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# Inferring the effects of past climate fluctuations on the distribution pattern of *Iranolacerta* (Reptilia, Lacertidae): Evidence from mitochondrial DNA and species distribution models

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ABSTRACT

A variety of different methods are available for investigating the effects of past climate fluctuation on biota. Among them, molecular phylogeography and species distribution modeling approaches have been shown to be especially useful tools to trace past climate induced modifications of species' geographic distributions. The results of both analytical approaches are here combined to better understand the influences of past climate changes on the fragmented distribution pattern of the lizard genus *Iranolacerta* that currently occurs in the northwest and central Zagros Mountains of Iran. While *Iranolacerta zagrosica* is restricted to few localities and cannot be modeled, the potential distribution of *Iranolacerta brandtii* suggested a large region of unfavorable habitat between northwest and the central Zagros Mountains populations. From the phylogenetic perspective, both species display deep genetic separation likely predating the Pleistocene. However, limited genetic diversity across this divided range of *I. brandtii* implies that the current separation is recent. Deeper genetic divergences were, nevertheless, uncovered within the northwest population. Since no recent geological events explain these results, the most likely explanation for such a distribution pattern is due to past climate fluctuations. Both sources of evidence suggest that during the early Holocene the northwest and Zagros populations of *I. brandtii* were connected, and the current pattern was shaped with their disconnection in the early Holocene. Further studies may identify potential glacial refugia for other species in this biodiverse region.

## 1. Introduction

During the Pleistocene, global temperatures underwent extreme fluctuations producing progressively larger ice sheets across Eurasia and North America (Webb and Bartlein, 1992). In the northern latitudes, glaciations, or periods with low temperatures left distinctive marks on the genetic diversity patterns of many taxa and have shaped their current genetic structures (Avise, 2000; Hewitt, 2000). Similarly, repeated cycles of range restriction to refugia during glacial periods and outward expansion during interglacials have shaped the current distribution pattern of many plant and animal species in Europe (Hewitt, 1999; Lesbarreres, 2009). On the other hand, currently arid regions such as much of North Africa and the Middle East experienced an alteration of dry and humid periods, which would have allowed lower or greater connectivity than currently for many mesic species (Schuster et al., 2006). The most recent glaciation, termed the Riss-Würm, reached its maximum about 18,000–21,000 years ago and in the Sahara and Middle East corresponded to a period of higher aridity than present (Ehlers and Gibbard, 2004). In contrast, after the end of the glaciations, conditions in this region during the Holocene Climatic Optimum (HGO) 9000–5000 years ago were much more humid than present (Kaufman et al., 2004).

Different approaches, comprising molecular phylogeography and species distribution modeling techniques (SDMs), are available to investigate the effects of such massive, often rapid changes in climatic conditions on species distributions. With the development of molecular methods it is now possible to investigate the geographical variation using multiple markers, and to deduce intraspecific phylogeographic structures (Taberlet et al., 1998; Avise, 2000). On the other hand, SDMs are now widely used to assess the potential distribution of species (Guisan and Thuiller, 2005; Jeschke and

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Strayer, 2008). Using SDMs, it can be assessed how a set of environmental factors influences the distribution patterns of a species. The models are based on the ecological niche concept, which assumes that the environmental (i.e. the Grinellean) niche of a species determines its large scale distribution, which is ultimately determined through its fundamental niche breadth and position. The latter is defined as the range of biotic and abiotic conditions in a multidimensional space, which allows the species to persist without immigration (Hutchinson, 1957; Soberón and Peterson, 2005; Soberón, 2007; Sillero, 2011). In practice, information derived from a number of environmental parameters is combined with known locations of presences and a model is fitted to describe the requirements of the target species (Anderson et al., 2003). A special case of SMDs are climate envelope models (CEMs) which focus only on the climatic niche of the species (Elith and Leathwick, 2009). SDMs are widely used to predict the potential distribution of rare species (Peterson and Vieglais, 2001; Pearson and Dawson, 2003; Pearson et al., 2007; Jiménez-Valverde et al., 2011).

Comparisons of the independent results of SDMs and molecular phylogeographic analyses extends the range of evolutionary biology studies even further by assessing geographic patterns of ecological and genetic variation in evolutionary processes (Cushman et al., 2006; Knouft et al., 2006; Chan et al., 2011). Comparing results from phylogeographic and SDM methods that utilize a heterogeneous set of quantitative and qualitative data obtained from a wide variety of sources with differing data types improves our understanding of evolutionary processes. In fact, it allows comparisons among results derived from independent, but complimentary methods. If they are coherent, the evolutionary hypotheses are then better supported (Kidd and Ritchie, 2006; Rödder et al., 2010).

