



## Circum-Mediterranean phylogeography of a bat coupled with past environmental niche modeling: A new paradigm for the recolonization of Europe?



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### ABSTRACT

The isolation of populations in the Iberian, Italian and Balkan peninsulas during the ice ages define four main paradigms that explain much of the known distribution of intraspecific genetic diversity in Europe. In this study we investigated the phylogeography of a wide-spread bat species, the bent-winged bat, *Miniopterus schreibersii* around the Mediterranean basin and in the Caucasus. Environmental Niche Modeling (ENM) analysis was applied to predict both the current distribution of the species and its distribution during the last glacial maximum (LGM). The combination of genetics and ENM results suggest that the populations of *M. schreibersii* in Europe, the Caucasus and Anatolia went extinct during the LGM, and the refugium for the species was a relatively small area to the east of the Levantine Sea, corresponding to the Mediterranean coasts of present-day Syria, Lebanon, Israel, and northeastern and northwestern

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Egypt. Subsequently the species first repopulated Anatolia, diversified there, and afterwards expanded into the Caucasus, continental Europe and North Africa after the end of the LGM. The fossil record in Iberia and the ENM results indicate continuous presence of *Miniopterus* in this peninsula that most probably was related to the Maghrebian lineage during the LGM, which did not persist afterwards. Using our results combined with similar findings in previous studies, we propose a new paradigm explaining the general distribution of genetic diversity in Europe involving the recolonization of the continent, with the main contribution from refugial populations in Anatolia and the Middle East. The study shows how genetics and ENM approaches can complement each other in providing a more detailed picture of intraspecific evolution.

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## 1. Introduction

The three peninsulas in southern Europe, the Iberian, the Italian and the Balkan, comprise refugia which not only made it possible for populations of species to survive during the ice ages (Taberlet et al., 1998), but also acted as “engines for speciation” (Hewitt, 2011). During the ice ages, isolated populations of many widespread species became genetically differentiated in the peninsulas and later repopulated the rest of Europe after the last glacial maximum (LGM). Based on the role played by these peninsulas, four paradigms of intraspecific genetic evolution in Europe have been defined (Habel et al., 2005; Hewitt, 1999). Under the grasshopper paradigm, the Balkan populations populated continental Europe more quickly than the Iberian and/or the Italian populations, which were confined to their own peninsulas by the Pyrenees and the Alps, respectively. Under the hedgehog paradigm, species dispersed out of their respective peninsulas in tandem and the differentiated Iberian, Italian and Balkan populations populated regions corresponding roughly to western, central and eastern Europe, respectively. The bear paradigm outlines a pattern where the Alps acted as a barrier to dispersal of the Italian populations after the LGM, whereas the Iberian and Balkan populations populated rest of Europe, meeting around central Europe (Hewitt, 1999). The most recently defined paradigm, the butterfly paradigm, outlines a scenario in which expansion took place out of differentiated populations in the Italian and Balkan/Anatolian peninsulas, but those in the Iberian peninsula were confined by the Pyrenees (Habel et al., 2005).

However, these paradigms are likely to be oversimplifications of the origins of intraspecific genetic evolution in Europe, especially at smaller geographic scales. For instance, smaller “refugia within refugia” have been suggested to exist within Iberia (Gómez and Lunt, 2007), Italy (Canestrelli et al., 2007), the Balkans (Previšić et al., 2009; Surina et al., 2011), and Anatolia (Bilgin, 2011). Additionally, local continental glacial refugia in central Europe have been suggested for many species, including the Carpathian Basin, Black Forest region, Pyrenean region, and Higher Tatras (Schmitt, 2007).

Recolonization of European populations may also have origins in glacial refugia farther to the east. For instance, in addition to the Balkan refugium, Anatolia has been shown to be a potential refugium, from where populations subsequently colonized Europe (Bilgin, 2011; Rokas et al., 2003). For some species, especially those inhabiting the taiga (e.g. Russian flying squirrel *Pteromys volans*), dispersal centers are found even farther to the east, in central Asia (Oshida et al., 2005). Recolonization of the Mediterranean basin by eastern source populations is also supported by a meta-analysis of species belonging to six phyla around the Mediterranean basin, showing that intra-specific genetic diversity generally decreases from east to west (Conord et al., 2012).

The details of the postglacial history of species found in Europe are far from simple, and for widely distributed species, reconstructing historical dispersal patterns requires sampling both at

continental and regional/local geographic scales. In this study we examined the phylogeography of a cave-dwelling bat species, the bent-winged bat, *Miniopterus schreibersii*, using a dense sampling strategy from around the Mediterranean basin and the Caucasus. The evolutionary history of *M. schreibersii* has been studied locally in different parts of Europe and Anatolia, yet a comprehensive study has not previously been conducted. The work at a regional level in and around the vicinity of Anatolia, including Bulgaria and Greece indicates the presence of two mitochondrial DNA clades (Bilgin et al., 2008a, 2006; Furman et al., 2009), which were recently shown to represent two different species (Bilgin et al., 2012; Furman et al., 2010b). Within *M. schreibersii*, Bilgin et al. (2008a) found that the southeastern Balkans could be a refugial region from which the rest of Anatolia was populated, while Furman et al. (2010a) suggested a Transcaucasian refugium for the recolonization of the eastern Black Sea coast by *M. schreibersii*. In a more continental perspective, although refugial populations have been suggested to exist in Iberia or Northern Africa (Ramos Pereira et al., 2009) or Thrace (the European part of Turkey) (Furman et al., 2010a), the issue has not been properly addressed using samples from throughout Europe, including the Italian peninsula, and North Africa. To better understand the details of the evolutionary history of *M. schreibersii* in the western Palearctic, we have collected and undertook genetic analyses on samples from 15 countries spanning North Africa, southern and central Europe, Anatolia, the Middle East and the Caucasus. We also coupled genetics data with Environmental Niche Modeling (ENM) of the current time frame and the LGM to investigate whether the hypothetical refugia determined by genetics data were supported by inferred LGM niche distributions. We were also able to formulate testable hypotheses for future investigations, showing the strength of combining genetics and ENM approaches.

## 2. Materials and methods

### 2.1. Field methods

For the study, sequence data available from GenBank from Turkey ( $n = 217$ ), Greece ( $n = 11$ ), Bulgaria ( $n = 17$ ) and Portugal ( $n = 302$ ) (Bilgin et al., 2008a, 2006; Furman et al., 2009, 2010a, 2010b; Ramos Pereira et al., 2009) were used, and additional samples ( $n = 337$ ) were collected from 28 locations in 15 countries including Russia, Lebanon, Cyprus, Greece (including Crete), Romania, Slovakia, Slovenia, Croatia, Italy, France, Serbia, Spain, Morocco and Tunisia (Fig. 1, Table 1). For the new samples, wing-punches (3–4 mm) were placed in 80% ethanol or dried in silica gel in the field (Puechmaille et al., 2011), and subsequently stored at  $-20\text{ }^{\circ}\text{C}$  until further processing.

### 2.2. Laboratory methods

Total DNA from each sample was extracted using a Roche High Pure PCR Template Preparation Kit, following the manufacturer's

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