Arboreal Ecology of Plethodontidae: A Review

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Lungless salamanders in the family Plethodontidae are widely distributed and the most diverse lineage of caudates. Plethodontids occupy forested and freshwater habitats, where they can achieve remarkable abundance and biomass. The majority of tropical plethodontids are arboreal. Though generally considered ground dwelling, a large proportion of temperate species have been observed climbing shrubs, trees, and herbaceous vegetation. Approximately 45% of terrestrial and semi-aquatic (not including permanently aquatic) plethodontid species are known to obligately or facultatively climb vegetation; yet, with the exception of tropical plethodontids, the importance of arboreal habits is generally underappreciated. The potential benefits of arboreality vary based on life history and geography but may include improved olfaction, increased foraging potential, shelter and nesting, and predator avoidance. Constraints on arboreality include increased water loss rates and morphological limitations. Recognition of arboreal habits as a relevant component of salamander ecology is important in rapidly changing landscapes with anthropogenic alterations to midstory and canopy communities.

THE caudate family Plethodontidae is widely distributed and the most diverse lineage of salamanders in the world. There are 448 known species within Plethodontidae, which account for 66% of all known salamander species worldwide (AmphibiaWeb, 2015). All except nine of those species occur in temperate North America and the New World tropics. Plethodontids are the only salamanders known to occur in the Southern Hemisphere. Although plethodontids are found in a variety of terrestrial and freshwater habitats, the majority of species are associated with forests (Petranka, 1998; Blankers et al., 2012). Many tropical plethodontids are generally or exclusively arboreal (Blankers et al., 2012), whereas North American plethodontids commonly frequent forest floor and streamside habitats (Petranka, 1998). Because there is not a term to distinguish between climbing exclusively on trees and climbing on multiple types of vegetation, for this paper, the term ‘arboreal’ refers to climbing all types of vegetation. With this definition, many temperate plethodontids are facultatively arboreal. However, because most temperate plethodontids spend a significant amount of time on and are primarily associated with the forest floor, observations of arboreal habits are often treated as peculiar or trivial behaviors. Ignoring the arboreal habits of many plethodontids may skew our perspective on the prevalence and potential importance of these habits and the importance of vegetation as a component of plethodontid habitats.

The goal of this review is to 1) describe and characterize the prevalence and distribution of arboreality in Plethodontidae, 2) discuss the evolution and economics of plant climbing behaviors, and 3) explore the relevance of arboreality to our understanding of salamander ecology in a rapidly changing world.

DESCRIPTION AND DISTRIBUTION OF ARBOREALITY

Despite many anecdotal reports, one might infer that arboreality is rare among salamanders based on the paucity of published literature on this behavior. The absence of published reports of arboreality and explicit studies of climbing behavior for many species reflects the perception or implicit belief that arboreality is an esoteric behavior or restricted to specialist species in tropical America. Yet integration of anecdotal and published reports suggest at least 45% of non-permanently aquatic, plethodontid salamanders have been observed climbing plants. For the remainder of this paper, all references to plethodontid salamanders as a group refer to non-permanently aquatic species. A list of all arboreal plethodontid species based on these reports was deposited in the Dryad Digital Repository (DRYAD; McEntire, 2015). The overwhelming majority (95%) of obligately arboreal salamanders occur in tropical forests and spend the majority of their lives in the canopy (e.g., Wake, 1987). At least 22% of tropical species are obligately arboreal (Fig. 1), and this estimate is likely conservative given limited information on the habits of many enigmatic tropical species. Canopy communities within the tropics are the centers of biodiversity, and many tropical plethodontids are associated with epiphytic plants such as bromeliads that provide moist microclimates in which to shelter, forage, and nest (Wake, 1987; Benzing, 1998; Bruce, 1998; Nadkarni and Solano, 2002).

