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What Drives Variation in Plethodontid Salamander Species Richness over Space and Time?

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ABSTRACT: Plethodontid salamanders have become model organisms for studying many fundamental questions in evolutionary biology, ecology, and behavior. Dozens of studies focused on geographic patterns of phenotypic and genetic variation have been conducted on plethodontids, such that we now have a deep understanding of how many species are in the family and where they occur. This body of work on patterns of speciation has been foundational to exploring the drivers of the major patterns of species richness in the family. Approximately 70% of the world's 696 extant species of salamanders are plethodontids. The distribution of plethodontid species diversity exhibits striking variation globally. Most plethodontids are concentrated into two hotspots of diversity, the Appalachian Highlands and the Mesoamerican Highlands. Moreover, within these montane centers of diversity more species are found in midelevation habitats than at the highest or lowest elevations. The clade has been highly successful in the New World tropics, which harbors more plethodontid species than the temperate zone. Here, I review new insights on the evolutionary and ecological causes of variation in plethodontid species richness over geographic space and evolutionary time. New hypotheses on the phylogenetic relationships of plethodontids and tools from comparative phylogenetics and biodiversity informatics have been critical to this recent progress. Threats to plethodontid diversity arising from global climate change are examined, as is the need to further study and to cross-validate forecasts of species' range dynamics with different modeling approaches and independent data.

Key words: Caudata; Climate; Diversity; Ecological limits; Montane; Niche; Speciation

SPECIES richness shows remarkable variation among regions across the globe (Ricklefs 2004), and among clades across the Tree of Life (Scholl and Wiens 2016). For example, tropical regions (and clades that inhabit them) are often more species rich than temperate regions (Mittelbach et al. 2007). Species richness also shows striking variation with elevation; montane regions are centers of diversity and endemism for many taxa (Myers et al. 2000; Graham et al. 2014). Understanding the underlying causes of this variation is a major goal of ecology and evolution. It is also critical for predicting how biodiversity will respond to global environmental changes.

What processes cause species richness to vary among regions and clades? Ultimately, factors that lead to variation in speciation, extinction, and dispersal impact patterns of species richness. In general, studies that explore the relationship between these three processes, and the number of species that a given region or clade harbors, have arrived at three general hypotheses for why species richness varies over space and time.

The first of these hypotheses involves variation in rates of net diversification (speciation minus extinction). If the abiotic or biotic conditions in different regions or habitats (Fischer 1960; reviewed in Mittelbach et al. 2007) impact diversification rates, then species richness patterns will vary across them. For example, differences in rates of diversification in terrestrial and marine habitats seem to explain the disparity in species richness on land vs. in the sea (e.g., Benton 2001; Wiens 2015). Similarly, some traits (e.g., herbivory in insects; Ehrlich and Raven 1964; Southwood 1973; Wiens et al. 2015) promote increased rates of diversification that in turn are associated with variation in species richness among clades.

Species richness might also vary in the absence of variation in diversification rates. For example, regions that have been occupied longer than others, as well as older

clades, are expected to contain more species (Wallace 1878; Wiens and Donoghue 2004; Fine and Ree 2006; McPeck and Brown 2007). This phenomenon is called the time-for-speciation effect. Under this hypothesis, limited dispersal from one region to another, and limited time for species to accumulate, drive variation in species richness among locations and clades.

Finally, some regions and clades might have higher carrying capacities of species and become saturated at higher levels of species richness (Raup 1972; Walker and Valentine 1984; Ricklefs 2007; Rabosky 2009). A key ingredient of this hypothesis is that resources are limited and vary across space and time, resulting in variation in the probability of extinction and speciation (reviewed in Pontarp and Wiens 2016). Various factors are thought to influence such ecological limits to richness, including climatic conditions (Currie et al. 2004) and the amount of phenotypic disparity among species (Rabosky and Adams 2012).

Great disparity in species richness exists among the 10 extant families of salamanders. Approximately 70% world's salamander species belong to Family Plethodontidae (459 out of 696 species; AmphibiaWeb 2017). Although plethodontids account for much of the world's salamander diversity, most of the clade's species are concentrated in two regions of endemism: the southern Appalachian Highlands of eastern North America, and the Mesoamerican Highlands of Mexico and Central America (Fig. 1). Moreover, within each of these montane centers of diversity, species richness varies elevationally, with more species occurring in habitats at intermediate elevations than at higher or lower elevations. As in many other taxa, plethodontids also exhibit higher species richness in the tropics than in the temperate zone.

