

Location-specific sympatric morphological divergence as a possible response to species interactions in West Virginia *Plethodon* salamander communities

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Summary

1. The competitive interactions of closely related species have long been considered important determinants of community composition and a major cause of phenotypic diversification. However, while patterns such as character displacement are well documented, less is known about how local adaptation influences diversifying selection from interspecific competition.

2. We examined body size and head shape variation among allopatric and sympatric populations of two salamander species, the widespread *Plethodon cinereus* and the geographically restricted *P. nettingi*. We quantified morphology from 724 individuals from 20 geographical localities throughout the range of *P. nettingi*.

3. *Plethodon nettingi* was more robust in cranial morphology relative to *P. cinereus*, and sympatric localities were more robust relative to allopatric localities. Additionally, there was significantly greater sympatric head shape divergence between species relative to allopatric communities, and sympatric localities of *P. cinereus* exhibited greater morphological variation than sympatric *P. nettingi*.

4. The sympatric morphological divergence and increase in cranial robustness of one species (*P. nettingi*) were similar to observations in other *Plethodon* communities, and were consistent with the hypothesis of interspecific competition. These findings suggest that interspecific competition in *Plethodon* may play an important role in phenotypic diversification in this group.

5. The increase in among-population variance in sympatric *P. cinereus* suggests a species-specific response to divergent natural selection that is influenced in part by other factors. We hypothesize that enhanced morphological flexibility and ecological tolerance allow *P. cinereus* to more rapidly adapt to local environmental conditions, and initial differences among populations have allowed the evolutionary response of *P. cinereus* to vary across replicate sympatric locations, resulting in distinct evolutionary trajectories of morphological change.

Key-words: character displacement, geometric morphometrics, historical contingency, species interactions.

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Introduction

Understanding how ecological processes affect phenotypic evolution has long been of interest to evolutionary ecologists. Closely related species are frequently more

divergent in phenotype in sympatry than in allopatry, and one explanation for this is ecological character displacement (Brown & Wilson 1956). Here, competition for limiting resources generates divergent selection between species, such that subsequent resource overlap is reduced (Losos 2000). When alternative explanations such as geographical clines or resource differences among locations are eliminated (Grant 1975; Schluter & McPhail 1992; Taper & Case 1992), this pattern

provides strong evidence of an evolutionary response to interspecific competition. Though much controversy has surrounded the prevalence of ecological character displacement, recent evidence suggests that this evolutionary process is widespread (Adams & Rohlf 2000; Simberloff *et al.* 2000; Melville 2002; Grant & Grant 2006; reviewed in Schluter 2000).

Because ecological character displacement links proximate selection pressures to evolutionary responses in morphological traits, it is believed to be an important factor determining community composition (Dayan & Simberloff 2005) and a major cause of adaptive diversification (Schluter 2000; Pfennig & Murphy 2003). Interestingly, while considerable effort has been devoted to documenting the existence of character divergence across a wide range of taxa (reviewed in Schluter 2000), few studies have examined the extent to which character displacement has evolved consistently in replicated communities of the same species. In several well studied natural systems, researchers have focused on whether divergent morphological change has evolved in multiple sympatric populations and if these patterns are qualitatively similar (Schluter & McPhail 1992; Losos 1992; Jastrebski & Robinson 2004). However, whether adaptation to local conditions have influenced the way in which populations responded to divergent selection has been given less consideration. Under certain conditions, similar selection pressures generated from interspecific competition can result in divergent phenotypic patterns that are not completely consistent between sympatric communities. Thus, while character displacement is likely an important process that shapes patterns of diversification, the influences on this process of historical contingency (the characteristics of the ancestral population) and adaptation to the local environment is less well understood (but see Losos 1992).

Terrestrial salamanders of the genus *Plethodon* provide an excellent opportunity to examine the evolutionary responses to community interactions. *Plethodon* are widely distributed in the forests of North America and considerable ecological research suggests that interspecific competition is widespread (Hairston 1980; Anthony, Wicknick & Jaeger 1997). Throughout north-eastern North America, the wide-ranging red-backed salamander *P. cinereus* completely surrounds the ranges of several sibling species with more restricted distributions. One species, the Cheat Mountain salamander *P. nettingi* is federally threatened, and is restricted to approximately 60 disjunct populations in West Virginia (Pauley 1991). Through extensive natural history work, the distribution and habitat characteristics of *P. nettingi* and *P. cinereus* have been documented. Field observations revealed that these species have largely disjunct distributions, with narrow sympatric zones (Pauley 1980, 1991). Further, the two utilize similar microhabitats, are site tenacious, and competitive release experiments suggest that both species defend territories (Wicknick & Pauley 1998). From these observations it was hypothesized that

interspecific competition dominated the interactions of the two species and that the distribution of *P. nettingi* has been restricted in part through competition (Highton 1972; Jaeger 1974; Pauley 1991, 2005). However, because *P. nettingi* is federally threatened, large experimental manipulations that directly test these hypotheses have not been performed.