The only temperate plethodontid genus that includes obligate (or near obligate) arboreal species is Aneides (Diefenbacher, 2008). Seasonal weather shifts and freezing temperatures in temperate zones force salamanders to periodically seek shelter away from the canopy. In most areas, these shelters are underground or in deep rock crevices, where temperatures remain above freezing. In the absence of freezing temperatures, tropical salamanders can exclusively utilize the many humid shelters located in the canopy. Therefore, obligate arboreality would be predicted less frequently in temperate compared to tropical regions. The three temperate plethodontid species found frequently in trees, and believed to dwell there, occur in temperate rainforests, where moss mats provide shelter and food resources. One of these species, Aneides ferreus, has been found inside the nests of Western Gray Squirrels (Sciurus griseus), where temperatures were higher than the surrounding air (Spickler et al., 2006). A fourth species, Aneides aeneus, can be classified as facultatively arboreal as it extensively climbs high into trees during the summer and has been found up to 21 m in the canopy (Waldron and Humphries, 2005; Thigpen et al., 2010) but retreats to rock outcrops in the winter. It has been speculated that A. aeneus was once highly arboreal, but the loss of American Chestnut (Castanea dentata) trees, which may have provided superior shelter compared to other tree species, restricted their current distribution to rock outcrops (Dodd, 2004).
In addition to the obligately arboreal species, 28% of tropical salamanders and 33% of temperate plethodontid species are facultatively arboreal (Figs. 1, 2). These species spend much of their time on and under the ground but emerge to climb plants under favorable conditions. Although arboreality is seldom reported in species descriptions for temperate species, a rigorous literature search and personal communication with experts has revealed that arboreality is common among temperate species. Arboreal behavior has been observed for 19 species of *Plethodon*, 13 species of *Desmognathus*, four species of *Eurycea*, four species of *Batrachoseps*, *Gyrinophilus porphyriticus*, *Hydromantes italicus*, *Ensatina eschscholtzii*, and *Pseudotriton ruber*. If arboreality is extended to include other climbing surfaces (rock faces and cave walls), the proportion of animals known to climb grows to 51% of temperate species. Whether salamanders distinguish between these two vertical surfaces remains unstudied, but several species known to climb plants are also frequently found on rock faces (Huheey and Brandon, 1973; Petranka, 1998; Casali et al., 2005; Lannoo, 2005).

The proportion of known species with arboreal behaviors changes slightly if temperate species with and without an aquatic larval stage are examined separately. This separation facilitates comparison of direct developing temperate and tropical species. Given this distinction, 47% of species with an aquatic larval stage and 31% of direct developing species have been observed displaying arboreal behaviors (17 of 36 and 31 of 100, respectively). These proportions are not significantly different (Fisher’s Exact test ($P = 0.1039$; GraphPad Quick Calcs, GraphPad software Inc., 2015).

Little information exists about facultative arboreality in tropical regions. High endemism and natural rarity combined with recent declines for many species has resulted in relatively little ecological or behavioral research on tropical species. Much of the published literature in this region focuses on phylogeography and species descriptions. Additional studies measuring the frequency of plant climbing would be useful in determining the utilization of plants as a microhabitat across the family. Currently, our knowledge of arboreality across plethodontid species, as measured by the number of species in an area that are reported as arboreal, is concordant with overall patterns of species richness (Fig. 3). This suggests that arboreality is common among all plethodontids that have terrestrial life stages, and that the form (facultative versus obligate) but not the prevalence of arboreal species varies geographically. However, populations or species may vary geographically in the prevalence of individual plant climbing depending on local climate and other environmental factors.

There have been few efforts to quantify the prevalence or amount of time individuals spend climbing and whether that varies geographically. Among 11 studies that quantified arboreal behavior, rates of plant climbing ranged from 0 to 88% of individuals (Table 1). Climbing rates may vary locally with weather and among populations or species depending on climate, which makes it difficult to characterize the extent to which individuals or species are facultatively arboreal. Because plethodontid activity is strongly governed by water loss (Jaeger, 1978; Feder and Lynch, 1982; Feder, 1983), one would expect higher percentages of individuals to climb plants during wetter conditions. Though most studies report observations from wet nights, it is notable that Jaeger (1978) observed 13% of surface-active *Plethodon cinereus* and Trauth et al. (2000) observed 23% of *P. caddoensis* climbing plants on relatively dry nights (Table 1).