Plethodontid salamanders have become model organisms for studying many fundamental questions in evolutionary biology and ecology (Wake 2009). Thanks to many studies over the last five decades that focused on geographic patterns of phenotypic and genetic variation in plethodon-

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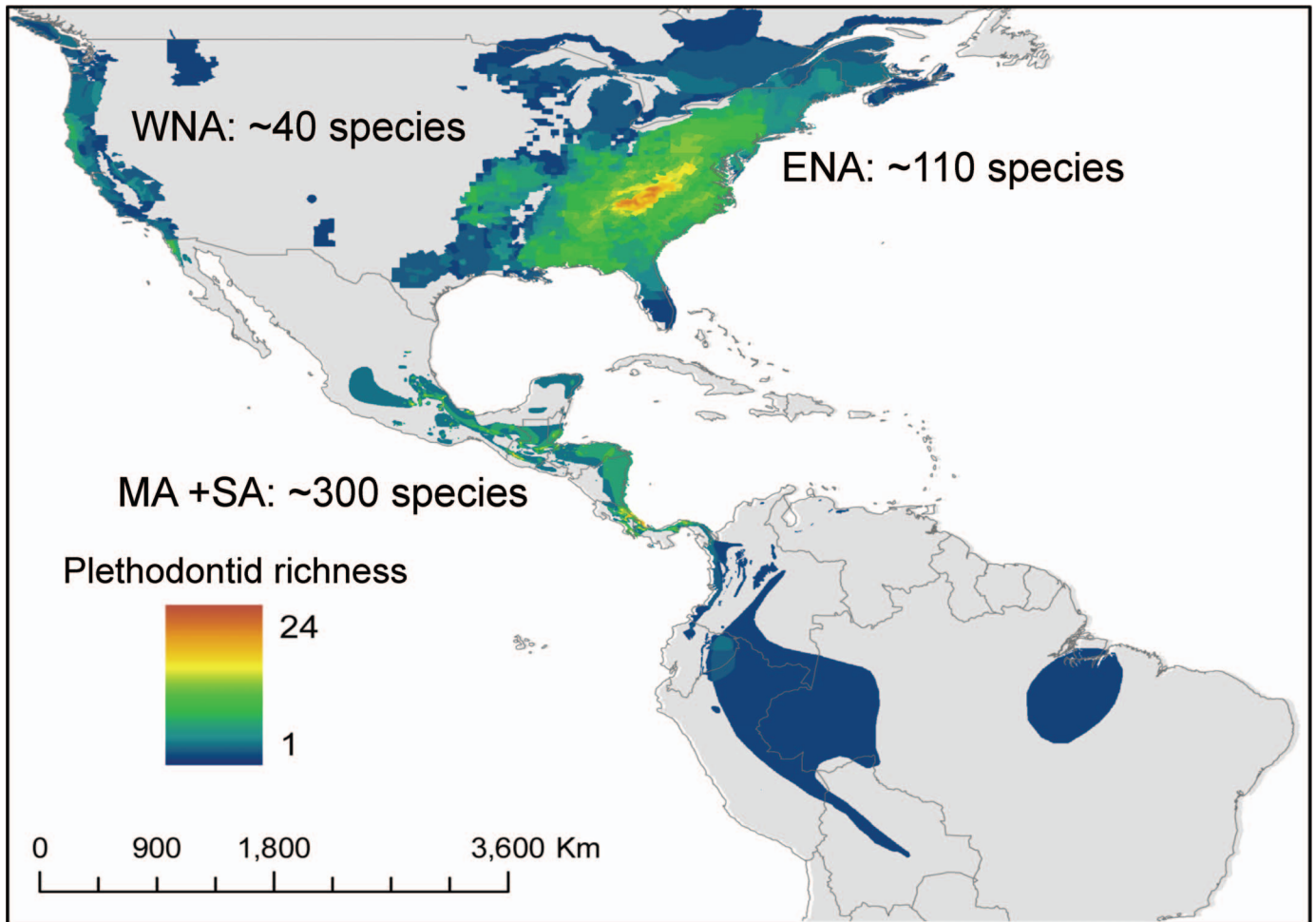