Despite current collecting restrictions on *P. nettingi*, other data can be examined to determine whether the resulting patterns are consistent with and corroborate the hypothesis of interspecific competition. For example, patterns of morphological divergence are frequently accentuated between species that compete in regions of sympatry. Character divergence has been identified in several salamander communities where interspecific competition has been documented (Adams & Rohlf 2000; Adams 2000, 2004). Further, in those communities, there was a direct association between biotic interactions, such as food exploitation or aggressive behaviour, and patterns of morphological diversification. Combining these observations with the previously stated hypothesis of competition (Pauley 1980), we predict that if interspecific competition occurs between *P. cinereus* and *P. nettingi*, there should be a pattern of sympatric phenotypic divergence that is greater than typical differences in allopatry. Our goal was to determine whether among population patterns of morphological variation were consistent with this hypothesis. We assessed patterns of phenotypic variation across replicated sympatric and allopatric populations to determine whether there was significant phenotypic variation among local populations of *P. nettingi* and *P. cinereus*, and whether sympatric phenotypic divergence was significantly greater than allopatric phenotypic differences. We also tested whether character shifts from allopatry to sympatry, and patterns of sympatric divergence, were consistent for both species.

Materials and methods

We obtained 724 adult specimens (273 *P. cinereus* and 451 *P. nettingi*) from the National Museum of Natural History (Washington DC, USA) from 20 West Virginia localities (sites) throughout the range of *P. nettingi*. Thirteen localities were single species allopatric sites containing either *P. cinereus* or *P. nettingi*, while seven localities were sympatric sites where both species were found (Fig. 1, Table 1).

We assessed patterns of morphological variation in two data sets: body size and head shape. These attributes were chosen because previous studies in *Plethodon* have demonstrated that patterns of variation in head shape and body size were related to ecological interactions in some communities (e.g. Adams & Rohlf 2000; Adams 2004). For body size, snout–vent length was recorded using Brown & Sharpe Mark IV digital calipers. For cranial morphology, head shape was quantified using landmark-based geometric morphometrics methods (Rohlf & Marcus 1993; Adams, Rohlf & Slice

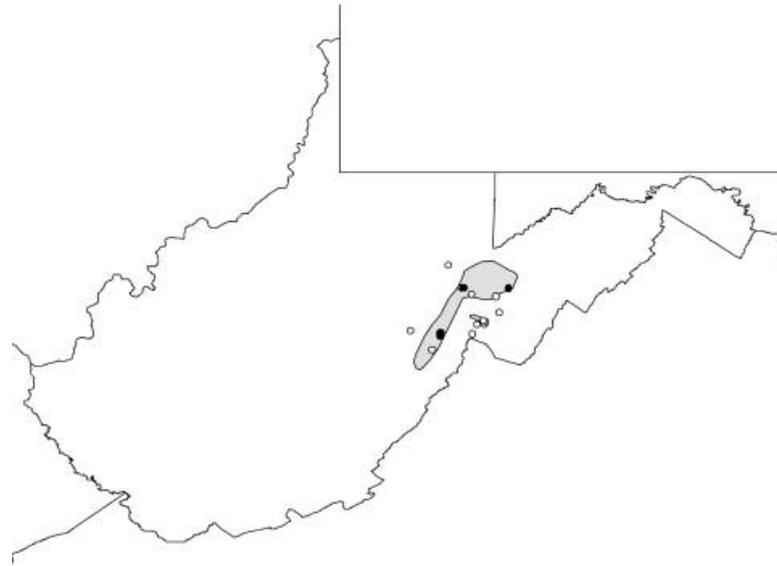


Fig. 1. Map of West Virginia, USA and the geographical localities of sites used in this study. Sympatric sites (black circles) and allopatric sites (open circles) are shown. The distribution of *Plethodon nettingi* is denoted as the shaded area (after GAA distribution map, IUCN, Conservation International and NatureServe 2004).

