



Original Article

# Salamander climbing behavior varies among species and is correlated with community composition

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Species coexistence is often facilitated by behavioral strategies that minimize competition for limited resources. Terrestrial, lungless salamanders (genus *Plethodon*) coexist in predictable assemblages of body size guilds, but little is known about the behavioral mechanisms that promote such coexistence. Here, we considered the hypothesis that *Plethodon* salamanders use climbing behavior to reduce competitive interactions, thereby promoting coexistence through spatial partitioning. To explore this hypothesis, we quantified the frequency of climbing behavior at field sites where small-bodied (*P. cinereus*) and large-bodied (*P. glutinosus*) species are always present, but an intermediate-bodied species (*P. montanus*) is either absent, introduced, or native. We observed that climbing behavior varied among size guilds so that the smallest species climbed most frequently, followed by the intermediate, and then the large species. Further, we identified several correlates of climbing behavior that may be shaped by intraspecific and interspecific competition. Climbing frequency was positively correlated with intraspecific competition and negatively correlated with interspecific competition in the small species, unrelated to competition in the intermediate species, and positively correlated with interspecific competition in the large species. Our results suggest that *Plethodon* size guilds might differentially utilize climbing behavior to facilitate spatial partitioning in dense populations and communities. Further, we show how competition intensity can shape the behavior of cohabitating species, and ultimately provide insight into how behavioral plasticity and microhabitat partitioning can promote species coexistence.

**Key words:** amphibian, competition, GLM, niche partitioning, *Plethodon*

## INTRODUCTION

Species coexistence is made possible through an array of behavioral, morphological, and physiological adaptations (Adams and Rohlf 2000; Siepielski and McPeck 2010; Seebacher and Krause 2017). Behavioral strategies, such as microhabitat use and foraging strategies, are particularly important for reducing competition between closely related species, which tend to be morphologically and physiologically similar (Schoener 1974; Sih et al. 2004; Siepielski and McPeck 2010). The ability to respond to ecological stressors through behavioral adaptations promotes the coexistence of closely related competitors through resource and niche partitioning (Sih et al. 2004). These adaptations arise in response to 2 major

types of competition, exploitative and interference competition. In communities with exploitative competition, adaptations often relate to food source utilization, including consumption of different-sized prey and foraging in different locations or at different times of day (Schoener 1974; Vanak et al. 2013; Moreno-Opo et al. 2016). In communities with interference competition, which involves direct physical disputes as well as physical avoidance, behavioral strategies often facilitate the spatial partitioning of available habitat (Schoener 1974; Toft 1985). However, exploitative and interference competition are not mutually exclusive. In many cases, interference or spatial avoidance behaviors are outcomes of exploitative competition over shared resources (Toft 1985; Ferry et al. 2016).

When space is limited, behavioral adaptations and microhabitat complexity may define species' capacity for spatial partitioning (Schoener 1974; Amarasekare 2003). This mechanism is evident in communities of Florida anoles, where invasion by *Anolis sagrei* has

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driven the native *Anolis carolinensis* to climb higher, ultimately resulting in the rapid evolution of larger toe pads (Stuart et al. 2014). Stuart et al. (2014) suggested that the shift in climbing behavior and microhabitat preference has arisen from exploitative competition over shared food sources between the coexisting anoles. Studies of behavioral variation in response to competitor composition, like the anole example above, can provide insight into species' spatial distributions across available microhabitats and broader ecological scales (Bowler and Benton 2004; Sih et al. 2004). However, few studies have directly explored behavioral plasticity across communities of similar species that differ in competitor composition and density.

Salamanders of the genus *Plethodon* are strictly terrestrial and are known to live in dense, speciose communities (Grover 1998; Petranks 1998; Adams 2007). Because *Plethodon* species share similar ecological functions, coexisting species undergo intense competition for limited resources (Hairston 1981). As a result, *Plethodon* communities are frequently comprised of up to 5 different species that are divided into body size guilds, or species of comparable sizes that use shared resources, such as prey or retreats, in similar ways (Hairston et al. 1987; Simberloff and Dayan 1991; Adams 2007). Guild-based community organization acts as a resource partitioning mechanism, reducing interspecific competition and increasing the likelihood of species coexistence (Adams 2007; Vignoli et al. 2009). Adams (2007) suggests that patterns of size guild composition in *Plethodon* communities arise in response to competition over limited resources.

