* decreased for forecasted 2050  
290 climate, especially at lower elevations (Fig 1; Supplemental Fig. 1). Notably, mean predicted  
291 ENM suitability for 2050 was lower than 99.6% (261/262) of the *P. montanus* occurrence sites  
292 that we used to train and test our models. While our experiment was not conducted to explicitly  
293 test the role of environmental suitability per se on salamander growth and survival, which would  
294 require multiple transplant locations across many more sites across the environmental suitability  
295 landscape, our results do support predictions that lower elevations will become more limiting for  
296 montane salamanders as temperatures increase (Milanovich et al. 2010; Gifford and Kozak 2012;  
297 Lyons et al. 2016). Moreover, changes in climate do not affect species independently, and can  
298 result in shifts in the distribution of competitors, prey, or predators, which could alter  
299 interspecific interactions and potentially compound the negative effects of changes in climate on  
300 population growth (Blois et al. 2013; Liles et al. 2017).

301

302 *Initial Body Condition*

303 Initial BCI was an important factor predicting observed trends in survival, growth, and  
304 reproductive condition in males; animals with higher BCI had higher survival rates, and males  
305 had higher reproductive condition. Our results for survival and reproductive condition agree with  
306 other studies that have examined the importance of body condition for individuals as well as  
307 populations (Wheeler et al. 2003; Karraker and Welsh Jr. 2006; Reading 2007; Janin et al. 2011).  
308 For example, Reading (2007) found that decreasing BCI in common toads, caused by warming  
309 climate, led to a decrease in survival and egg production. Our study shows that healthier  
310 individuals (i.e., those with higher body conditions) are afforded a greater probability of survival;  
311 however, for montane salamanders in low elevation habitats, this higher body condition may not  
312 be enough. As climate is expected to become less favorable for montane salamanders, especially  
313 at lower elevations, monitoring these low elevations populations is of increasing importance  
314 because at least 55% of montane plethodontids (lower elevation limit is greater than or equal to  
315 1,000m) are threatened with extinction (IUCN 2016). Moreover, key life history characteristics  
316 such as body condition are relatively easy to collect and can provide an effective tool for  
317 identification of populations at risk (Janin et al. 2011).

318 Interestingly, animals that started the experiment with a greater BCI had lower rates of  
319 SVL changes and more negative changes in mass yet those same males had larger, darker testes  
320 indicative of greater reproductive condition (Sayler 1966; Peacock and Nussbaum 1973). This  
321 suggests that males with a greater BCI may put more energy into reproduction rather than growth  
322 during this life stage; this trend was strong for the males in our experiment (Supplemental Fig.  
323 5). Tradeoffs between growth and reproduction in wild animals have been well-documented  
324 (e.g., Reznick 1983, 1985); for example, in *P. cinereus*, brooding females allocated less

325 resources to growth compared to non-brooding females regardless of food availability (Yurewicz  
326 and Wilbur 2004).

327

### 328 *Origin Population*

329 We found that where an individual originated was a significant predictor of survival;  
330 individuals from lower elevations had higher survival than individuals from mid and high  
331 populations (Fig. 2) irrespective of their transplant location. One of the limitations in our data  
332 was our inability to control for relatedness, maternal effects, or genotype-environment  
333 interactions (e.g., Via and Lande 1985; Sinervo 1990; Bernardo 1996; Bronikowski 2000), all of  
334 which could have added unknown sources of variation to our data. This was out of necessity as it  
335 would not have been feasible to assess reproductive condition in a natural setting for salamanders  
336 that take at least three years to mature (N.M.C. *unpublished data*). However, patterns of survival  
337 in our transplant experiment may suggest interacting effects of local adaptation and phenotypic  
338 plasticity; individuals originating from low elevations were transplanted to elevations that  
339 represent either locally adapted conditions (i.e., low elevation) or better conditions (i.e.,  
340 transplanted to higher elevations than origin). On the other hand, individuals who originated  
341 from mid and high elevations experienced locally adapted conditions or better conditions (when  
342 transplanted from mid elevation to high elevation only), or worse conditions (i.e., when  
343 transplanted to elevations lower than origin). This variation in survival may be explained, at least  
344 in part, by temperature, which decreased with increasing elevation (PRISM, 2017). Although low  
345 and mid elevations show similar ENM suitability, the scale at which these variables were  
346 measured (~1 km) may not have been fine enough to adequately characterize these habitats. For  
347 example, Gifford and Kozak (2012) found that lower elevations, though they appeared to have  
348 identical habitats to higher elevations, contained microclimates that constrained *P. jordani*, a  
349 montane salamander. Future studies can refine hypotheses concerning local adaptation and  
350 phenotypic plasticity in salamanders by splitting clutches or otherwise controlling for genetic  
351 factors; however, this technique is logistically challenging for many *Plethodon* species.