Table 1. Location of geographical localities (sites) used in this study

Site type	Species	Latitude	Longitude	County	Description
Allopatry	N	38-512°N	79-897°W	Pocahontas	Back Allegheny Mountain
Allopatry	C	38-606°N	79-846°W	Randolph	Forest Rt. 27 NNE of US Rt. 250
Allopatry	C	38-622°N	79-625°W	Pocahontas	Forest Rt. 112 N of WV Rt. 28
Allopatry	C	38-644°N	80-042°W	Randolph	NW of Old Fort
Allopatry	N	38-686°N	79-548°W	Pendleton	SW of Spruce Knob
Allopatry	C	38-686°N	79-598°W	Pendleton	Forest Rt. 112 N of WV Rt. 28
Allopatry	N	38-706°N	79-540°W	Pendleton	NW of Spruce Knob
Allopatry	C	38-714°N	79-553°W	Pendleton	Spruce Knob
Allopatry	C	38-770°N	79-449°W	Pendleton	N of Riverton
Allopatry	C	38-876°N	79-469°W	Pendleton	US Rt. 33, S of Pendleton-Randolph Cty line
Allopatry	C	38-891°N	79-631°W	Randolph	US Rt. 33, W of Harman
Allopatry	C	38-938°N	79-702°W	Randolph	Bickle Knob
Allopatry	C	39-091°N	79-790°W	Tucker	US Rt. 219, N of Montrose
Sympatry	CN	38-615°N	79-844°W	Pocahontas	Gaudineer Knob
Sympatry	CN	38-629°N	79-842°W	Pocahontas	Gaudineer Knob
Sympatry	CN	38-933°N	79-387°W	Randolph	Near headwaters of South fork of Red Creek
Sympatry	CN	38-936°N	79-681°W	Randolph	Bickle Knob
Sympatry	CN	38-936°N	79-691°W	Randolph	Bickle Knob
Sympatry	CN	38-937°N	79-686°W	Randolph	Bickle Knob
Sympatry	CN	38-939°N	79-682°W	Randolph	Bickle Knob

Species codes are as follows: C = *P. cinereus*; N = *P. nettingi*.

2004). First we obtained digital images of the left-lateral side of each head using a Nikon DXM-1200 digital camera mounted to a Nikon SMZ1500 stereomicroscope. We then digitized the location of 11 external biologically homologous landmarks from the skull and mandible (Fig. 2) using TpsDIG (Rohlf 2004). Variation in the position of the mandible relative to the skull was standardized by rotating the mandible of all specimens to a fixed angle relative to the skull (Adams 1999). Nonshape variation was then removed using a generalized Procrustes analysis (GPA: Rohlf & Slice 1990), which superimposed specimens to a common location after accounting for differences in position, orientation

and scale. From the aligned specimens shape variables were then generated as partial warp scores from the thin-plate spline (Bookstein 1991) and standard uniform components (Rohlf & Bookstein 2003). The set of principal component scores from all principal component axes that expressed variation (i.e. all nontrivial dimensions) fully described head shape, and were used in all multivariate statistical analyses.

Patterns of body size and head shape variation were investigated using two-factor ANOVA and MANOVA, respectively, where species, community type (allopatric or sympatric), and their interaction were treated as explanatory factors. The interaction term from this model

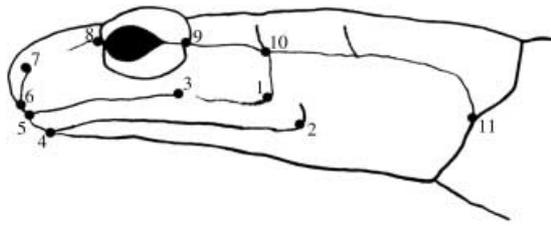


Fig. 2. Positions of 11 landmarks used in this study. All landmarks were digitized from the left-lateral view of the skull (modified from Adams 2004).

assessed whether species-specific responses across community types were similar for the two species. However, a significant interaction was not sufficient to determine whether greater sympatric morphological divergence had occurred, because convergence or other non-consistent patterns could also generate significant interactions (Adams & Collyer 2007). Therefore, to evaluate the more specific hypothesis of character displacement, we performed a direct comparison of sympatric morphological divergence with allopatric morphological divergence using a randomization procedure.