When 2 or more *Plethodon* species of a similar size guild co-occur, morphological traits may diverge to reduce competition (Adams 2007). For example, cranial and jaw morphology has diverged in sympatric populations of *P. cinereus* and *P. hoffmani* in Pennsylvania (Adams 2000; Adams and Rohlf 2000) and *P. cinereus* and *P. nettingi* in West Virginia (Adams et al. 2007), relative to allopatric populations. In these cases, morphological differentiation drove a functional shift in jaw strength and closure speed, thereby partitioning prey. A sole limiting resource in *Plethodon* communities is yet to be determined, though suggested factors include food and space to forage, burrow, and nest (Fraser 1976; Jaeger 1978; Jaeger 1979; Hairston et al. 1987; Rissler et al. 2000).

To compensate for intra- and inter-guild competition not accounted for by physiological and morphological mechanisms, *Plethodon* salamanders display a range of behaviors, including aggressive territorialism and biting, shifting burrows, staggered feeding schedules, and potentially climbing off-ground vegetation (Fraser 1976; Jaeger 1979; Rissler et al. 2000; Roberts and Liebgold 2008). Because *Plethodon* salamanders are relatively reclusive and occur under leaf litter and other cover objects (e.g., rocks and logs), many behavioral studies occur in highly controlled laboratory settings. Therefore, much remains unknown about microhabitat use under competitive pressures in wild *Plethodon*

communities comprised of multiple size guilds, though several studies have examined the use of daytime surface retreats (Gabor 1995; Faragher and Jaeger 1997; Caruso 2016). This is especially true of climbing behavior, which is diminished in lab settings where natural vegetation is absent.

While climbing behavior is often anecdotally noted in *Plethodon* species, we lack an understanding of why, and how often, these animals climb off the forest floor (McEntire 2016). In fact, we lack records of climbing behavior for most *Plethodon* species. Previous studies suggest that plethodontids may climb to increase olfactory cue detection and homing ability (Madison and Shoop 1970), to exploit additional foraging space or an alternative prey pool (Jaeger 1978), or to avoid predation (Roberts and Liebgold 2008). Given the high densities of individuals observed in *Plethodon* communities, it is possible that climbing behavior promotes spatial partitioning, thereby reducing interference competition as well as resource competition for space on the forest floor.

In this study, we examined climbing behavior in *Plethodon* communities to better understand its potential role in promoting species coexistence. Specifically, we were interested in the relationships between community composition and climbing behavior in 3 coexisting *Plethodon* species that represent 3 distinct body size guilds: small *P. cinereus*, intermediate *P. montanus*, and large *P. glutinosus*. Using field observations, we addressed the following questions: 1) Does the frequency of climbing behavior vary among species of different body size guilds? and 2) Is climbing behavior correlated with the number of active interspecific and intraspecific competitors? We predicted that climbing frequency differs among *Plethodon* body size guilds to promote spatial partitioning when climbable, aboveground microhabitat is available. Further, we predicted that climbing behavior is correlated with community composition such that salamanders are more likely to climb when the number of interspecific competitors increases. We suspected that this relationship would vary among size guilds, and that the small-bodied *P. cinereus* would be most sensitive to an increase in interspecific competitors. Overall, our study explores the ways in which community composition and the presence of competitors shapes the behavior of cohabitating species, and ultimately provides insight into how behavioral plasticity and microhabitat partitioning can promote coexistence.