### EVOLUTION AND ECONOMICS OF ARBOREALITY

The prevalence of arboreality among species across temperate and tropical ecosystems suggests arboreality among Plethodontidae is either conserved or has evolved multiple times. Regardless of whether this behavioral trait is highly conserved or evolved repeatedly, its prevalence across pletho-
A dontid species suggests arboreality has adaptive benefits. This raises several important questions: (1) what fitness benefits would select for obligate or facultative arboreality; (2) what fitness costs limit arboreality; and (3) among facultatively arboreal species, what local factors determine whether individuals climb vegetation?

**Economics of obligate arboreality.**—In rainforests, arboreality offers sites for nesting and shelter (Wake, 1987; Bruce, 1998; Spickler et al., 2006) and foraging opportunities (Wake, 1987; Spickler et al., 2006). Tropical forest canopies support diverse and productive communities largely because epiphytic plants and moss mats provide abundant prey. Epiphytic plants (e.g.,

**Fig. 3.** Map (A) shows the number of species with known arboreal tendencies (both facultatively and obligately arboreal species); (B) shows the number of plethodontid salamanders found in the Americas based on ranges for 375 species of salamander (174 of 193 known to climb and 164 of 233 non-aquatic species not known to climb). These ranges were obtained through the IUCN and are limited to species in the Americas where all but nine species occur and to current IUCN species designations (some species have been split following genetic information, but this is not yet reflected in the distributions from IUCN).

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency of climbing</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Desmognathus carolinensis</em></td>
<td>22% (7 of 32) [wet]</td>
<td>Black Mountains area, Clingman’s Peak, North Carolina</td>
<td>Hairston, 1949</td>
</tr>
<tr>
<td><em>Desmognathus wrighti</em></td>
<td>88% (7 of 8) [wet]</td>
<td>Black Mountains area, Clingman’s Peak, North Carolina</td>
<td>Hairston, 1949</td>
</tr>
<tr>
<td><em>Eurycea bislineata</em></td>
<td>58% (11 of 19) [wet]</td>
<td>Canada</td>
<td>LeGros, 2013</td>
</tr>
<tr>
<td><em>Hydromantes italicus</em></td>
<td>77% [overall; wet and dry]</td>
<td>Italy</td>
<td>Casali et al., 2005</td>
</tr>
<tr>
<td><em>Plethodon caddoensis</em></td>
<td>21% (11 of 52) [dry]</td>
<td>Ouachita National Forest, Montgomery County, Arkansas</td>
<td>Trauth et al., 2000</td>
</tr>
<tr>
<td><em>Plethodon cinereus</em></td>
<td>13 to 60% [dry and wet nights, respectively]</td>
<td>Blackrock Mountain, Shenandoah National Park, Virginia</td>
<td>Jaeger, 1978</td>
</tr>
<tr>
<td><em>Plethodon cinereus</em></td>
<td>23% [wet]</td>
<td>Mountain Lake Biological Station, Salt Pond Mountain, Giles County, Virginia</td>
<td>Roberts and Liebgold, 2008</td>
</tr>
<tr>
<td><em>Plethodon glutinosus</em></td>
<td>0–65% and 4–87% [NA]</td>
<td>Smoky and Balsam mountains, North Carolina</td>
<td>Hairston et al., 1987</td>
</tr>
<tr>
<td><em>Plethodon hubrichti</em></td>
<td>76% [wet]</td>
<td>Virginia</td>
<td>Kramer et al., 1993</td>
</tr>
<tr>
<td><em>Plethodon idahoensis</em></td>
<td>0.20% [overall; wet and dry]</td>
<td>Lincoln County, Montana</td>
<td>Wilson and Larsen, 1988</td>
</tr>
<tr>
<td><em>Plethodon jordani</em></td>
<td>0–65% and 4–87% [NA]</td>
<td>Smoky and Balsam mountains, North Carolina</td>
<td>Hairston et al., 1987</td>
</tr>
<tr>
<td><em>Plethodon shermani</em></td>
<td>15% [wet]</td>
<td>North Carolina</td>
<td>Lewis et al., 2014</td>
</tr>
</tbody>
</table>
bromeliads) extract moisture from the atmosphere in cloud forests (Benzing, 1998). In turn, these plants provide ideal shelter for salamanders by retaining moisture, stabilizing temperature, and providing habitat for prey (Wake, 1987; Benzing, 1998). The temperate rainforests of the Pacific Northwest of the U.S. also offer wet, moderate, maritime climates that support moss mats in the canopy, providing shelter and foraging for Aneides (Spickler et al., 2006).