For this analysis we first calculated the observed divergence between species in each of the seven sympatric sites, using the Euclidean distance between sympatric locality means as a measure of morphological divergence. The average sympatric divergence was then estimated from these values. Next, we calculated the morphological divergence between all possible pairings of allopatric localities of the two species using Euclidean distance. We then randomly chose seven allopatric distances (to compare with the seven observed sympatric values), determined their average, and compared this value with the average sympatric divergence. This was repeated 9999 times, and the proportion of randomly chosen values (plus the observed) that exceeded the average sympatric divergence determined whether the observed sympatric divergence was greater than expected from chance. This procedure assessed patterns of morphological divergence while accounting for variation among sites, and was performed separately on both body size and head shape data (for related procedures see Schluter & McPhail 1992; Adams & Rohlf 2000; Adams 2004; Collyer & Adams 2007).

Finally, we determined whether sympatric shifts in head shape were consistent for both species by examining patterns of dispersion among shape means. We used a measure of multivariate variance to describe the dispersion of locality means with respect to one another (e.g. among allopatric *P. cinereus*). First, the head shape means for all localities were used to determine the overall means for each of the four species–community combinations (average allopatric *P. cinereus*, average allopatric *P. nettingi*, etc.). We then calculated the Euclidean distances (D) between locality means and their respective group mean, and for each species–community combination, determined the average multivariate distance to the group mean (\bar{D}). A distribution of random average distances was then generated by shuffling locality means with respect to community type, and the observed multivariate variance was compared with random values to determine whether these values were greater than expected from random chance.

Morphological patterns were visualized through a principal components analysis (PCA) of shape, where site means were projected on PC axes, and thin-plate spline deformation grids were generated to graphically describe patterns of shape variation.

Results

We found significant variation in body size between species and between community types, but not for their interaction (Table 2a). *Plethodon nettingi* was significantly larger than *P. cinereus* ($\bar{X}_{P. cinereus} = 39.0$ mm SVL; $\bar{X}_{P. nettingi} = 42.3$ mm SVL), and both species were significantly smaller in sympatry relative to allopatry. Using the randomization procedure, we found no evidence of sympatric body size divergence, as the observed sympatric divergence was not greater than was expected from randomly paired allopatric localities ($P_{\text{Rand}} = 0.4087$, NS). The latter finding was in contrast to observations in other *Plethodon* communities, where competition resulted in sympatric divergence of body size (e.g. Adams 2000).

When head shape was examined, a factorial MANOVA revealed significant differences between species, between community types, and in their interaction (Table 2b). Unlike body size, however, our resampling procedure found strong evidence of sympatric head shape

Table 2. (a) Analysis of variance for sources of body size variation

Source	d.f.	MS	<i>F</i>	<i>P</i>
Species	1	665.39	66.39	< 0.0001
Community type	1	276.06	27.55	< 0.0001
Species × community type	1	4.88	0.49	0.48 NS

(b) Multivariate analysis of variance for sources of head shape variation

Source	Exact <i>F</i>	d.f.	<i>P</i>
Species	15.38	17, 704	< 0.0001
Community type	4.39	17, 704	< 0.0001
Species × community type	4.51	17, 704	< 0.0001

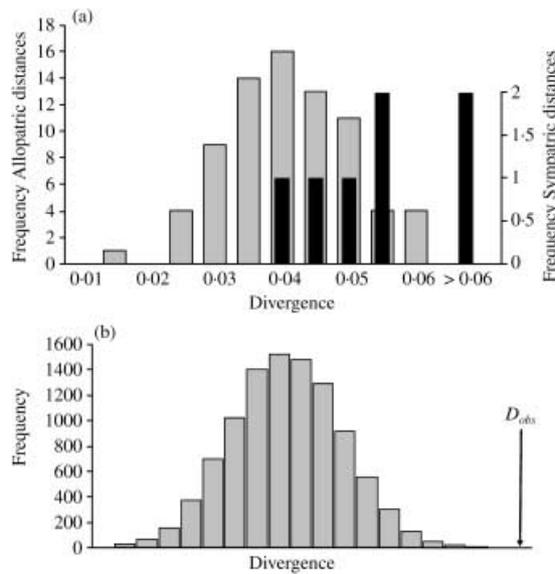


Fig. 3. (a) Distribution of morphological shape divergence between randomly paired allopatric populations (grey) and distribution of the observed sympatric morphological shape divergence (black). (b) Distribution of average allopatric shape divergence for 9999 randomly chosen sets of seven distances. The observed average sympatric shape divergence is denoted with an arrow.

divergence, as the observed sympatric head shape divergence was significantly greater than was expected from chance ($P_{Rand} = 0.001$; Fig. 3). Thus for head shape, we found a pattern of significant sympatric phenotypic divergence between *P. cinereus* and *P. nettingi*, which was consistent with our predictions.