352

### 353 *Transplant Location*

354 The abiotic environment, represented by transplant location in this experiment, was an  
355 important predictor for both growth and survival; salamanders that were transplanted to low  
356 elevations responded with the lowest survival and lowest growth (both mass and SVL) rates (Fig.  
357 3). These results also conform to *in situ* observations; warmer summer temperatures were  
358 associated with reduced growth rates in *P. cinereus* (Muñoz et al. 2016) and lower elevations had  
359 lower survival than higher elevations in *P. montanus* (Caruso and Rissler 2017). Our results  
360 support the hypothesis that amphibian distributions are influenced at the southern or lower  
361 elevation range limits by abiotic variables (Buckley and Jetz 2007; Gifford and Kozak 2012;  
362 Cunningham et al. 2016; Lyons et al. 2016), although here we did not explicitly test the relative  
363 influence of biotic factors. It should be noted, however, that climatic barriers at the lower  
364 elevational limit are not universal for plethodontids and biotic variables may be more important.

365 For example, *Desmognathus wrighti* is precluded from suitable lower elevations via predation by  
366 larger and more aquatic desmognathines (Organ 1961; Crespi et al. 2003), while *P. shendadoah*  
367 is outcompeted from non-talus slopes by *P. cinereus* (Jaeger 1970). Nonetheless we demonstrate  
368 here, that for the montane endemic *P. montanus*, the abiotic environment, specifically hotter and  
369 drier conditions (Fig. 1; Supplemental Fig. 1), likely limits its lower elevation distribution,  
370 similar to *P. jordani* (Gifford and Kozak 2012).

371         Though we did not modify or augment prey availability, we believe that prey availability  
372 was an unlikely source of variation in our results. First, all mesocosms had mesh screen and  
373 holes drilled along the side and bottom that were large enough to allow for smaller arthropods to  
374 enter the mesocosms. Second, local soil and leaf litter, which contained prey sources, were added  
375 to each mesocosm; thereby, minimizing variation among mesocosms within a transplant  
376 replicate. Lastly, we noted an abundance of prey items within the mesocosms when extracting  
377 the resident salamander at the end of the experiment, and during dissection to assess reproductive  
378 condition animals had prey items in their gut, indicating recent feeding (gut-passage time in *P.*  
379 *cinereus* is 1 – 2 weeks; Merchant 1970; Gabor and Jaeger 1995). While we do not suppose that  
380 prey populations affected our experiment, future shifts in salamander abundance could have big  
381 consequences for ecosystem function. Due to their large numbers in forest ecosystems (Burton  
382 and Likens 1975; Milanovich and Peterman 2016), salamanders can exhibit strong top-down  
383 effects on invertebrate populations; their presence is associated with reduced leaf-litter  
384 decomposition and overall carbon retention (Wyman 1998; Rooney et al. 2000; Walton et al.  
385 2006; Best and Welsh 2014; but see Walton and Steckler 2005; Homyack et al. 2010; reviewed  
386 in Walton 2013). Therefore, declines of salamander populations may have a negative feedback,  
387 in which the loss of salamander biomass reduces forest carbon sequestration, potentially  
388 accelerating anthropogenic climate change, resulting in further reductions in areas of suitable  
389 climate for salamander persistence.