METHODS

We performed a field study to observe salamander climbing behavior in 3 *Plethodon* communities in the Blue Ridge Mountains of southwest Virginia, USA (Table 1). The small- and large-bodied species, *P. cinereus* and *P. glutinosus*, respectively, were present in all 3 communities (Table 1). The intermediate-sized species, *P. montanus* (previously classified as *P. jordani*), was either absent, introduced by humans approximately 80 years prior to our study, or native

Table 1  
Site information for salamander field surveys

Community	Locality	N*	Coordinates (decimal degrees)	Elevation (m asl)
<i>P. montanus</i> absent	War Spur Trail	8	37.39366, -80.50329	1100
<i>P. montanus</i> absent	Wind Rock	8	37.40896, -80.52584	1200
<i>P. montanus</i> introduced	Hunter's Branch	16	37.37140, -80.52389	1150
<i>P. montanus</i> native	Dismal Creek A	8	37.24781, -80.86457	1100
<i>P. montanus</i> native	Dismal Creek B	8	37.25381, -80.85507	1000

Small and large *Plethodon* body size guilds are present in each community type, while the status of the intermediate guild (*P. montanus*) varies.  
\*N = number of 15 × 3 m transects.

(Rissler et al. 2000; Table 1). The number of active salamanders of each size guild varied among the communities, therefore our field sites represented a range of niche overlap (Figure 1). Thus, our study design provided a unique opportunity to quantify the effects of competitor abundance on climbing behavior, without experimental manipulation.

In each community type, we established 16, 15 × 3 m transects at randomly generated coordinates within a 1.6 km<sup>2</sup> area. Transects were separated by at least 20 m to reduce the possibility of recounting the same individual on a given survey. For the communities where *P. montanus* was either absent or native, we split survey efforts between 2 localities separated by at least 1 km. Since there is only one known *P. montanus* introduction site, we were limited to a single locality for this community type. To reduce climatic variation among communities, we chose sites within a narrow altitudinal range (1000–1200 m above sea level; Table 1).

We surveyed each transect 3 times within a 7-week period during June and July 2015, with at least 24 h between each survey to minimize disturbance (Otto et al. 2013). We randomized the survey order within each locality and conducted all surveys within 24 h of a rain event to maximize the number of salamanders available for aboveground sampling (O'Donnell and Semlitsch 2015). During each survey, 2–4 people crawled along the transect in a straight line and counted all surface-active salamanders of each species. The same 3 biologists led all surveys and trained all observers prior to data collection. For each salamander observed, we recorded whether it was on the ground (not climbing) or off the ground (climbing). We considered a salamander to be off the ground if it was observed on a plant (i.e., tree or understory vegetation) or a cover object at least 1 inch above the ground. Our study design minimized the likelihood that observed climbing behaviors were a result of climatic variability by performing all surveys on wet nights within a single season.

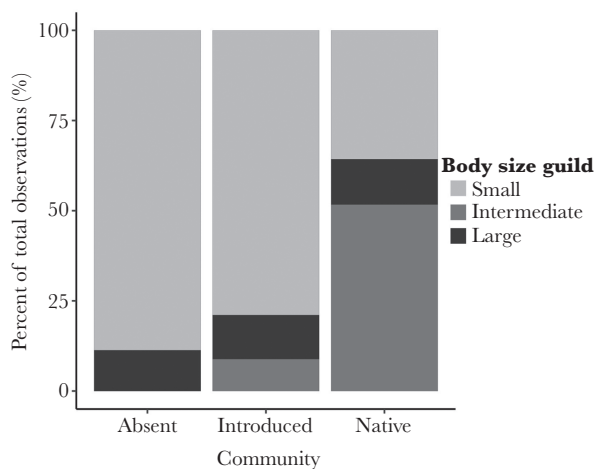
To account for variation in the amount of climbable structures among transects, we recorded the number of trees (diameter at breast height > 5 cm) and density of understory vegetation within each transect. We quantified understory vegetation by taking 3 pictures along each transect, at approximately 1.3 m above the ground. We estimated the density of understory vegetation as the percent

ground cover of vegetation in each photo using color segmentation and binary processing tools in ImageJ software (National Institute of Health, Bethesda, MD). For all analyses, we use the mean percent ground cover for understory vegetation within each transect.

