



Pleistocene range shifts, refugia and the origin of widespread species in western Palaearctic water beetles



David García-Vázquez^a, David T. Bilton^b, Garth N. Foster^c, I. Ribera^{a,*}

^a Institute of Evolutionary Biology (CSIC-Universitat Pompeu Fabra), Passeig Marítim de la Barceloneta 37, 08003 Barcelona, Spain

^b Marine Biology and Ecology Research Centre, Plymouth University, Drake Circus, Plymouth PL4 8AA, UK

^c Aquatic Coleoptera Conservation Trust, 3 Eglinton Terrace, Ayr KA7 1JJ, Scotland, UK

ARTICLE INFO

Article history:

Received 30 January 2017

Revised 2 June 2017

Accepted 10 June 2017

Available online 15 June 2017

Keywords:

Glacial refugia

Dytiscidae

Hydraenidae

Quaternary glaciations

Range expansion

Mediterranean Peninsulas

Central Asia

ABSTRACT

Quaternary glacial cycles drove major shifts in both the extent and location of the geographical ranges of many organisms. During glacial maxima, large areas of central and northern Europe were inhospitable to temperate species, and these areas are generally assumed to have been recolonized during interglacials by range expansions from Mediterranean refugia. An alternative is that this recolonization was from non-Mediterranean refugia, in central Europe or western Asia, but data on the origin of widespread central and north European species remain fragmentary, especially for insects. We studied three widely distributed lineages of freshwater beetles (the *Platambus maculatus* complex, the *Hydraena gracilis* complex, and the genus *Oreodytes*), all restricted to running waters and including both narrowly distributed southern endemics and widespread European species, some with distributions spanning the Palearctic. Our main goal was to determine the role of the Pleistocene glaciations in shaping the diversification and current distribution of these lineages. We sequenced four mitochondrial and two nuclear genes in populations drawn from across the ranges of these taxa, and used Bayesian probabilities and Maximum Likelihood to reconstruct their phylogenetic relationships, age and geographical origin. Our results suggest that all extant species in these groups are of Pleistocene origin. In the *H. gracilis* complex, the widespread European *H. gracilis* has experienced a rapid, recent range expansion from northern Anatolia, to occupy almost the whole of Europe. However, in the other two groups widespread central and northern European taxa appear to originate from central Asia, rather than the Mediterranean. These widespread species of eastern origin typically have peripherally isolated forms in the southern Mediterranean peninsulas, which may be remnants of earlier expansion-diversification cycles or result from incipient isolation of populations during the most recent Holocene expansion. The accumulation of narrow endemics of such lineages in the Mediterranean may result from successive cycles of range expansion, with subsequent speciation (and local extinction in glaciated areas) through multiple Pleistocene climatic cycles.

© 2017 Elsevier Inc. All rights reserved.

1. Introduction

The Quaternary was a period of drastic cyclical climatic changes, with multiple glacial–interglacial periods, ultimately driven by variations in the earth's orbit known as Milankovitch cycles. Milankovitch–driven climate oscillations led to large changes in the size and location of the geographic distribution of many species, in some cases resulting in speciation due to the higher probability of isolation of small populations in areas under new selection regimes (Dynesius and Jansson, 2000). These Pleistocene climatic oscillations and the subsequent shifts in ecological

conditions, with the repeated fragmentation of populations during glacials and interglacials, have long been hypothesised to have driven the origin of most extant Holarctic species (e.g. Rand, 1948; Mayr, 1970).

Pleistocene climatic changes were especially drastic in northern latitudes of the Palearctic region, since during the Last Glacial Maximum the European ice sheet covered most areas north of 52°N, with permafrost north of 47°N (Dawson, 1992). Large areas of central and northern Europe therefore became inhospitable to temperate taxa during glacials; in stark contrast to the Mediterranean peninsulas, which retained more temperate climate and vegetation (e.g. Huntley, 1988; Bennett et al., 1991). However, despite the fact that most of central and northern Europe and regions of Asia at similar latitudes were exposed to extremely cold conditions (Dawson, 1992), there were areas on the slopes of mountain ranges

* Corresponding author.

E-mail address: ignacio.ribera@ibe.upf-csic.es (I. Ribera).

and along river valleys where moister conditions prevailed (Soffer, 1990), allowing the local survival of temperate biota in these northern/eastern refugia (e.g. Stewart et al., 2009; Schmitt and Varga, 2012).

Two main scenarios could account for the origin of the current central and northern European fauna. Firstly, there is the traditional model of postglacial range expansion from Mediterranean refugia (e.g. Hewitt, 2000), in which central and northern Europe were colonized by northward range expansions mainly from the Iberian, Italian, Balkan and Anatolian peninsulas at the end of the last glaciation. According to this model, populations of most European species were confined to refugial areas in southern Mediterranean peninsulas during glacial maxima, from which they would have re-colonized the continent during interglacials (although Hewitt, 2000 also recognised the important role of the Carpathians as providing potential refugia). Whilst such a scenario is well established for some taxa, it is not ubiquitous. A second possibility is that the colonization of central and northern Europe at the end of the Last Glacial was from non-Mediterranean source areas in eastern Europe and Asia (Bilton et al., 1998). According to this view, the isolation of the Mediterranean peninsulas during glacial cycles led to speciation, preventing gene flow with the new colonisers of central and northern Europe during subsequent interglacials. For taxa conforming to this model, southern peninsulas are centres of endemism rather than being a source of colonists (Bilton et al., 1998; Schmitt and Varga, 2012).