PCA indicated that the major axis of shape variation (PC1) corresponded with the shape distinction of

P. cinereus and *P. nettingi*. These findings graphically confirmed the species-specific differences identified in MANOVA. When thin-plate spline deformation grids were examined, we found that populations of *P. nettingi* were relatively more robust in their cranial region as compared with *P. cinereus* (Fig. 4). In particular, *P. nettingi* displayed a relatively deeper head and a relatively expanded posterior of the lower jaw as compared with *P. cinereus* (Fig. 4). Further, sympatric *P. nettingi* were generally more extreme along PC1 as compared with allopatric *P. nettingi*, implying that they exhibited a relative increase in cranial robustness. Interestingly, when comparing allopatric and sympatric localities of *P. cinereus*, the pattern was considerably more varied. For *P. cinereus*, sympatric localities appeared more dispersed in morphospace relative to allopatric localities, and to both allopatric and sympatric localities of *P. nettingi* (Fig. 4). Statistically evaluating multivariate dispersion indices confirmed this observation. There was no difference in variation among allopatric and sympatric locality means for *P. nettingi* ($\bar{D}_{symp} = 0.022$; $\bar{D}_{allo} = 0.017$; $P_{Rand} = 0.5776$), but variation among sympatric locality means was significantly greater than among allopatric locality means for *P. cinereus* ($\bar{D}_{symp} = 0.036$; $\bar{D}_{allo} = 0.020$; $P_{Rand} = 0.0025$). Variation among sympatric *P. cinereus* locality means was also significantly greater than among sympatric *P. nettingi* locality means ($P_{Rand} = 0.0349$), implying that variation was enhanced among sympatric *P. cinereus* populations. Therefore, while phenotypic shifts from allopatry to sympatry appear somewhat consistent in *P. nettingi*, the phenotypic changes observed in *P. cinereus* are considerably more variable and locality specific.

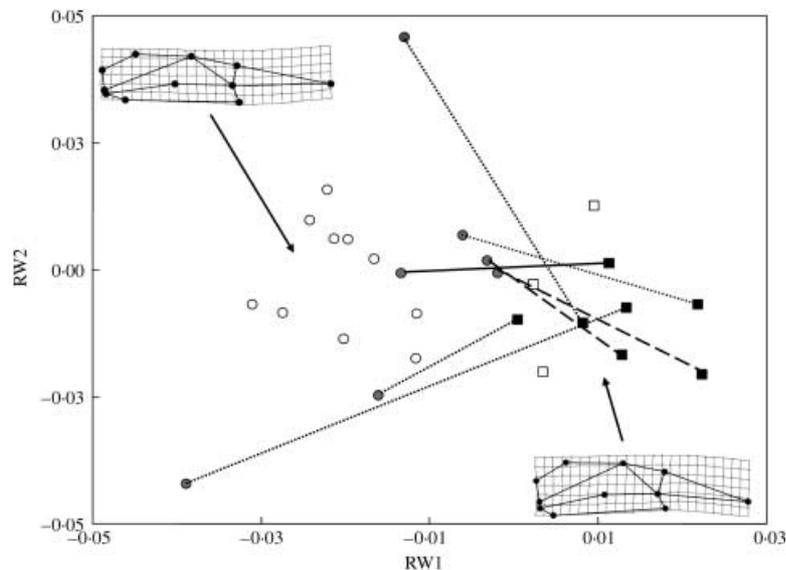


Fig. 4. Relative warp plot of least squares means for each site, with *P. cinereus* displayed as circles and *P. nettingi* displayed as squares (the first two axes describe 49% of the variation in shape). Allopatric sites are open symbols and sympatric sites are shaded symbols. Means for species at sympatric sites are connected with lines that correspond to the following geographical regions (small dash = Bickle Knob; long dash = Gaudineer Knob; solid line = NW of Old Fort; see Table 1). Thin-plate spline deformation grids for representative samples are shown.

Discussion

The competitive interactions of closely related species have long been considered important determinants of community composition and the evolution of morphological diversity. However, while divergence from competition is well documented, much less is known about how adaptation to the local environment influences the diversifying selection of interspecific competition. In this study we examined morphological variation among allopatric and sympatric populations of two *Plethodon* salamander species in West Virginia to determine whether phenotypic patterns were consistent with the hypothesis of interspecific competition. We found significant variation in body size across geographical localities, but no evidence of greater sympatric body size divergence. In contrast, we found both significant head shape variation across localities and significantly greater sympatric phenotypic divergence in head shape. Further, while phenotypic shifts from allopatry to sympatry were relatively consistent for *P. nettingi*, shifts for *P. cinereus* were more varied, with sympatric localities exhibiting significantly greater morphological dispersion than allopatric localities.