The dominant physiological constraint for obligate arboreality is water loss, as lungless plethodontids require moist skin for cutaneous gas exchange (Jaeger, 1978; Feder and Lynch, 1982). Abundance of moist shelters within the canopy of tropical and some temperate rainforests alleviates much of this pressure and facilitates obligate arboreality. In the absence of these shelters, salamanders climbing on vegetation may be exposed to lower relative humidity and greater wind speed than on the surface of the ground. Arboreal salamanders in the tropics have more robust bodies than non-arboreal species (Blankers et al., 2012). This difference in body shape may reduce water loss rates by reducing their surface area to volume ratios. However, increased robustness may be limited as a way to reduce water loss because mass acts as a limiting factor for climbing ability, and, consequently, larger animals tend to be less arboreal than smaller ones (Alberch, 1981).

Arboreality also requires morphological adaptations that may trade off with adaptations for using underground retreats. Obligately arboreal plethodontids frequently have highly specialized morphologies, especially in their foot shape and toe webbing (Alberch, 1981). Wake (1987) described a general morphology of bromeliad-dwelling (specialist) salamanders as having a small overall size, long prehensile tails, long limbs, widely spread digits, and frontally directed eyes. All of these traits contribute to the salamanders’ ability to cling to and forage on slippery, vertical surfaces (Alberch, 1981). Cave and rock associated plethodontids frequently have similar morphological adaptations for climbing such as wider toe tips, webbing, prehensile tails, and projectile tongues (Diefenbacher, 2008; Saunders, 2009).

Most tropical plethodontid salamanders also have free projectile tongues, whereas most temperate species have attached protrusible or attached projectile tongues that are effective only at close range and require more bodily movement to search for and capture prey (Lombard and Wake, 1986). The more robust bodies of some tropical plethodontids may accommodate the musculature needed to retract a projectile tongue. Similarly, highly arboreal Aneides have broad toe tips and prehensile tails, although their tongues are attached at the anterior margin instead of freely projectile.

In contrast to arboreal forms, fossorial plethodontids generally have slender bodies with shorter legs that facilitate retreat into small underground crevices and burrows (Petranka, 1998). Oedipina and Batrachoseps have short legs, small feet, and an elongated body, which allows them to easily navigate fossorial habitats (Wake, 1987). There are naturally some exceptions to these generalizations, but the patterns among tropical plethodontids suggest a morphological trade off between effective use of arboreal and fossorial habitats.

**Economics of facultative arboreality.**—Temperate zones are less likely to support obligate arboreality because seasonality dictates a need to seek shelters that remain above freezing. In addition, some temperate zone forests may be too dry to allow animals to remain in arboreal habitats, and the general absence of epiphytic plants limits the availability of moist refuges within the canopy. Nonetheless, many temperate plethodontids climb vegetation opportunistically and with high frequency, suggesting advantages to facultative arboreality within temperate systems. Several hypotheses about the benefits of plant climbing within the temperate zone have been proposed, including increased prey quality or abundance (Jaeger, 1978), increased detection of olfactory cues (Madison and Shoop, 1970), and avoidance of predators (Roberts and Liebgold, 2008).