FIG. 1.—Map showing species richness of plethodontid salamanders across the major regions of endemism in the New World. ENA = Eastern North America, WNA = Western North America, MA + SA = Middle America + South America. Europe and Asia are omitted for illustrative purposes. The species richness scale indicates the number of regionally sympatric species. The approximate species richness of each region is illustrated on the map.

tids, we now have a deep understanding of how many species are in the family and where they occur (e.g., Highton 1962, 1972, 1995; Wake 1966, 1970, 1987; Wake and Lynch 1976; Hanken 1983; Wake and Yanev 1986; Highton et al. 1989; Tilley and Mahoney 1996; Hanken and Wake 1998; Jockusch et al. 2001, 2002; Anderson and Tilley 2003; Tilley et al. 2008). This rich body of literature on species distributions and patterns of speciation has been foundational to progress in understanding the major patterns of species richness in the clade.

Here, I review recent progress in our understanding of the evolutionary and ecological determinants of plethodontid salamander diversity. My discussion considers several questions: Why are there so many montane species? Why are there more tropical than temperate plethodontids? Is there evidence that regions and communities have become saturated with species? Can variation in carrying capacities or ecological limits explain regional variation in plethodontid richness? What is the fate of plethodontid diversity in the face of global climate change? New hypotheses on the phylogenetic relationships of species, the ability to estimate the timing and rates of diversification within and among major areas of endemism, and tools from biodiversity informatics have been critical to addressing these long-

standing questions about patterns of plethodontid species richness.

WHY ARE THERE SO MANY MONTANE PLETHODONTIDS?

Emmett Reid Dunn was the first to ponder the causes of the remarkable richness of plethodontids in the southern Appalachian Highlands compared to adjacent lowland physiographic provinces (Dunn 1926). Dunn's hypothesis that the southern Appalachians are so plethodontid rich because they are the center of origin for the group no longer appears tenable (Vieites et al. 2007). Nevertheless, why many taxa (including plethodontid salamanders) reach their greatest species richness in montane regions, and in particular at intermediate elevations, remains a fundamental question (Graham et al. 2014).

Plethodontids are lungless and require cool, moist environments for efficient cutaneous respiration. Given that hotspots of diversity for the group like the southern Appalachians harbor more habitats with these conditions, one might readily conclude that climatic conditions drive high montane species richness. Marshall and Camp (2006) found that plethodontid species richness across North America is positively correlated with environmental variables

related to available moisture. Similarly, regional and local richness for plethodontids across the New World (eastern North America, western North America, and Mesoamerica + South America) are negatively correlated with temperature and positively correlated with precipitation (Kozak and Wiens 2012). Despite the ubiquity of species richness gradients and their association with climate, it is only recently that researchers have begun to identify the factors that generate them (Ricklefs 2004). Climate alone does not directly increase or decrease the number of species that occur in a given location. Ultimately, such correlations must arise because climatic variables impact the processes of speciation, extinction, and dispersal.

Two general hypotheses that link elevational variation in species richness to these biogeographic processes have been proposed. The montane species-pump hypothesis predicts that montane regions have high species richness because topographic heterogeneity increases opportunities for allopatric and parapatric speciation (Moritz et al. 2000; Rahbek and Graves 2001; Smith et al. 2007), and/or reduces rates of extinction. Under this hypothesis, more species accumulate per unit of time at middle elevations in montane regions, resulting in a correlation between a lineage's diversification rate (speciation rate minus extinction rate), and its elevation. In turn, this leads to greater species diversity than in the lowlands or at the highest elevations where there is little topographic complexity and climatic zonation to result in the geographic and/or ecological isolation required for speciation (Hall 2005; Fjeldsa and Rahbek 2006; Cadena et al. 2011).

Alternatively, middle elevations in montane regions (or the climatic conditions that are now associated with them) are more species rich because they have been inhabited longer, allowing more time for speciation and species to accumulate without the need for postulating variation in rates of speciation or extinction at different elevations. This phenomenon is called the time-for-speciation effect (Stephens and Wiens 2003), and Smith et al. (2007) coined it as the montane museum hypothesis. A key prediction of the montane museum hypothesis is a positive correlation between the number of species occurring in an elevational band and the amount of time that elevational band has been colonized.

