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Phylogeographic incongruence of codistributed amphibian species based on small differences in geographic distribution

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Abstract

Codistributed species may display either congruent phylogeographic patterns, indicating similar responses to a series of shared climatic and geologic events, or discordant patterns, indicating independent responses. This study compares the phylogeographic patterns of two similarly distributed salamander species within the Pacific Northwest of the United States: Cope's giant salamander (*Dicamptodon copei*) and Van Dyke's salamander (*Plethodon vandykei*). Previous studies of *P. vandykei* support two reciprocally monophyletic lineages corresponding to coastal populations, located from the Olympic Mountains to the mouth of the Columbia River, and inland populations within the Cascade Mountains. We hypothesized that *D. copei* would have a congruent phylogeographic pattern to *P. vandykei* due to similarity in distribution and dependence upon similar stream and stream-side habitats. We test this hypothesis by estimating the phylogeny of *D. copei* using ~1800 bp of mitochondrial DNA and comparing it to that of *P. vandykei*. Sympatric populations of *D. copei* and of *P. vandykei* display an identical phylogeographic pattern, suggesting similar responses within their shared distribution. Populations of *D. copei* occurring outside the range of *P. vandykei* displayed high levels of genetic divergence from those sympatric to *P. vandykei*. Overall, phylogeographic patterns between the two species were ultimately incongruent due to the high divergence of these allopatric populations. These results provide an example of codistributed species displaying overall incongruent phylogeographic patterns while simultaneously displaying congruent patterns within portions of their shared geographic distribution. This pattern demonstrates that a simple dichotomy of congruent and incongruent phylogeographic patterns of codistributed species may be too simplistic and that more complex intermediate patterns can result even from minor differences in species' ranges.

Keywords: AU test; Bayesian hypothesis testing; Biogeography; Columbia River; Comparative phylogeography; *Dicamptodon*; Pacific Northwest parametric bootstrap; *Plethodon*; SH test

1. Introduction

A central objective of comparative phylogeography is to test codistributed species for concordant phylogeographic patterns (Bermingham and Moritz, 1998; Schneider et al., 1998; Avise, 2000; Argobast and Kenagy, 2001; Zink, 2002). Studies that reveal concordance among codistributed biota often provide evidence that a shared series of past events similarly shaped their genetic patterns. Comparative phylogeography enhances our understanding about the role of climatic, geological, and ecological forces in shaping the geographic distribution and intraspecific variation of species comprising an ecosystem. While a variety of studies have demonstrated phylogeographic congruence among codistributed taxa (Avise, 1992; Schneider et al., 1998; Riddle et al., 2000), a comparable number have also revealed incongruence (Zink, 1996; Taberlet et al., 1998; Hewitt, 1999). Discovery of incongruent phylogenies among codistributed species may suggest independent responses to shared evolutionary events due to different ecologies, life histories, or post-glacial expansion routes (Bowen and Avise, 1990; Taberlet et al., 1998; Michaux et al., 2005; Rocha et al., 2005), or may result from "pseudo-incongruence" in which codistributed species respond independently

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to different evolutionary events occurring at different times (Donoghue and Moore, 2003). Incongruence among population-level phylogenies may also be due to variation in the microevolutionary processes, such as lineage sorting or effective population size, that are responsible for generating the patterns of population-level divergence (Mason-Gamer and Kellogg, 1996). Additionally, underlying concordance in phylogenetic topologies may be masked by variation in the geographic patterns of population processes such as extinction, dispersal, sympatric diversification, or a lack of evolutionary response to vicariance (van Veller et al., 1999; Crisci et al., 2003). Phylogeographic incongruence among codistributed species suggests that evolution of biotic communities is often neither a synchronized nor a concerted event (Hewitt, 1999; Sullivan et al., 2000; Brunsfeld et al., 2001; Carstens et al., 2005a). Phylogeographic patterns of codistributed species may also be incongruent while simultaneously displaying patterns of shared responses to past climatic or geologic events (Sullivan et al., 2000). The combination of these findings indicate that phylogeographic patterns of codistributed species are often influenced by differing ecologies, life history traits and population processes.