Increased foraging potential was commonly assumed to be the reason for plant climbing behaviors and has been explored in four studies of two species of Plethodon. A foundational study for this hypothesis was conducted on Plethodon cinereus. That study attributed increased volumes of food in the stomachs of animals collected on plants (compared to individuals collected on the ground) to increased foraging success when climbing (Jaeger, 1978). A dietary study on another species, P. shermani, found arboreal invertebrates present in the diet, which also suggested that salamanders forage when climbing (Mitchell and Taylor, 1986). However, a later study on P. shermani found similar diets and volume of prey between individuals collected on plants and those collected on the ground (Lewis et al., 2014). Additionally, Roberts and Liebgold (2008) estimated that potential prey items for P. cinereus were less abundant on plants compared to the ground, suggesting better foraging potential on the ground.

There are a number of potential reasons for the equivocal findings among these four studies. Jaeger (1978) suggested that prey may be easier to capture on plants than in the complex matrix of leaf litter, and therefore, arboreal prey may be more available to salamanders even though it may be less abundant than forest floor-dwelling prey. Further, differences in the abundance or types of vegetation among sites may affect arboreal prey availability, and the relative availability of arboreal versus leaf litter prey may vary seasonally. A potential limitation of all these studies are the assumptions that prey found in a salamander’s stomach were captured in the microhabitat where the animal was captured and that there are distinct arboreal and ground-dwelling taxonomic groups of prey (Jaeger, 1978; Mitchell and Taylor, 1986; Roberts and Liebgold, 2008; Lewis et al., 2014). Salamanders may capture litter-dwelling prey before ascending plants and plant-dwelling prey before descending back to the ground. Some common invertebrates in salamander diets occur in both habitats, either because those invertebrates also climb vegetation (e.g., ants and spiders) or because they drop from plants into the leaf litter (e.g., caterpillars that are pupating or fall during storms). The movement of potential prey between habitats may confound the use of diets to study salamander arboreality, but it may also be a reason that salamanders are facultatively arboreal. Salamanders may alter their climbing behavior in response to variation in the availability of litter versus arboreal prey.

Plethodontids frequently use chemosensory information to interact with their surroundings, and salamanders may be able to more efficiently detect or orient toward the sources of olfactory cues when climbing. Above the ground there is less disruption of airflow, and climbing was proposed to increase their detection of olfactory cues and influence homing behavior (Madison and Shoop, 1970). Plethodon jordani use olfactory cues to home when displaced (Madison, 1969), and displaced salamanders were frequently observed climbing
plants when homing. It is not clear whether detection of olfactory cues explains arboreality when salamanders are not homing. Plethodontids use olfactory cues to remain within territories (Jaeger et al., 1995), locate mates (Marco et al., 1998), and identify predators (Maerz et al., 2001; Madison et al., 2002; Sullivan et al., 2002), but no study has linked arboreality to chemical ecology in any of these contexts. Roberts and Liebgold (2008) proposed predator avoidance as a benefit of plant climbing when they found that *P. cinereus* climbed higher on vegetation following tail autotomy compared to individuals with their tails left intact.