This study identifies a pattern of sympatric morphological divergence consistent with the hypothesis of interspecific competition; namely, that morphological differences between species were greater in sympatry than in allopatry. This pattern also corroborates results from other studies that imply competition between *P. cinereus* and *P. nettingi* (see Wicknick & Pauley 1998). Interestingly, phenotypic divergence and character displacement has also been observed in other *Plethodon* communities where competition has been documented. For instance, competition for food between *P. cinereus* and *P. hoffmani* was associated with sympatric head shape divergence (Adams & Rohlf 2000; Adams 2000), and levels of aggressive interference between *P. jordani* and *P. tayahalee* (Hairston 1980; Nishikawa 1985) was associated with sympatric head shape divergence (Adams 2004). In each case, at least one sympatric species evolved a more robust cranial morphology in the presence of congeners, and a similar pattern was identified in this study for *P. nettingi*. Whether this is a general pattern throughout multispecies *Plethodon* communities remains to be determined.

In addition, we identified nonconsistent patterns of phenotypic divergence across replicated sympatric localities, and found that *P. cinereus* exhibited greater variation in head shape among sympatric localities than *P. nettingi*. The increase in among-population phenotypic variance in sympatric *P. cinereus* is noteworthy, and suggests a species-specific response to divergent natural selection that is influenced in part by other factors. In other naturally replicated systems such as sticklebacks (Schluter & McPhail 1992), pumpkinseed sunfish (Jastrebski & Robinson 2004), *Anolis* lizards (Losos 1992) and even other *Plethodon* salamanders (Adams 2004), patterns of phenotypic divergence evolved

in a similar manner, and were qualitatively consistent across multiple sympatric communities. However, in our study the pattern of phenotypic divergence was more complicated. While divergence occurred in all sympatric communities, the specific manner in which head shape diverged was not consistent from community to community (see vectors connecting sympatric populations: Fig. 4). Therefore, in these communities, the evolutionary response to interspecific competition was both the result of probable competitive effects and adaptation to environmental effects at particular geographical locations (historical contingency). Unlike MANOVA, our resampling approach was capable of identifying this more complex pattern, as it accounted for among-site variation while still assessing divergence patterns among community types. Because other ecological systems likely have similarly complex patterns resulting from interspecific interactions, we expect that employing a resampling scheme analogous to the approach outlined here will have considerable utility in future community ecology studies.

Several possible factors, other than interspecific competition, could influence the evolutionary trajectory of sympatric divergence, such as historical contingency and adaptation to the local environment. In this case, because the enhanced variation between replicate sympatric populations was restricted to one species, we suggest that species-specific factors may be responsible. We hypothesize that adaptation to the local environment has generated differences in the source populations of *P. cinereus* that invaded sympatric localities, and these initial differences allowed the evolutionary response of *P. cinereus* to vary across replicate sympatric locations. Several lines of evidence support this hypothesis. First, *Plethodon cinereus* is most widely distributed species in the genus and therefore experiences the widest range of environmental conditions. Second, local populations of *P. cinereus* exhibit significant morphological differences, and this morphological variation is associated with differences in habitat and local food resources (Maerz, Myers & Adams 2006). Finally, *P. cinereus* exhibits considerable variation in other ecologically relevant phenotypic traits across its range, including aggressive behaviour (Wise 1995) and territoriality (e.g. Griffis & Jaeger 1998; Quinn & Graves 1999). Together, these patterns suggest that *P. cinereus* has considerable morphological and behavioural flexibility, which may enable it to adapt relatively quickly to local environmental conditions. If interspecific competition is subsequently experienced, initial differences between replicate sympatric populations of *P. cinereus* could then generate responses to diversifying selection that follow different evolutionary trajectories. The result is that character divergence is observed in sympatry, but the exact nature of phenotypic diversification is a combination of selection and local historical effects. Alternatively, variation in the intensity of competition with *P. nettingi* at different locations coupled with differences between replicate sympatric populations of *P. cinereus* could also lead to a similar evolutionary response. Fine-scale

studies of micropopulation variation of morphology in sympatry and allopatry, combined with a phylogenetic hypothesis for those populations, will allow these hypotheses to be examined.

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