The following analyses were used to determine whether climbing behavior varied among *Plethodon* body size guilds and whether it was correlated with competitor abundance. To determine whether climbing behavior varied among size guilds, we used a generalized linear model (GLM) with a logit link function to account for the binomial nature of our response variable (climbing or not climbing). We included body size guild and understory vegetation as explanatory variables. We quantified competition as the number of intra-specific and interspecific competitors observed within a transect during each survey. This represents the number of surface-active salamanders during a given survey, rather than the “superpopulation,” which would also account for salamanders belowground or unavailable for sampling (O'Donnell and Semlitsch 2015). Actual abundance estimates were not necessary, as we were interested in how the number of active competitors relates to climbing behavior. For each guild, we ran a GLM with a logit link function that included climbing behavior as the response variable. We chose to run separate models for each species to tease apart the relative effect of each competitor on the climbing behavior of each focal species. Explanatory variables included the number of intraspecific and interspecific salamanders observed in each transect during each survey, as well as the interactions between each competitor and understory vegetation. We chose to include understory vegetation as a fixed, rather than random, effect because we were interested in whether competition interacted with available microhabitat predictably, rather than stochastically. While *Plethodon* species can also climb up to 2–3 m on tree trunks, we chose not to include trees as an environmental variable in our analysis for 2 reasons. First, the complexity of understory vegetation, relative to tree trunks, provides far more opportunities for salamander climbing and foraging. Second, trees were underrepresented in our transects with a median of 7 trees per transect, relative to understory vegetation with a median of 30% ground cover in each transect.

## RESULTS

We observed a total of 2964 salamanders: 2189 *P. cinereus*, 420 *P. montanus*, and 355 *P. glutinosus* (Table 2). Of these observations, 595 individuals were found climbing (Table 2). We found that the probability of climbing was significantly different among size guilds ( $\chi^2 = 38.49$ ;  $P < 0.001$ ) and positively related to the density of understory vegetation ( $\chi^2 = 105.93$ ;  $P < 0.001$ ; Figure 2). The interaction between size guild and understory vegetation was non-significant ( $\chi^2 = 3.61$ ;  $P = 0.16$ ). In habitats with median understory vegetation (30% ground cover), the predicted probability of climbing was 0.24 (95% CI: 0.22–0.26) for the small species, 0.17 (95% CI: 0.14–0.21) for the intermediate species, and 0.10 (95% CI: 0.07–0.14) for the large species. For each percent increase in understory vegetation, the odds of climbing increased by a factor of 1.03 (95% CI: 1.02–1.03) when averaged across all species. In habitats with maximal vegetation (100% ground cover), predicted probability of climbing was 0.69 (95% CI: 0.59–0.76) for the small species, 0.51 (95% CI: 0.33–0.70) for the intermediate species, and 0.16 (95% CI: 0.05–0.41) for the large species. We assessed model fit using a likelihood ratio test and found that our model fit the data significantly better than an intercept-only (null) model for climbing probability ( $\chi^2 = 148.03$ ;  $df = 5$ ;  $P < 0.001$ ).



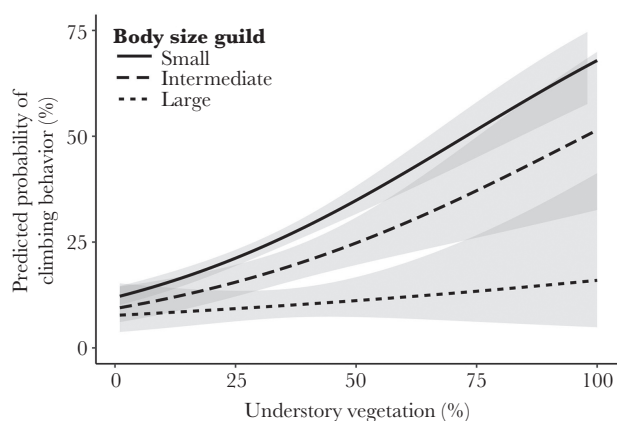
**Figure 1**

Comparison of species observations during field surveys among communities where the intermediatesized *Plethodon* species (*P. montanus*) is either absent, introduced or native.