The primary motivator for plethodontid salamanders to cease activity is water loss (e.g., Feder, 1983; Peterman and Semlitsch, 2014), so facultative arboreality should also be proximately and ultimately governed by water loss. Jaeger (1978) demonstrated that *Plethodon cinereus* lose water at a faster rate while climbing plants but suggested salamanders would need to spend a smaller amount of time hunting on vegetation because of improved foraging success. However, Hairston (1949) described activity patterns for *Desmognathus wrighti* and *D. carolinensis* and observed both species on vegetation later in the evening for several hours (it is not known if these were the same individuals). Additionally, individual *D. ocoee*, *P. teyahalee*, and *P. shermani* have been observed remaining on leaves for several continuous hours at mid and upper elevations in North Carolina (pers. obs.). These observations suggest the potential for water loss may not always be significantly higher on vegetation, or that salamanders are using other means such as behaviorally positioning themselves on vegetation to reduce water loss. Some species may have developed greater resistance to water loss that permits prolonged plant climbing. A recent study found elevation differences in resistance to water loss with animals from lower elevations having a higher resistance to water loss allowing estimated activity time to closely resemble higher elevation populations (Riddell and Sears, 2015). This geographic variability suggests plasticity or local adaptation to the environment and may also apply when animals are climbing.

Morphological tradeoffs may also explain facultative arboreality in some temperate plethodontids. A study comparing morphology and microhabitat use found no distinct relationship among temperate species (Blankers et al., 2012) but did not include information about temporary use of arboreal microhabitats. Nonetheless, many temperate plethodontid species are morphologically intermediate to the highly arboreal and fossorial forms seen in tropical climates. The need to use subterranean burrows to escape winter temperatures, frost, and periodic droughts likely requires a relatively slender form that constrains the evolution of more robust body forms that are associated with climbing and reduced water loss. Temperate species, while generally intermediate in form, do vary in size, limb length, and robustness (Adams et al., 2009), which may be related to relative differences in arboreal tendencies (but this has not been evaluated). Similarly, in the tropics, salamanders typically found in moss mats have a less distinct overall morphology but generally are slender with short legs (Wake, 1987). This intermediate morphology may reflect more facultative tendencies and the prevalence of moss mats in both ground level and arboreal habitats. Different body forms may also use different strategies to maintain arboreal behaviors. For example, the few species of *Oedipina* (elongate salamanders with reduced limbs) known to climb may use surface tension to cling to branches rather than specialized limbs and feet (Wake, 1987).

As previously mentioned, cave and rock associated plethodontids have similar morphologies to obligately arboreal species (Diefenbacher, 2008; Saunders, 2009). This suggests potential for salamanders with these morphologies to facultatively climb on different substrates, including vegetation, depending on availability. *Hydromantes* salamanders in Italy and California are known to inhabit caves and have specialized morphologies associated with climbing (Adams and Nistri, 2010). Many of these habitats are devoid of vegetation, thus restricting any tendency for arboreality. When arboreal habitat is available, at least one species (*Hydromantes italicus*) is known to frequently climb vegetation as well as cave walls (Casali et al., 2005). Similarly, *Aneides aeneus* utilizes both arboreal habitats and rock outcrops, further suggesting potential translation of form to multiple habitats.

Extensive facultative climbing also exists in tropical areas. This behavior is less well studied in tropical climates, but many of the aforementioned constraints and benefits may also apply to tropical species. A large part of tropical diversity and biomass exists in the canopy, making arboreality a beneficial behavior for increased foraging potential. Climbing ability related to morphology may restrict the capacity for species to remain in the canopy permanently. Tropical species may also facultatively climb plants due to chemosensory information. Predator avoidance is unlikely to be a motivating factor for arboreality in the tropics, as Wake (1987) reported higher rates of tail loss in arboreal animals compared to other species. Further research would greatly enhance our understanding of facultative arboreality in tropical forests.

An understudied aspect of facultative arboreality is its potential relationship to interspecific interactions. Montane forests within southern Appalachia and Neotropical cloud forests harbor a high density and diversity of species. Interspecific competition and intra-guild predation have been proposed as structuring mechanisms for temperate salamander communities (Hairston, 1987; Hairston et al., 1987; Bruce, 2008). Facultative arboreality may influence the community structure through habitat partitioning if certain species or ages climb at different frequencies. Climbing also may change the frequency of direct interactions simply by increasing the potential surface area of a habitat by adding vertical surfaces. Future studies about differential climbing ability and propensities among species could help understanding of possible intra-guild salamander interactions.

