



The phylogeography of an alpine leaf beetle: Divergence within *Oreina elongata* spans several ice ages

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ABSTRACT

The genetic landscape of the European flora and fauna was shaped by the ebb and flow of populations with the shifting ice during Quaternary climate cycles. While this has been well demonstrated for lowland species, less is known about high altitude taxa. Here we analyze the phylogeography of the leaf beetle *Oreina elongata* from 20 populations across the Alps and Apennines. Three mitochondrial and one nuclear region were sequenced in 64 individuals. Within an mtDNA phylogeny, three of seven subspecies are monophyletic. The species is chemically defended and aposematic, with green and blue forms showing geographic variation and unexpected within-population polymorphism. These warning colors show pronounced east–west geographical structure in distribution, but the phylogeography suggests repeated origin and loss. Basal clades come from the central Alps. Ancestors of other clades probably survived across northern Italy and the northern Adriatic, before separation of eastern, southern and western populations and rapid spread through the western Alps. After reviewing calibrated gene-specific substitution rates in the literature, we use partitioned Bayesian coalescent analysis to date our phylogeography. The major clades diverged long before the last glacial maximum, suggesting that *O. elongata* persisted many glacial cycles within or at the edges of the Alps and Apennines. When analyzing additional barcoding pairwise distances, we find strong evidence to consider *O. elongata* as a species complex rather than a single species.

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1. Introduction

The Quaternary has proved a turbulent time for the flora and fauna of northern Europe. This period of Earth's history, from around 2.6 million years ago, has witnessed alternating glacial and interglacial periods driven by interactions between tectonic and orbital forces (Webb and Bartlein, 1992; Williams et al., 1998; EPICA community members, 2004). The fluctuating climate would have had profound effects on population migration and survival, the results of which are still apparent in the community composition and genetic diversity of recent organisms (Bennett, 1990). During glacial periods, when large areas of northern Europe were covered by the growing ice shelf and permafrost, most lowland species survived in southern refugia in the Iberian, Italian and Balkan Peninsulas (Hewitt, 1996, 2000, 2004; Taberlet et al., 1998). Recolonization of temperate regions was affected by mountain

ranges such as the Pyrenees or the Alps acting as barriers to some species, so that the contributions of different refugia varied in different taxa. For example, all northern European populations of *Chorthippus parallelus* and *Alnus glutinosa* emerged from the Balkans, whereas in *Erinaceus* and *Quercus* species, western, central and eastern regions were colonized independently from the Iberian, Italian and Balkan refugia, respectively (Hewitt, 1999). This periodic extinction and recolonization shaped the genetic landscape of Europe, determining the large-scale patterns of spatial genetic structure and diversity (Hewitt, 1996, 2001; Gratton et al., 2008; Fussi et al., 2010).

Whilst these patterns have been well documented for many lowland species, much less is known about the influence of ice ages on high altitude animals (Pauls et al., 2006; Schmitt et al., 2006; Haubrich and Schmitt, 2007; Schmitt, 2009). They provide a contrast with the lowland taxa, since the current warm climate represents a period in which their range has probably contracted. Climate cycles may therefore have led currently isolated populations to have come repeatedly into contact during cold periods as their suitable habitat expanded. For the alpine flora, long-term refugia within the Alps and at their northern, southern and eastern

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borders have been proposed on the basis of recent molecular studies (Stehlik et al., 2001; Stehlik, 2002; Schönswetter et al., 2005). Such results have important implications for the community ecology of montane habitats. If many animal and plant species survived *in situ* this suggests a long period for coevolution and local adaptation, which would not have been available to most of the more recently assembled communities of the northern lowlands.

Here we address the bias towards lowland taxa by presenting the phylogeography of the alpine leaf beetle *Oreina elongata* (Suffrian, 1851) (Coleoptera: Chrysomelidae). This species is adapted to survival at high altitudes, with isolated populations found across the Alps and Apennines at altitudes of 1200–2500 m above sea level (Margraf et al., 2003, 2007; Röder et al., 2008). Seven allopatric subspecies have been described based on differentiation of male genitalia (the aedeagus) and cuticle microstructure (Ruffo, 1946; Franz, 1949; Daccordi and Ruffo, 1976, 1986). These herbivorous beetles feed on hosts from two tribes of the Asteraceae: when feeding on *Cirsium* (Cynareae) larvae and adults synthesize cardenolides, whereas individuals feeding on *Adenostyles* or *Senecio* (Senecioneae) encounter plant-produced pyrrolizidine alkaloid N-oxides (PAs) that they are able to sequester (Dobler et al., 1996; Hsiao and Pasteels, 1999; Röder et al., 2007; Verdon et al., 2007). This chemical defense is accompanied by what appears to be warning coloration in bright metallic patterns, with blue, green and mixed populations known. Color pattern does not covary with the type of defense, and the within-population polymorphism is unexpected, because learning by predators would be expected to generate positive frequency-dependent selection and lead to monomorphism (Mallet and Joron, 1999).