**Table 2**  
Climbing frequency of each *Plethodon* species in each community type

Community	Locality	Species	Number observed*	Number observed climbing*	Percent climbing
<i>P. montanus</i> absent	War Spur Trail	<i>P. cinereus</i>	404	99	24.50%
		<i>P. glutinosus</i>	29	5	17.24%
		<i>P. montanus</i>	-	-	-
<i>P. montanus</i> absent	Wind Rock	<i>P. cinereus</i>	542	44	8.12%
		<i>P. glutinosus</i>	92	2	2.17%
		<i>P. montanus</i>	-	-	-
<i>P. montanus</i> introduced	Hunter's Branch	<i>P. cinereus</i>	1033	306	29.62%
		<i>P. glutinosus</i>	160	17	10.63%
		<i>P. montanus</i>	116	21	18.10%
<i>P. montanus</i> native	Dismal Creek A	<i>P. cinereus</i>	131	23	17.56%
		<i>P. glutinosus</i>	26	3	11.54%
		<i>P. montanus</i>	123	16	13.01%
<i>P. montanus</i> native	Dismal Creek B	<i>P. cinereus</i>	79	15	18.99%
		<i>P. glutinosus</i>	48	5	10.42%
		<i>P. montanus</i>	181	39	21.55%

\*Observations are summed across replicate surveys and transects for each locality.



**Figure 2**  
Predicted probability of climbing behavior for small, intermediate, and large *Plethodon* body size guilds in relation to available climbing habitat. The shaded area represents standard error.

In our second set of analyses, we determined the relationship between climbing probability and competitor abundance for each species. We found that climbing probability in the small species, *P. cinereus*, was significantly and positively affected by the number of intraspecific competitors ( $\chi^2 = 123.57$ ;  $P < 0.001$ ; Figure 3A) and understory vegetation ( $\chi^2 = 72.59$ ;  $P < 0.001$ ). Our models predict a 4-fold increase in the climbing probability of *P. cinereus* in transects where intraspecific competition intensity was the highest (climbing probability = 0.56, density = 2.07 *P. cinereus*/m<sup>2</sup>) relative to transects where intraspecific competition was lowest (climbing probability = 0.14, density = 0.02 *P. cinereus*/m<sup>2</sup>) when all other variables were held at their mean values. Additionally, we found a significant interaction between the number of intermediate-bodied competitors and understory vegetation ( $\chi^2 = 11.56$ ;  $P = 0.001$ ; Figure 3B) and the number of large-bodied competitors and understory vegetation ( $\chi^2 = 18.31$ ;  $P < 0.001$ ; Figure 3C) on climbing behavior in *P. cinereus*. In both cases, the probability of climbing decreased as the number of interspecific competitors increased. Yet, the large competitor had a greater effect on the odds of climbing than the intermediate competitor (odds ratios = 1.19 and 1.06, respectively). We assessed model fit using a likelihood ratio test and found that our model fit the data significantly better than the null model ( $\chi^2 = 236.14$ ;  $df = 7$ ;  $P < 0.001$ ).