390         In conclusion, we first provide experimental support for the hypothesis that the abiotic  
391 environment constrains the lower elevation limits of *Plethodon montanus*, which is consistent  
392 with predictions for amphibians, and more specifically, montane salamanders (e.g., Gifford and  
393 Kozak 2011; Cunningham et al., 2016; Lyons et al. 2016). Importantly, by using a reciprocal  
394 transplant experiment, we were able to test the relative influence of origin population and  
395 transplant location simultaneously; our results (i.e., AICc-selected variables and variable  
396 importance; Table 1; Supplemental Tables 1-3), suggest that the abiotic environment (transplant  
397 location) has more influence on survival and growth than population identity (origin population).  
398 Warmer and/or drier conditions can result in reduced surface activity, increased metabolism,  
399 increased water loss, as well as reductions in growth and survival in plethodontids (Caruso et al.  
400 2014; Riddell and Sears 2015; Catenazzi 2016; Connette et al. 2015; Muñoz et al. 2017; Caruso  
401 and Rissler 2017). Continued trends towards warmer and drier climates in the Appalachian  
402 region will likely lead to reductions in population growth unless compensated by an increase in  
403 immigration or reproduction (Tavecchia et al. 2016; Gaston 2009). These data are important not  
404 just because they add to the growing body of literature seeking to understand what determines  
405 the limits of a species' range (Gaston 2003), but they further suggest a worrisome forecast for  
406 montane salamanders under predicted future climate changes.

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615 **Table 1:** Estimates for the parameters included in the top model set ( $\Delta AICc < 2$ ) for each  
 616 response (Supplemental Tables 1-4). Interactions are denoted by ":", and bolded terms indicate  
 617 significant variables (i.e., 95% CI do not overlap zero). Relative importance of each parameter is  
 618 shown along with the number of models in the top model set that contain each variable (n).

Response	Parameter	Estimate	Lower 95% CI	Upper 95% CI	Variable <sup>19</sup> Importance (n)
Survival	<b>Intercept</b>	<b>0.501</b>	<b>0.014</b>	<b>0.988</b>	—
	<b>BCI</b>	<b>3.673</b>	<b>0.961</b>	<b>6.384</b>	<b>1.00 (5)</b>
	Transplant (Mid)	0.521	-0.094	1.136	0.67 (3)
	Transplant (High)	0.399	-0.297	1.095	
	<b>BCI:Transplant (Mid)</b>	<b>4.449</b>	<b>0.654</b>	<b>8.243</b>	<b>0.55 (2)</b>
	BCI:Transplant (High)	3.487	-0.393	7.367	
	<b>Origin (Mid)</b>	<b>-0.676</b>	<b>-1.338</b>	<b>-0.014</b>	<b>0.53 (3)</b>
	Origin (High)	-0.390	-1.007	0.228	
Rate of SVL Change	<b>Intercept</b>	<b>0.00091</b>	<b>0.00067</b>	<b>0.00114</b>	—
	<b>BCI</b>	<b>-0.00115</b>	<b>-0.00188</b>	<b>-0.00042</b>	<b>1.00 (2)</b>
	<b>Transplant (Mid)</b>	<b>0.00034</b>	<b>0.00010</b>	<b>0.00059</b>	<b>0.65 (1)</b>
	Transplant (High)	0.00001	-0.00022	0.00023	
Rate of Mass Change	Intercept	0.00060	-0.00028	0.000147	—
	<b>BCI</b>	<b>-0.00662</b>	<b>-0.00942</b>	<b>-0.00382</b>	<b>1.00 (2)</b>
	Origin (Mid)	-0.00059	-0.00130	0.00012	1.00 (2)
	Origin (High)	-0.00042	-0.00121	0.00037	
	<b>Transplant (Mid)</b>	<b>0.00144</b>	<b>0.00058</b>	<b>0.00230</b>	<b>1.00 (2)</b>
	Transplant (High)	0.00051	-0.00030	0.00132	
	BCI:Origin (Mid)	0.00274	-0.00084	0.00632	0.62 (1)
	BCI:Origin (High)	-0.00254	-0.00700	0.00192	

620 **Figure 1:** Relationship between ENM suitability and latitude, longitude, and elevation. Current  
621 (blue squares), future (red triangles) and the difference between future and current (purple  
622 circles) are shown.

623

624 **Figure 2:** Relationship between survival of *P. montanus* and A) origin population, and B)  
625 transplant location and BCI. Error bars denote 95% CI, lines show predicted probability of  
626 survival and dots indicate data points for low (dotted line, open squares), mid (solid line, closed  
627 circles) and high elevations (dashed line, closed triangles).

628

629 **Figure 3:** Influence of transplant location and BCI on rates A) of SVL and B) mass change.  
630 Lines show predicted fit, and dots indicate data points for low (dotted line, open squares), mid  
631 (solid line, closed circles) and high elevations (dashed line, closed triangles).

632

633 **Figure 4:** Reproductive condition (testes pigmentation) of *P. montanus* and BCI. Shaded ribbon  
634 denotes 95% CI of predicted fit (solid line).