The three mountain ranges, the Azerbaijan in the northwest, the Alborz in the north and the Zagros in the west of Iran are well-known barriers for the distribution of lacertid lizards, tribe Lacertini, to the west (Anderson, 1999; Arnold et al., 2007; Ahmadzadeh et al., 2008). In this area and neighbouring regions as well, the species of the small Lacertini often display fragmented ranges (Arnold, 1973; Nilson et al., 2003; Pavlicev and Mayer, 2009). The fragmented distribution pattern of *Iranolacerta* species offers an interesting model that can be examined with such integrated approaches. *Iranolacerta* is a small genus comprising *Iranolacerta brandtii* De Filippi, 1863 and *Iranolacerta zagrosica* (Rastegar-Pouyani and Nilson, 1998), both of which are native Iranian species with a limited distribution (Anderson, 1999; Arnold et al., 2007; Ahmadzadeh et al., 2008). *I. brandtii* is present in northwestern Iran in Azerbaijan Provinces and discontinuously in Esfahan Province. Two subspecies have been described, the nominate subspecies and *I. b. esfahanica* that was reported by Nilson et al. (2003) from the Zagros Mountains in the Esfahan province of Iran, although there are also doubtful records in the Caucasus (In den Bosch, 1996; Anderson, 1999; Nilson et al., 2003; Rezazadeh et al., 2010). *Iranolacerta zagrosica* is known only from around the type locality also in the Zagros Mountains (Rastegar-Pouyani and Nilson, 1998). The habitat type is rocky and vertical slopes. It lives in sympatry but not syntopic with *I. b. esfahanica* (Rastegar-Pouyani and Nilson, 1998; Anderson, 1999; Nilson et al., 2003; Arnold et al., 2007).

The influences of past climate fluctuations on the geographical distribution of the genetic diversity in this area is still poorly known. Therefore, in this study, we investigated the evolutionary history of *I. brandtii* and *I. zagrosica* in the light of past climate change, by linking the independent results of two different analytical approaches, i.e. SDMs and phylogeography. Specific questions were: (1) What shaped the current biogeographic pattern? (2) Which is the level of genetic variability between the two species and the two subspecies of *I. brandtii*?, and (3) Can this group be used as a model to examine the influences of the Northwestern and Zagros mountains on biogeographical patterns in the light of climate change and post-glacial events?

## 2. Materials and methods

### 2.1. Specimens and species records

Specimens used in this study and respective locations are listed in Table 1. A comprehensive sampling was conducted across the whole distribution areas of *I. brandtii* and *I. zagrosica* from the Azerbaijan provinces and the central Zagros Mountains in Iran (Fig. 1). The samples are classified in three main groups; (i) Esfahan–Central Zagros including four *I. zagrosica* and two *I. b. esfahanica* specimens, (ii) Azerbaijan–Tabriz comprising the specimens from Sahand Mountains and Verzeghan and (iii) Azerbaijan–Ardabil, with additional samples from the North. All specimens from (ii) and (iii) areas are considered *I. b. brandtii.* All known geographic records of *I. brandtii* ($n = 10$) were used for SDM development (see below).

### 2.2. Phylogenetic analyses

Total genomic DNA from each specimen was extracted using standard saline methods (Sambrook et al., 1989). Polymerase chain reaction (PCR) amplifications were performed for fragments of three different mitochondrial DNA (cytochrome *b*, 16S and 12S ribosomal RNA) genes. The amplification and sequencing of three mtDNA gene fragments, was performed using the primers Cytb1/cb2R, 16SL/16SH, and 12Sa/12Sb (Kocher et al., 1989; Hedges et al., 1991). PCR reactions were carried out in a 25 μl total volume, containing 2.5 μl reaction Buffer, 1.5 mM of $MgCl_2$, 0.5 mM each

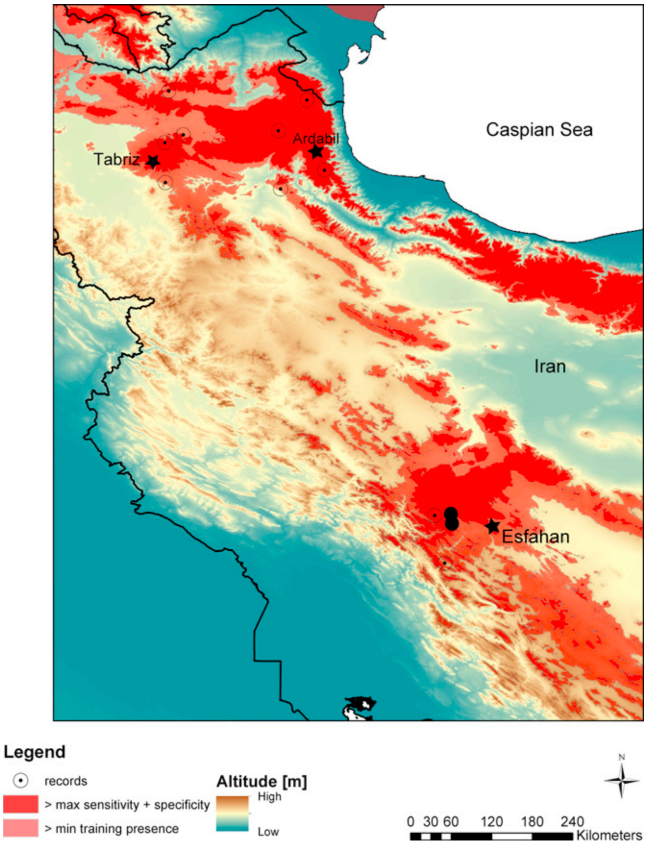

**Fig. 1.** The map showing the sampling sites for specimens sequenced in this study (dots: *I. brandtii*; black circles: *I. zagrosica*) and also the current estimated potential distribution of *I. brandtii* as estimated by Maxent models.