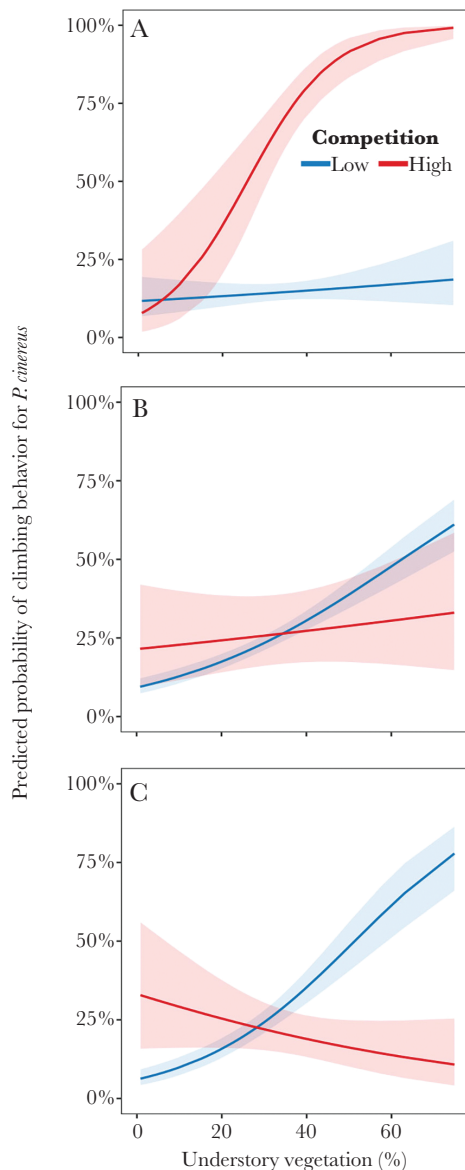
For the intermediate-sized *P. montanus*, understory vegetation was the only significant predictor of climbing behavior of the variables we explored ( $\chi^2 = 12.98$ ;  $P < 0.001$ ). All other variables and their interaction terms were non-significant, including the number of small competitors ( $\chi^2 = 1.68$ ;  $P = 0.20$ ), the number of large competitors ( $\chi^2 = 2.30$ ;  $P = 0.13$ ), and the number of intraspecific competitors ( $\chi^2 = 0.17$ ;  $P = 0.68$ ). We assessed model fit using a likelihood ratio test and found that our model fit the data significantly better than the null model ( $\chi^2 = 19.80$ ;  $df = 7$ ;  $P = 0.006$ ).

For the large species, *P. glutinosus*, the GLM for climbing probability poorly fit the data ( $\chi^2 = 9.43$ ;  $df = 7$ ;  $P = 0.08$ ). Preliminary data visualization suggested that of the variables we explored, the most important driver of climbing behavior in *P. glutinosus* was the number of small interspecific competitors. Thus, we reduced our model to test the effects of understory vegetation, the number of small-bodied competitors, and the interaction between competition and vegetation on climbing probability. The reduced model proved to be a better-fit than the null model ( $\chi^2 = 8.86$ ;  $df = 3$ ;  $P = 0.03$ ) and showed that the climbing behavior of *P. glutinosus* was significantly affected by the number of small competitors such that the probability of observing climbing behavior in *P. glutinosus* increased as the number of active *P. cinereus* increased ( $\chi^2 = 5.41$ ;  $P = 0.02$ ; Figure 4). Understory vegetation ( $\chi^2 = 0.56$ ;  $P = 0.45$ ) and the interaction between competition and understory ( $\chi^2 = 2.89$ ;  $P = 0.09$ ) were nonsignificant. Our model predicted an 8.49-fold increase in the climbing probability of *P. glutinosus* in communities with the highest density of *P. cinereus* (climbing probability = 0.43, density = 2.07 *P. cinereus*/m<sup>2</sup>) relative to communities with the lowest density of *P. cinereus* (climbing probability = 0.05, density = 0.02 *P. cinereus*/m<sup>2</sup>) when understory was held at a mean value.

## DISCUSSION

In this study, we surveyed representatives of 3 *Plethodon* size guilds across communities to better understand the relationships between species size, competitor abundance, and climbing behavior. As anticipated, the availability of climbing structures, in the form of understory vegetation was strongly and positively related to climbing frequency. However, size guilds differentially utilized vegetation for climbing. On average, the smallest species was most likely to climb, followed by the intermediate, and then the large species. Further, we found correlations between competitor abundance