The relatively recent assembly of a comprehensive time-calibrated phylogeny for nearly all species of plethodontids occurring across eastern North America (Kozak et al. 2009) has been critical to understanding whether the southern Appalachian Highlands are so rich in plethodontid species because they act as species pump or as a museum. Kozak and Wiens (2010a) combined this phylogenetic information with ancestral-state reconstruction and comparative phylogenetic methods to estimate both the timing of colonization of different elevations across eastern North America and the rate at which lineages diversify along the elevational gradient. They found no evidence that diversification rates have been faster in the mountains than in the adjacent lowlands. Instead, they found that elevational variation in plethodontid richness was explained by the amount of time that different elevations have been colonized, with intermediate elevation habitats in the Appalachian Highlands being occupied the longest and accumulating the most species. In light of these phylogenetic inferences, it seems that in eastern North America plethodontid species do not originate

any more rapidly in montane habitats than they do in the adjacent Piedmont or Coastal Plain. Rather, there are more plethodontid species in midelevation habitats in the southern Appalachian Highlands because they have been occupied longer.

The limited dispersal of plethodontids to the lowest and highest elevation habitats appears to be driven by long-term specialization of lineages to the climatic conditions currently occurring at middle elevations (i.e., niche conservatism), leading to a greater buildup of species in this ancestral environment. In particular, wider daily fluctuations in temperature and warmer and drier conditions seemingly set the lower elevation range limits of montane endemics (Kozak and Wiens 2006, 2010a). It is important to point out that the climatic regimes currently at middle elevations have almost certainly shifted in elevation over the time period that plethodontids have inhabited eastern North America. The presence of many pairs of sister species of plethodontids that inhabit similar climatic conditions in adjacent mountain ranges, but that are separated by harsher climates in the lowlands, illustrates this dynamic of shifting species' ranges. These sister species originated when their ancestors that were once more continuously distributed in the lowlands when the climate was cooler tracked their favored climatic conditions to higher elevations and became isolated in separate mountain ranges (Kozak and Wiens 2006). Cooling and warming cycles of climate, coupled with long-term conservatism of species' climatic niches, have likely been important in generating many of the montane-endemic plethodontids that inhabit the southern Appalachian Highlands today. Intriguingly, such climate-associated cycles of allopatric isolation have not resulted in higher rates of diversification in the southern Appalachian Highlands, given the lack of support for the montane species-pump hypothesis (Kozak and Wiens 2010a).

The midelevation peak for plethodontid species richness in the Mesoamerican Highlands also appears to be driven by the montane museum phenomenon at middle elevations (Wiens et al. 2007). However, the general way in which populations become sundered to form new species in tropical vs. temperate mountains differs. Specifically, there seems to be a greater propensity for speciation to be associated with climatic-niche divergence along tropical mountain slopes (Kozak and Wiens 2007; Wake 2009).

WHY ARE THERE MORE TROPICAL THAN TEMPERATE PLETHODONTIDS?

Not only are most of the world's salamanders plethodontids, the majority of plethodontid species (302 of 459 species, AmphibiaWeb 2016) are also restricted to the New World tropics. Many groups of animals and plants exhibit greater species richness in the tropics than in the temperate zone. In general, many taxa might be more species rich in the tropics because they originated there, allowing more time for speciation, with subsequent dispersal to temperate regions being limited by the inability of species to evolve tolerance to freezing temperatures and/or strong seasonality in temperature (Wiens et al. 2006). However, the timing of colonization of tropical vs. temperate habitats cannot explain the pattern of high tropical richness for plethodontid salamanders.