In the present study we analyzed the genetic structure of 20 populations of *O. elongata* from across the whole species distribu-

tion. Sequencing of regions of three mitochondrial genes and one nuclear gene was used to answer the following questions:

1. Did *O. elongata*, as a representative of the high altitude fauna, survive the cold periods of the Quaternary *in situ* in the Alps and Apennines?
2. What does the phylogeography suggest about the evolution of color pattern in the species?

In order to infer the timescale over which differentiation is likely to have arisen, we make use of an approximate molecular dating method based on a review of published gene-specific mtDNA substitution rates to answer a further question:

3. Was divergence within *O. elongata* a product of the last glacial cycle or is the differentiation more ancient?

2. Materials and methods

2.1. Sampling

Between 2001 and 2007, *O. elongata* were collected from 20 populations covering the whole distribution (Alps and Apennines), including most of the sites where the species is known to exist, and all of the seven described subspecies (Ruffo, 1946; Franz, 1949; Daccordi and Ruffo, 1976, 1986; Kippenberg, 1994) (Fig. 1 and Table 1). Samples were preserved in pure ethanol and stored at -20°C , apart from the individuals from GLE that were dried specimens from a collection. For most populations, three individuals were chosen for the phylogeographic analysis, using only males to be sure of accurate identification based on genitalia (except for PDC, the holotype location for *O. elongata zoiai*, for which only

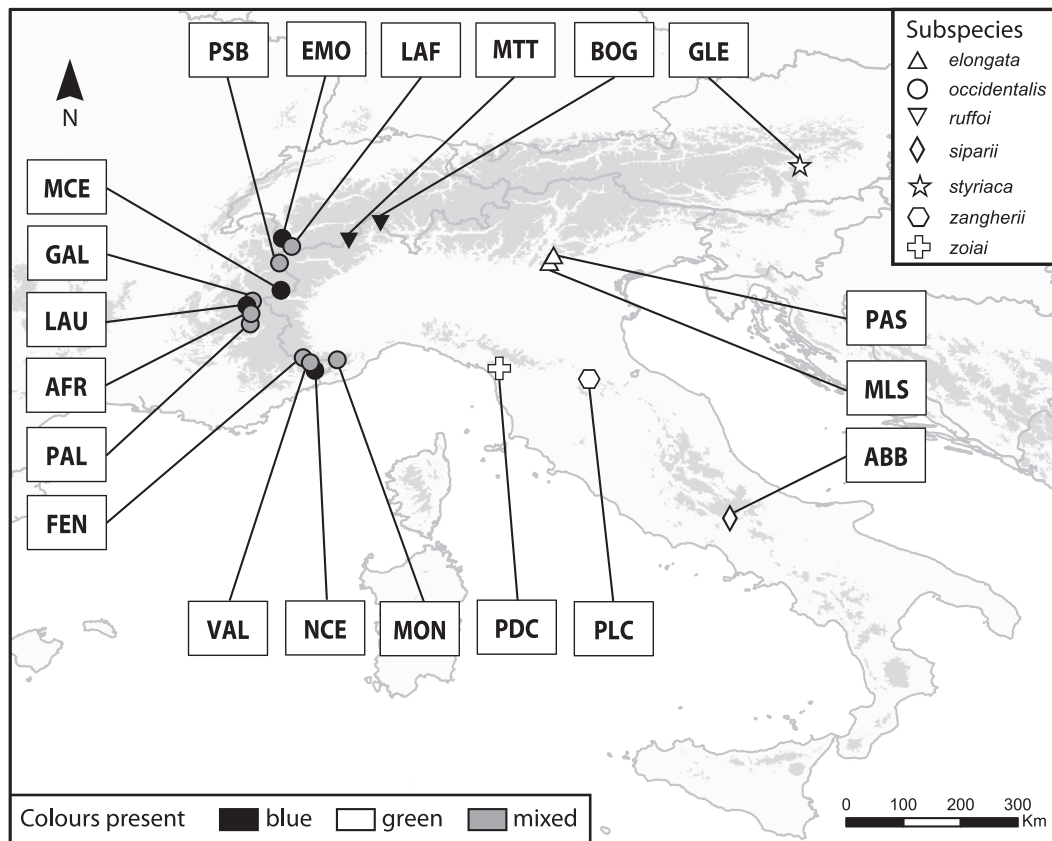


Fig. 1. Distribution of the 20 sampled populations of *O. elongata* in Italy and neighboring countries, showing their subspecies (symbols) and color morphs present (shading). Topographic shading in the Alps and Apennines shows altitudes above 1000 m.

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