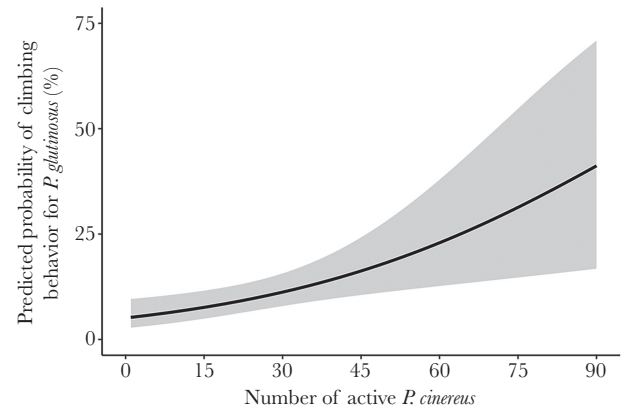


**Figure 3**

Interactive effects of microhabitat availability and competition on climbing behavior in *P. cinereus*. The panels illustrate the predicted effects of (A) intraspecific competition, (B) interspecific competition with an intermediate-sized competitor (*P. montanus*), and (C) interspecific competition with a large competitor (*P. glutinosus*). The colors represent competitor density, where the competing guild is either present in relatively high (red) or low (blue) densities. The shaded area represents standard error.

and climbing behavior, though the relative importance of intraspecific and interspecific competitor abundance was species-specific. For the smallest species, climbing behavior strongly increased with the abundance of intraspecific competitors, but decreased with the abundance of interspecific competitors. For the large species, climbing behavior increased with the number of small interspecific competitors. Finally, of the variables we considered, climbing behavior in the intermediate species was only driven by vegetation density and was seemingly unaffected by competition.

Variation in climbing behavior among *Plethodon* size guilds suggests that behavioral niche partitioning may be a mechanism of coexistence. While the amount of understory vegetation was a



**Figure 4**

Relationship between competitor abundance and climbing behavior in *P. glutinosus*. The number of active small-bodied salamanders (*P. cinereus*) was the strongest predictor of climbing behavior for the large-bodied species (*P. glutinosus*). The shaded area represents standard error.

strong predictor of climbing behavior, *Plethodon* size guilds differentially utilized available aboveground microhabitat. At all understory vegetation densities, the large *P. glutinosus* had a lower likelihood of climbing than both the intermediate *P. montanus* and the small *P. cinereus*. This trend may be the result of body size limitations, where *P. glutinosus* and, to a lesser degree, *P. montanus* are limited to climbing larger vegetation while the smaller *P. cinereus* can climb a broader range of understory structures. Additionally, *P. glutinosus* is more likely to remain near the entrance of underground burrows during nocturnal activity than the 2 smaller species, which may provide an alternative foraging ground (Rissler et al. 2000). The use of burrows may be advantageous over understory vegetation, as they provide a quicker retreat from potential threats (AJ Navarro, personal observation). Further research should investigate the ecological tradeoffs of microhabitat use in *Plethodon* communities to better understand the impacts of spatial partitioning on individual fitness and population dynamics.

The abundance of competitors seems to affect the climbing behavior of the small *P. cinereus* to a higher degree than the 2 larger guilds. Climbing behavior of *P. cinereus* strongly increased with the abundance of intraspecific competitors. As the abundance of *P. cinereus* increased, shared resources of the size guild may have become limited, thus increasing competition. An elevated climbing frequency may compensate for intensified competition by providing alternate foraging grounds as well as an escape from intraspecific aggressive interference and territorialism on the forest floor (Jaeger 1978; Mathis 1990; Roberts and Liebgold 2008). Thus, we propose that understory vegetation may vertically expand hospitable habitat and foraging opportunities for *P. cinereus*, thereby increasing carrying capacity and promoting larger population sizes.

Unlike intraspecific competition, interspecific competition appeared to reduce climbing frequency in *P. cinereus*. This was especially apparent in the presence of the large competitor, *P. glutinosus*. We find this result surprising given that *P. glutinosus* is the least likely to utilize understory vegetation for climbing and occurs in relatively low densities across all community types. A recent study found no aggressive interference competition between juvenile *P. glutinosus* and adult *P. cinereus* for available space (i.e., earthworm burrows; Ransom 2011). Though adult *P. glutinosus* are too large to use earthworm burrows, it is possible that higher densities of *P. glutinosus* indicates greater availability of burrows, in general, for all species

to exploit as retreats or foraging grounds. If true at our study sites, *P. cinereus* may have used available burrows, rather than climbing, to avoid resource competition or aggressive interference. Another study found evidence of exploitative competition between the 2 species, though it varied with ontogeny (Price and Secki Shields 2002). When exploitative competition is high and understory vegetation provides an alternative source of food, the larger species may outcompete *P. cinereus* for climbing microhabitat. However, it is unclear whether *P. cinereus* avoids climbing in the presence of larger species, potentially exploiting other spatial resources on the forest floor, or is aggressively prevented from accessing understory vegetation through interference competition.