Such biogeographical isolation of Mediterranean peninsular populations has been suggested previously for small mammals (Bilton et al., 1998) and some insects (e.g. Cooper et al., 1995). Amongst aquatic Coleoptera, the absence of fossil remains of southern species in the abundant central and northern European Quaternary subfossil record (Abellán et al., 2011) supports a view of Mediterranean peninsulas as areas of endemism, rather than significant sources of postglacial colonists. Data from extant species also suggest that current southern endemics have not contributed to the diversity of northern areas (e.g. *Hydrochus* (Hydrochidae), Hidalgo-Galiana and Ribera, 2011; or *Enicocerus* (Hydraenidae), Ribera et al., 2010). Some central and northern European species may have had their origin in Mediterranean peninsulas, but in such cases it appears that the taxa concerned were those whose refugia were located in the northernmost areas of the peninsulas, on the margins of deglaciated areas (e.g. Ribera et al., 2010 for *Enicocerus*, and García-Vázquez and Ribera, 2016 for *Deronectes*), successful expansion possibly being aided by physiological adaptations in such species (Calosi et al., 2010; Cioffi et al., 2016).

Despite increased understanding of the evolution of the European insect fauna in recent decades, data on the origin of widespread central and northern European species, which should have necessarily experienced recent expansions of their geographical ranges, remain severely limited. Here we study a suite of such species, using molecular phylogeographic data to clarify their temporal and geographic origin and to better understand the role of the Pleistocene glacial cycles in driving their diversification. We examined species groups from three genera of freshwater beetles, in two different families, whose representatives colonized water independently: (1) the *Hydraena gracilis* complex (“*Haenydra*” lineage, family Hydraenidae); (2) the *Platambus maculatus* complex (family Dytiscidae) and (3) *Oreodytes sanmarkii* (C.R. Sahlberg) and *O. davisii* (Curtis) (family Dytiscidae). All taxa concerned are typical of running waters, and include both widespread European and narrowly distributed southern endemic species (Trizzino et al., 2013; Nilsson and Hájek, 2017a,b). They do, however, differ in functional traits and evolutionary histories (see below), facts which contribute to the generality of our conclusions.

Using a combination of mitochondrial and nuclear data we reconstruct the phylogenetic relationships, age and geographical

origin of the western Palaearctic species of these three widely distributed lineages, to better understand the effects of Quaternary glacial cycles on their diversification and current distributions.

2. Material and methods

2.1. Taxonomic background and taxon sampling

2.1.1. *Hydraena gracilis* complex

The genus *Hydraena*, currently with ca. 900 species distributed worldwide (Trizzino et al., 2013) is the largest genus within the family Hydraenidae and probably the most diverse amongst the aquatic Coleoptera (Jäch and Balke, 2008). Within *Hydraena*, the “*Haenydra*” lineage includes ca. 90 species with a north Mediterranean distribution (Trizzino et al., 2013). They are usually found in clean, fast flowing waters, often in mountain streams, from the Iberian Peninsula to Iran and the Urals, but are absent from North Africa (Ribera et al., 2011; Trizzino et al., 2011, 2013; Jäch, 2015). Many species of this lineage have very restricted distributions, often limited to a single valley or mountain system, but there are also a few species with very wide geographical ranges.

In this work we focus on the most widespread species of “*Haenydra*”, *Hydraena gracilis* Germar and its closest relatives in the *H. gracilis* complex *sensu* Jäch (1995), which includes seven recognised species and one subspecies (Trizzino et al., 2013). *Hydraena gracilis* is widely distributed across almost the whole of Europe, ranging from southern France eastwards to Ukraine and northwards to Finland, including the British Isles (Fig. 1). Previous molecular studies, albeit on a limited number of specimens (Ribera et al., 2011), suggested that despite its widespread distribution, genetic differences across its geographic range were minimal. Jäch (1995), however, found morphological differences between specimens from the Balkans and the rest of Europe, supporting the recognition of the subspecies *H. gracilis balcanica* d’Orchymont. *Hydraena gracilis* is absent from the Iberian and Anatolian peninsulas, where it is replaced by different species of the complex (Fig. 1). *Hydraena gracilidelphis* Trizzino, Valladares, Garrido & Audisio is the westernmost species of this group, endemic to the Iberian Peninsula (mainly in the north but with some records in the southwest) and the French Pyrenees (Trizzino et al., 2012). The Anatolian Peninsula and adjacent areas are occupied by three species: *H. anatolica* Janssens distributed in northern and eastern Anatolia and parts of the Caucasus and northwestern Iran; *H. graciloides* Jäch in northern Turkey; and *H. crepidoptera* Jäch known only from two northern Turkish provinces (Kastamonu and Sinop). The other two species of the complex, *H. nike* Jäch and *H. elisabethae* Jäch, are endemic to two Aegean islands; Samothraki and Thassos respectively (Trizzino et al., 2013).

We studied a total of 48 specimens from five of the seven species of the *H. gracilis* complex (we could not obtain fresh specimens of the two Aegean Island endemics) from 37 different localities, covering the full geographical range of the studied species (Fig. 1; Table S1). As outgroups we used three closely related species of the wider *H. gracilis* lineage within “*Haenydra*” (Trizzino et al., 2011; Table S1).

2.1.2. *Platambus maculatus* complex

The genus *Platambus* contains 66 recognised species (Nilsson and Hájek, 2017a) and has a wide distribution, being present in the Palearctic, Nearctic, Neotropical and Oriental regions, and is currently divided into eight species-groups (Nilsson and Hájek, 2017a). Amongst these the *P. maculatus* group - as defined by Nilsson (2001) - is the largest, with 24 species distributed across Asia and Europe. In a molecular phylogeny of Agabinae Ribera et al. (2004) recovered a paraphyletic *Platambus*, with the

Download English Version:

<https://daneshyari.com/en/article/5592327>

Download Persian Version:

<https://daneshyari.com/article/5592327>

[Daneshyari.com](https://daneshyari.com)