The temperate rainforests within the Pacific Northwest of the United States are a well-known example of an area with codistributed species known for their high endemism (Brunsfeld et al., 2001). Considerable effort has gone into constructing a regional perspective on the phylogeographic patterns of these endemic organisms (Brunsfeld et al., 2001; Soltis et al., 1997; Carstens et al., 2005a). The codistributed amphibian assemblage within the mesic forest ecosystem of the Pacific Northwest provides an ideal opportunity to test for concerted responses to past climatic and geologic events (Carstens et al., 2005a). This assemblage includes diverse and distantly related amphibian species such as tailed frogs (*Ascaphus truei*, *A. montanus*.), Pacific giant salamanders (*Dicamptodon* spp.) and plethodontid salamanders (*Plethodon idahoensis*, *P. vandykei*) (Carstens et al., 2005a). Previous studies on this assemblage have demonstrated a concordant response to the uplift of the Cascade Mountains ~2 to 5 mya, resulting in reciprocally monophyletic lineages corresponding to coastal populations and disjunct interior populations within the northern Rocky Mountains (Nielson et al., 2001; Carstens et al., 2004; Steele et al., 2005; Carstens et al., 2005b). The disjunct populations of amphibians found within the Rocky Mountains share similar geographic distributions and intraspecific studies reveal a common pattern of shallow phylogenetic structuring in these species, suggesting recent colonization events within the Rocky Mountains (Nielson et al., 2001; Carstens et al., 2004; Carstens et al., 2005b). Coastal lineages of this amphibian assemblage also share similar geographic distributions. However, detailed comparative studies have not yet been conducted on these coastal populations to test for concerted responses to past climatic or geologic events.

Studies of codistributed amphibian assemblages in the Pacific Northwest have primarily focused on broad scale phylogeography within a genus and the deep genetic divergence between coastal and disjunct inland lineages. In contrast, this study adds a new dimension by focusing on the comparative phylogeography of species that share small fragmented distributions restricted to coastal temperate rainforest. Two of the codistributed amphibians within this mesic forest ecosystem are the Cope's giant salamander (*Dicamptodon copei*) and the Van Dyke's salamander (*Plethodon vandykei*). These species are endemic to the Pacific Northwest of the United States, have similarly fragmented distributions, and are similarly dependent upon stream and stream-side habitats. The geographic distribution of each species is split into three mountainous regions within the Pacific Northwest: Olympic Mountains, Willapa Hills, and Cascades Mountains (Fig. 1). The Cope's giant salamander is a neotenic species and usually remains in an aquatic form throughout it life (Nussbaum, 1976), while the Van Dyke's salamander is considered to be the most aquatic *Plethodon* species in North America and lives in seeps and streamside splash zones (Brodie, 1970; Petranka, 1998). Several other species of salamander that are strongly associated with streams also occur in the study area (*Rhyacotriton* spp.) but each has a distribution restricted to just one of these mountainous regions (Good and Wake, 1992). The combination of a similarly fragmented distribution and shared dependence on stream habitat makes *D. copei* and *P. vandykei* ideal for testing hypotheses of concerted or independent responses to past climatic and geologic events. Because other mesic forest amphibians show similar responses to past geologic events in the Pacific Northwest, (Carstens et al., 2005a) it is reasonable to predict that these two species should also have concordant phylogeographic topologies.

Results from two previous studies on *P. vandykei* provide a clear phylogeographic hypothesis (Howard et al., 1993; Wilson and Larsen, 1999) which is used to test the phylogeographic topology of *D. copei*. Both electrophoretic (Howard et al., 1993) and morphological (Wilson and Larsen, 1999) studies consistently revealed two reciprocally monophyletic lineages corresponding to coastal populations, located in the Olympic Mountains and the Willapa Hills, and inland populations within the Cascade Mountains (Fig. 1). Populations within these two areas are thought to have been isolated since the late Pleistocene (Wilson and Larsen, 1999) and are separated by lowland areas of glacial and alluvial deposits that appear to limit dispersal (Wilson et al., 1995). Both studies also reveal that populations within the Olympic Mountains are indistinguishable from those in the Willapa Hills, indicating recent expansion of *P. vandykei* into the Olympic Mountains. To test the hypothesis that *D. copei* has a similar phylogeographic history, mitochondrial DNA is used to estimate a phylogeny and elucidate past demographic patterns within *D. copei*. The resulting phylogeny is tested for concordance with that of *P. vandykei* using a variety of phylogenetic comparison tests.