Surprisingly, and in contrast to the other 2 size guilds, the climbing behavior of *P. montanus* was not significantly related to competitor abundance. Given the species' intermediate size, the niche of *P. montanus* should strongly overlap with *P. cinereus* and *P. glutinosus*. As such, we expected the climbing behavior of this species to be driven by the abundance of interspecific competitors. However, the larger resource pool granted to *P. montanus* by its intermediate body size may allow the species to escape competitive pressures. The intermediate guild has access to a broader size range of prey than the small *P. cinereus* and access to a greater variety of microhabitats (e.g., climbable structures and burrows) than the large *P. glutinosus*. *Plethodon montanus*' ability to exploit a wider variety of resources than the other *Plethodon* species in the community may reduce the species' limiting resources, making it less subject to competition than the small and large species (Siepielski and McPeck 2010). These results support previous conclusions that coexisting *P. glutinosus* and *P. montanus* do not display competitive exclusion (Rissler et al. 2000). Less restricted by limited resources, *P. montanus*' climbing behavior may be significantly related only to the availability of climbable substrate. Understory vegetation promotes species coexistence by generating microhabitat differentiation (Mouquet and Loureau 2002). *P. montanus* may have made use of such habitat differentiation by responding with increased climbing behavior.

For all analyses, we used a single species to represent each body size guild. We recognize that variation in climbing behavior may be due to other species-specific traits, but previous studies suggest that body size is a profound driver of ecological variation among our focal species, and therefore, is a likely driver of behavioral differences (Adams 2007). Relatedly, variation in surface area to volume ratios may contribute to behavioral differences among size guilds. Smaller species, which have higher surface area to volume ratios, lose water more rapidly than larger species and may experience physiological benefits or costs when climbing understory vegetation (Spight 1968; Gifford 2016; McEntire 2016). Further work is needed to determine whether our observations are consistent in other communities of co-occurring small, intermediate, and large *Plethodon* species. We also suggest that future studies pair field observations with experimental manipulations to tease apart the effects of temperature, moisture, prey availability, and competition on climbing frequency.

In this study, we observed 3 coexisting *Plethodon* body size guilds differentially utilizing available microhabitat and propose that climbing behavior may be impacted by competition intensity. These suggestions support the proposition of McEntire (2016), that differences in climbing frequency of salamander species may influence community structure and spatial microhabitat partitioning. Our surveys suggest that the large species dominates the forest floor, the small species dominates understory vegetation, and the intermediate sized species is flexible in its use of available microhabitat. Our

observations support the idea that behavioral plasticity can enable coexistence of similar species competing for limiting resources, although the limiting resource driving such interspecific competition in *Plethodon* communities is yet to be determined (Sih et al. 2004). We provide correlative evidence for behavior-facilitated resource partitioning in coexisting *Plethodon* size guilds, especially between small- and large-bodied species. *Plethodon glutinosus*, *P. montanus*, and *P. cinereus* display spatial partitioning and plasticity in climbing behavior, possibly in response to increasing microhabitat availability and interspecific aggressive interference, feasibly promoting the coexistence of 3 size guilds.

Behavioral plasticity, such as the climbing behavior described in Virginia *Plethodon* communities, may reduce competition and promote coexistence of sympatric species. Behavioral mechanisms of coexistence have been proposed in numerous communities, including scavenging birds, large African carnivores, Florida anoles, and now *Plethodon* salamanders (Vanak et al. 2013; Stuart et al. 2014; Moreno-Opo et al. 2016). In the face of global climate change and community structure shifts, we propose further examination of behavioral strategies that reduce exploitative and interference competition in a greater number of communities. Understanding how closely related coexisting species might behaviorally respond to changing environmental conditions could enhance the predictability of species and community shifts on spatial and temporal scales.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Mezebish et al. (2018).

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