Wake (1966) and Wake and Lynch (1976) hypothesized, based on biogeographic patterns of generic and adaptive diversity, that plethodontids originated in the New World temperate zone. Bolitoglossines then expanded into the New World tropics sometime between the Cretaceous and early Tertiary periods as their associated forested habitats shifted southward into the highlands of northern Mexico in response to large-scale cooling. Recent time-calibrated phylogenies (e.g., Vieites et al. 2007, 2011; Rovito et al. 2015; Shen et al. 2016) and ancestral-state reconstruction of the family's major areas of endemism support this hypothesis and indicate that this colonization event occurred approximately 40–50 mya (Kozak and Wiens 2010b; Rovito et al. 2015). Thus, there has actually been less time for the buildup of species richness in tropical habitats given that the family has inhabited the temperate zone longer than the tropics. Instead, major clades of tropical plethodontids have undergone higher rates of diversification than temperate ones, resulting in greater species richness in the tropics. It is worth noting that high species richness of tropical plethodontids is driven primarily by Mesoamerica; South America was colonized very recently by comparison, and consequently, has low plethodontid richness (Elmer et al. 2013).

What drives higher rates of diversification in tropical plethodontids? A classic explanation is that the high productivity of warm and wet tropical habitats increases carrying capacities and thereby reduces rates of extinction, resulting in greater species richness (Currie et al. 2004). Unlike many groups of organisms that exhibit high tropical richness, however, plethodontid diversity does not peak in the lowland tropics where these climatic conditions prevail. As in eastern North America, plethodontid species richness in Mesoamerica is greatest at intermediate elevations in the mountains where the climatic conditions more closely resemble those in the temperate zone (i.e., the ancestral area for the family) than in lowland tropical rainforests. Accordingly, understanding why tropical mountains might promote elevated rates of diversification is at the heart of understanding the latitudinal gradient in plethodontid species richness.

In a classic paper, Janzen (1967) showed that limited seasonal variation in temperature in the tropics generates greater climatic zonation across elevational gradients. Because of the greater seasonality of temperature at higher latitudes, the climates of elevationally separated sites in temperate mountains will overlap more than those in tropical mountains. He suggested these differences in climatic zonation select for broad and overlapping thermal tolerances among species in the temperate zone and for climatic specialists with narrower thermal tolerances in the tropics. As a result, the cost of dispersal is greater in tropical than in temperate mountains, leading to more climatic barriers to dispersal and, in turn, leading to higher rates of speciation attributable to allopatric isolation across intervening unsuitable habitats at lower elevations (Ghalambor et al. 2006). Kozak and Wiens (2007) hypothesized that such climatic zonation could also increase opportunities for gradient (parapatric) speciation in tropical mountains, whereas in the temperate zone, only the climatic difference between the mountaintops and valleys might be strong enough to promote speciation (Kozak and Wiens 2006, 2007; Shepard and Burbrink 2008, 2011; but see Rissler and Apodaca 2007).

If there also has been greater opportunity for gradient speciation in the tropics, then overall, tropical sister species should exhibit less overlap in their elevational distributions and thermal niches than temperate sister species (Kozak and Wiens 2007).

Kozak and Wiens (2007) used geographic information system (GIS) data to calculate the overlap in the elevational distributions and thermal niches in 30 pairs of sister species (14 tropical, 16 temperate). They found patterns that were consistent with the hypothesis that divergence across climatic gradients has been more prevalent in the tropics than in the temperate zone. On average, tropical sister species show significantly less elevational and thermal overlap than temperate sister species, indicating the additional potential for gradient speciation to occur along tropical mountain slopes. Such a pattern could present more opportunities for speciation in tropical than in temperate mountains. It is doubtless that allopatric isolation associated with niche conservatism has also played an important role in speciation in the tropical mountains as well (e.g., Parra-Olea et al. 2001; Rovito et al. 2012, 2013).

Does the seemingly greater association of speciation with climatic divergence in tropical mountains underlie the higher rate of diversification of plethodontids in the tropics? More rapid shifts in the climatic niches of tropical species might be expected to accelerate rates of diversification if the occurrence of incipient sister species in different environments is a cause of reproductive isolation between them (e.g., if populations of one species cannot establish themselves and persist in the geographic range of the other; Sobel et al. 2010), leading to higher rates of allopatric and parapatric speciation. If so, then one would predict a positive relationship between the rates at which species' climatic niches evolve and the rates at which the clade containing them diversifies. Kozak and Wiens (2010b) combined phylogenetic and GIS climate data for 250 species of plethodontids inhabiting the temperate zone and the tropics. They found that rates of diversification and climatic-niche evolution were positively correlated across 16 major clades, and that both rates were particularly rapid in tropical regions. Diversification rates were especially elevated in the *Eladinea* clade, in which species inhabit the greatest range of climatic niches, ranging from lowland tropical forest to the páramo of the highest mountains. In the case of *Eladinea*, low overlap with other bolitoglossine clades (and consequently greater ecological access to a range of climatic zones) might be associated with these rapid climatic niche shifts, given that rates of diversification are also highest where few clades geographically overlap (Kozak and Wiens 2010b). Thus, rapid shifts between elevational climatic regimes seem to accelerate rates of diversification, resulting in greater plethodontid species richness in the tropics.