**ARBOREALITY AND CHANGING FOREST ENVIRONMENTS**

Recognition of the prevalence of arboreality and its potential importance to many plethodontids has pertinent applications to conservation and management. One of the primary drivers of global amphibian declines is the degradation of remaining forest habitats (e.g., Collins and Storfer, 2003). Widespread logging, species invasions, and land development are altering the composition and structure of many forests and have been linked to declines in salamander populations (e.g., Herbeck, 1998; Maerz et al., 2009; Connette and Semlitsch, 2013; Wood and Williams, 2013). The observed declines can be directly linked to loss of shelters and leaf litter (e.g., Maerz et al., 2009) and indirectly influenced by altered microclimates (e.g., Fetcher et al., 1985). Many of these processes result in simplified land-
scenes with reduced leaf litter and downed woody debris. This simplification has a negative impact on salamanders (see Clipp and Anderson, 2014).

Less attention has been given to human alteration of the vertical complexity of forests. The loss of historically dominant tree species with particular structural effects on forest habitats such as the American chestnut (Castanea dentata) has been proposed as a contributing factor to declines in highly arboreal species such as Aneides aeneus (and possibly a decline in their arboreal habits; Cupp, 1991; Dodd, 2004; Waldron and Humphries, 2005). Invasions of Hemlock Wooly Adelgid (Adelges tsugae) have opened the canopies of Appalachian cove forests, resulting in the rapid expansion of midstory shrubs such as Rhododendron (e.g., Spaulding and Rieske, 2010). The presence or absence of these midstory plants in gaps created by tree death influence local humidity, air temperature, soil temperature, and soil moisture (Clinton, 2003). These microhabitat differences influence salamander activity and therefore fitness (Feder, 1983). Midstory vegetation has an increasingly patchy distribution resulting from high levels of deer (Odocoileus virginianus) browse and the deliberate actions associated with residential development. Invasive species such as earthworms are altering understory and midstory forest communities in northeastern North America, including shifting worm casts resulting from high levels of deer (Odocoileus virginianus) browse and the deliberate actions associated with residential development. Invasive species such as earthworms are altering understory and midstory forest communities in northeastern North America, including shifting worm casts resulting from high levels of deer (Odocoileus virginianus) browse and the deliberate actions associated with residential development. Invasive species such as earthworms are altering understory and midstory forest communities in northeastern North America, including shifting worm casts resulting from high levels of deer (Odocoileus virginianus) browse and the deliberate actions associated with residential development.

In tropical regions, widespread land use change has had documented negative effects on many fauna, primarily through overall habitat degradation (i.e., Turner, 1996; Foley et al., 2005). Deforestation directly removes shelters and foraging potential for highly arboreal animals. Indirectly, deforestation alters microclimate because trees themselves provide increased local humidity and reduce temperatures (Fetcher et al., 1985). Additionally, climate change is already linked to the lifting of cloud cover and declines in the bromeliads (Kessler, 2002; Tabarelli, 2006) that are essential to supporting arboreal amphibians including many plethodontids. The epiphytic diversity and dependence on cloud formation makes cloud forests one of the habitats most at risk to climate change (Benzing, 1998).

CONCLUSION

It is challenging to draw meaningful linkages between the importance of arboreality, particularly facultative arboreality, and the ecology of plethodontids when the prevalence of the behavior is not recognized and often relegated to incidental and anecdotal observations. Nonetheless, the literature has accumulated a sufficient number of accounts to illustrate the widespread and frequent use of arboreal habitats by plethodontid salamanders. Vegetative structure should be considered an integral part of salamander habitat, and arboreal ecology should be incorporated into future studies. Considering the prevalence of arboreality among plethodontids, learning more about arboreal ecology for salamanders may be essential for conservation in a rapidly changing landscape.

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