ECOLOGICAL LIMITS AND PATTERNS OF PLETHODONTID RICHNESS

Many neontological and paleontological studies have explored the idea that there are ecological limits to how many species can coexist because of competition for finite resources (e.g., Raup 1972; Walker and Valentine 1984; Rabosky and Glor 2010; Machac et al. 2013), and that variation in these ecological saturation points might explain

variation in species richness among regions and clades (Rabosky 2009). This hypothesis predicts that the number of species in a given clade or region will initially rise to a given carrying capacity, and then plateau and remain constant over millions of years resulting in no relationship between the timing of colonization (or the age of a clade) and diversity. Molecular phylogenies have become a popular tool for testing the ecological-limits hypothesis because they allow researchers to estimate the rate at which species have accumulated within a clade or region, and whether this rate has changed over time. A declining rate of species accumulation is often interpreted as evidence that there are ecological limits to how many species can coexist (Rabosky 2009). However, many of these studies include little or no ecological data relevant to the coexistence of species at either regional or local scales. Moreover, signatures of declining rates of species accumulation in molecular phylogenies can occur for many nonecological reasons (Cusimano and Renner 2010; Burbrink and Pyron 2011).

The idea that patterns of species richness in plethodontids (local and regional) are driven by ecological limits seems plausible for a variety of reasons. Many ecological studies have demonstrated that ecological interactions such as competition and predation structure plethodontid communities (Hairston 1980, 1981, 1986; Adams and Rohlf 2000; Adams 2007, 2010). Previous studies have also revealed that rates of species accumulation have declined over time in many major clades of plethodontids (Kozak and Wiens 2010b). In at least one clade (*Desmognathus*), the decline is seemingly associated with the long-term stability in the ecomorphology of lineages and in the structuring of communities over space and time (Kozak et al. 2005), patterns that are consistent with the idea of ecological saturation over time. Finally, plethodontids are morphologically conserved (Wake et al. 1983), which might be expected to limit local and regional species diversity if morphological disparity is a critical to how many species can ultimately coexist.

Nevertheless, overall there appears little evidence that ecological limits to plethodontid diversity explain patterns of species richness at regional and local scales. For example, Kozak and Wiens (2012) found that both regional and local diversity for major areas of plethodontid endemism increase with the timing of colonization. Although within some regions the relationship between the timing of colonization and diversity seems to plateau at the local scale, communities that have been occupied the longest are still the most species rich, indicating that differences in the carrying capacities of regions do not explain the variation in species richness within or among them.

Rabosky and Adams (2012) suggested that variation in the species richness of major clades of plethodontids is explained by ecological limits to clade diversity. Specifically, they found a positive relationship between the rates of morphological evolution for clades and their species richness. They hypothesized that clades undergoing faster rates of morphological evolution expand more in ecological space, and therefore attain greater species richness. While this hypothesis is appealing, other than failing to find a strong positive relationship between clade age and species richness among clades (a pattern that might have explanations other than

ecological limits; Wiens 2011; Kozak and Wiens 2016a), they did not test any predictions of the ecological-limits hypothesis.

A key prediction of the ecological-limits hypothesis (following from the assumptions of Rabosky and Adams 2012) is that older clades with slower rates of evolution in ecologically important traits will have reached their ecological limits, and therefore show stronger declines in diversification over time. Therefore, if there are ecological limits on clade richness related to rates of phenotypic evolution, then patterns of decelerating diversification among clades should be associated with interactions between ages of clades and their rates of phenotypic evolution. Alternatively, there might be a faster decline for diversification rates of clades that experience slower rates of morphological evolution, regardless of their age. Relatively few studies have empirically tested predictions of this hypothesis with relevant ecological data (e.g., Machac et al. 2013; Pinto-Sanchez et al. 2014; Price et al. 2014).

Using phylogenetic multiple regression, Kozak and Wiens (2016b) found no evidence that slowing diversification within clades is related to an interaction between clade age and rates of shape or size evolution, demonstrating that older clades undergoing slower rates of morphological evolution are not more saturated with species than younger clades having faster rates of change in these traits. They also found that clades with slower rates of morphological evolution are not more saturated with species than clades with faster rates of phenotypic change. This overall lack of evidence that ecological limits to diversity underlie variation in species richness of major plethodontid clades seems to be corroborated by other studies. For most major clades of plethodontids, ecological radiation and microhabitat evolution are decoupled from size and shape evolution (e.g., Blankers et al. 2012). Kozak et al. (2009) also showed that the major clades of plethodontids that occur sympatrically in eastern North America (*Desmognathus*, *Plethodon*, and *Spelerpini*) have undergone parallel and convergent patterns of morphological evolution, such that sympatric species in different clades are actually more morphologically similar than expected by chance. Thus, morphological similarity of species does seem not preempt the diversification of coexisting clades. Finally, the results of Rabosky and Adams (2012) show that phenotypic disparity increases within clades over time, indicating that morphological space within these clades has not become saturated over time. Overall, it appears that rates of climatic-niche evolution explain most of the variation in richness among plethodontid clades, whereas rates of morphological evolution and ecological limits to diversity do not (Kozak and Wiens 2016b).

CLIMATE CHANGE AND THE FATE OF PLETHODONTID DIVERSITY

The finding that long-term specialization for montane climates underlies patterns of elevational diversity in plethodontids, and that this climatic specialization seems to prevent montane species from colonizing lowland habitats is particularly sobering in the face of global climate change. Unlike montane regions like the sky islands of the desert Southwest, where desert conditions in the adjacent lowlands restrict montane species to high elevations, the lower elevational range limits of many montane endemic pletho-

dontids are not associated with dramatic gradients in temperature and precipitation. In eastern North America, highland and lowland habitats are generally similar; both consist primarily of temperate deciduous forest (Delcourt and Delcourt 1980). Yet, recent studies suggest that energetic and physiological constraints associated with specialization for subtle elevation differences in climate are likely to drive the lower elevation range limits of many montane plethodontids (Bernardo and Spotila 2006; Gifford and Kozak 2012; Lyons et al. 2016).

The significance of this climatic specialization in the context of global climate change becomes even more apparent if one examines patterns of plethodontid diversity at a broader scale. For example, plethodontids spread from the temperate zone to the tropics approximately 40–50 mya. In colonizing the New World tropics many clades seem to have conserved the ancestral temperate niche by following a climatic path of least resistance. Although bolitoglossines have invaded lowland tropical habitats, most species are found in intermediate elevation habitats in the mountains where the climatic conditions more closely resemble those in the temperate zone. Together, these patterns indicate that even small changes in temperature could erode the ranges of montane plethodontids and effectively push them off the mountaintops. Given that montane endemics are a dominant element of the diversity in plethodontid hotspots like the Appalachian and Mesoamerican Highlands, it seems natural to predict that extinction risks to plethodontids are the greatest in such regions.

Rovito et al. (2009) documented that the elevational ranges of some tropical bolitoglossines have shifted upward over a 30-yr period, and that some species that inhabited narrow elevational zones have seemingly disappeared altogether, patterns that are consistent with climate-change-induced range contractions. Range forecasts from correlative niche models (models that use point locality data across the species range to model habitat suitability) predict large range contractions and extinctions of montane plethodontids inhabiting the Appalachian and Mesoamerican highlands (Parra-Olea et al. 2005; Milanovich et al. 2010). These predictions are quite alarming. In particular, Milanovich et al. (2010) forecast that by 2050, even under a moderate degree of warming, no climatically suitable habitats will remain for the 27 plethodontid species currently found in Great Smoky Mountains National Park.

While such forecasts and possible threats to plethodontid diversity should be taken seriously, they also deserve further cross-validation with independent data and different methods for modeling species' climatic niches. For example, the deep phylogeographic structure of codistributed plethodontids in the Appalachians (Tilley and Mahoney 1996; Highton and Peabody 2000; Crespi et al. 2003; Kozak et al. 2005, 2006; Weisrock and Larson 2006) indicates long-term persistence of species and communities through interglacials in which the global mean annual temperatures are similar to those of today (Petit et al. 2009). Indeed, studies on a variety of taxa and regions, including plethodontids, suggest that the reason many mountains may be more species rich than adjacent lowland regions is because they have been inhabited for longer periods of evolutionary time, thereby allowing a greater buildup of diversity (Fjeldsa and Lovett 1997; Smith et al. 2007; Wiens et al. 2007; Li et al. 2009;

Kozak and Wiens 2010a). The warming predicted by correlative models requires that species were repeatedly extirpated across most of their current ranges in the southern Appalachians in response to past warming events and that these species-rich communities subsequently reassembled, a possibility that seems at odds with the ancient ages of lineages and deep intraspecific genetic structure found in plethodontids across the region. This is not to say that the low dispersal abilities, conservatism of the climatic niche, and rates of contemporary warming might not threaten the ability of plethodontids to respond to climate change. It simply calls for further scrutiny of the forecasts that arise from correlation-based niche models.

The increasing ability to obtain large multi-locus datasets documenting genetic variation across the genome, along with molecular phylogeographic tools for inferring the effective sizes and demographic histories of populations (Hickerson et al. 2010), present a wealth of opportunities to explicitly test the ability of different classes of models to accurately predict range dynamics of seemingly sensitive organisms like plethodontids under shifting climates. For example, models can be hindcasted to predict the spatial locations, connectivity, and size of climatically suitable habitats at particular points in the past (e.g., Graham et al. 2006). Genetic data within and among populations can then be used to test for the molecular signatures of the demographic processes predicted by the models (e.g., population growth vs. stability, fragmented vs. continuous populations; Richards et al. 2007; Carnaval et al. 2009; Chan et al. 2011). If a particular model fails to hindcast past locations where populations were large and stable based on patterns of molecular variation, then it probably should not be employed to forecast future range dynamics. Such data on the past responses of species provide a means to cross-validate the predicted vulnerability of species in the future, but as of yet, remain virtually untapped. Luxbacher (2014) used such an approach to compare the performance of a correlative niche model and a mechanistic niche model for *Plethodon* salamanders that uses organismal physiology rather than point locality data across the species' range to model habitat suitability. Using *Plethodon jordani* in the Great Smoky Mountains as an example, Luxbacher (2014) found that both models effectively predicted the species' current distribution. However, the mechanistic model predicted a distribution under historical conditions (last glacial maximum) that was much more consistent with the population structure and demographic history of the species inferred from population-genetic data.

CONCLUSIONS

Plethodontid salamanders have been model organisms for many fundamental questions in evolution, ecology, and behavior. Yet, the answers to questions about why the clade's species diversity varies within and among its major areas of endemism have remained elusive. Using new information on the phylogenetic relationships of species and tools from comparative phylogenetics and biodiversity informatics has been critical to addressing why there are so many montane plethodontids, why the tropics are more species rich than the temperate zone, and whether ecological limits influence variation in plethodontid diversity. The most species rich

locations in the Appalachian and Mesoamerica highlands (i.e., middle elevations) are so rich in plethodontids not because they increase rates of diversification, but because they have been inhabited longer than other areas. Higher rates of diversification associated with faster rates of climatic niche evolution in tropical mountains appear to underlie the overall disparity in plethodontid richness between the New World tropics compared to the temperate zone. Specialization over evolutionary timescales for subtle differences in climate has played an important role in generating these latitudinal and elevational gradients in plethodontid richness. Overall, there appears to be little evidence for ecological limits to plethodontid richness related to variation in carrying capacities among different habitats, or to the morphological disparity among species of coexisting clades. Range erosion associated with climate change has been identified as a major threat to plethodontid diversity, especially in montane regions like the Appalachian and Mesoamerican highlands. However, cross-validation of predictions from niche models with independent data is needed to produce more robust forecasts of how plethodontids will respond to changes in climate.

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