Perspectives in Plant Ecology, Evolution and Systematics 16 (2014) 265–278

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

Review

Patterns and processes in plant phylogeography in the Mediterranean Basin. A review

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ARTICLE INFO

Article history:
Received 13 March 2014
Received in revised form 10 July 2014
Accepted 11 July 2014
Available online 21 July 2014

Keywords:
Glacial refugia
Latitudinal patterns
Mediterranean Basin
Phylogeography
Spatio-temporal concordance
Straits

ABSTRACT

Phylogeography, born to bridge population genetics and phylogenetics in an explicit geographic context, has provided a successful platform for unveiling species evolutionary histories. The Mediterranean Basin, one of the earth's 25 biodiversity hotspots, is known for its complex geological and palaeoclimatic history. Aiming to throw light on the causes and circumstances that underlie such a rich biota, a review of the phylogeographic literature on plant lineages from the Mediterranean Basin is presented focusing on two levels. First, phylogeographic patterns are examined, arranged by potential driving forces such as longitude, latitude – and its interaction with altitude –, straits or glacial refugia. Spatial coincidences in phylogeographic splits are found but, in comparison to other regions such as the Alps or North America, no largely common phylogeographic patterns across species are found in this region. Factors contributing to phylogeographic complexity and scarcity of common patterns include less drastic effects of Pleistocene glaciations than other temperate regions, environmental heterogeneity, the blurring of genetic footprints via admixing over time and, for older lineages, possibly a greater stochasticity due to the accumulation of responses to palaeoclimatic changes. At a second level, processes inferred in phylogeographically framed studies that are potential drivers of evolution are examined. These include gradual range expansion, vicariance, long-distance dispersal, radiations, hybridization and introgression, changes in reproductive system, and determinants of successful colonization. Future phylogeographic studies have a great potential to help explaining biodiversity patterns of plant groups and understanding why the Basin has come to be one of the biodiversity hotspots on earth. This potential is based on the crucial questions that can be addressed when geographic gaps are adequately filled (mainly northern Africa and the eastern part of the region), on the important contribution of younger lineages – for which phylogeographic approaches are most useful – to the whole diversity of the Basin, and on the integration of new methods, particularly those that allow refining the search for spatio-temporal concordance across genealogies.

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http://dx.doi.org/10.1016/j.ppees.2014.07.002

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Introduction

The Mediterranean Basin comprises a large territory around the Mediterranean Sea that is characterized by a Mediterranean climate, that is to say, mild rainy winters and hot dry summers. According to Quézel and Médail (2003) the Mediterranean region in a bioclimatic sense spans an area of 2,300,000 km^2, whose limits have sometimes been suggested as coinciding with the natural distribution range of the olive tree (*Olea europaea* L.) (Fig. 1). It extends approx. 4000 km along an east–west axis and approx. 1600 km along a north–south axis.

This region is of considerable biological interest because of its rich biota compared to the surrounding areas and is considered one of the earth's 25 biodiversity hot-spots (Myers et al., 2000). At the plant species level, i.e., in floristic terms, the Mediterranean region contains a flora that includes c. 24,000 species of which c. 60% are endemics (Greuter, 1991) whereas, for instance, all of tropical Africa has a comparable plant richness (30,000 taxa) in a surface area four times larger (Médail and Quézel, 1997). Compared to higher latitudes, 80% of all European plant endemics are Mediterranean (Comes, 2004). This richness is attributed to a number of factors including palaeogeologic and palaeoclimatic history, ecogeographical heterogeneity, human influence (Blondel and Aronson, 1999; Blondel et al., 2010) and a high percentage of species with narrow distribution ranges (Humphries et al., 1999; Thompson, 2005).

Geological and palaeoclimatic complexity is characteristic of the Mediterranean region. Its geological evolution involves complicated interactions between orogenic processes and widespread extensional tectonics (Rosenbaum et al., 2002). The area was formed during the Cenozoic simultaneously with the convergence of the African and Eurasian Plates and three associated smaller plates, Iberia, Apulia and Arabia (Dercourt et al., 1986; Krijgsman, 2002). The western Mediterranean was particularly active tectonically and consisted during the Oligocene of several small blocks that were remnants of a Paleozoic mountain chain, the Hercynian belt (Rosenbaum et al., 2002). Rotation, migration and collision processes along more than 30 Mya resulted in those small blocks located in the current territories of the Betic-Rif ranges, the Balearic Islands, the Kabylies, Corsica, Sardinia, and Calabria. The eastern Mediterranean region (Hellenic arc and Aegean basin) is more recent and its present configuration is the result of the collision of the Arabian plate with stable Eurasia in middle Miocene, which closed the connection between the Tethys Sea and the Indian Ocean (Krijgsman, 2002).

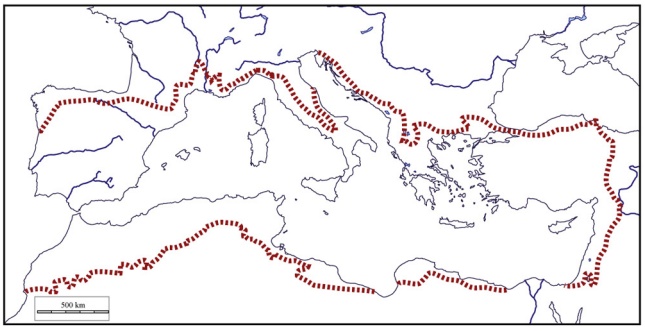

Fig. 1. Delimitation of the Mediterranean region according to bioclimatic criteria. Redrawn from Quézel and Médail (2003).

The palaeoclimatic history of the Mediterranean Basin included important long-term changes such as the gradual global cooling since the Oligocene (Zachos et al., 2008) and an aridification that started c. 9–8 Mya (van Dam, 2006). During the Late Miocene, subduction processes in the westernmost Mediterranean caused the closure of the marine gateways that existed between the Atlantic Ocean and the Mediterranean Sea, leading to the desiccation of the Mediterranean Sea that is known as the Messinian Salinity Crisis (MSC) 5.96–5.33 Mya (Hsü, 1972; Krijgsman, 2002). This period was followed by the establishment of a Mediterranean type climate, around 3.2 Mya (Suc, 1984). In addition, the Basin has been influenced by cyclical climatic changes, driven by the Milankovitch oscillations, due to periodical shifts in the earth's orbit and axial tilt that decreased their periodicity to 100 ky during the Pleistocene (Imbrie et al., 1993; Jansson and Dynesius, 2002).

Phylogeography has shed light on the evolutionary history of current plant species by bridging population genetic approaches and phylogenetic focuses, or micro- and macroevolution, as the father of the discipline put it (Avise et al., 1987). The geographic coverage of phylogeographic investigations has been more intense in regions such as North America (Brunsfeld et al., 2001; Soltis et al., 2006) and the Alps (Schönswetter et al., 2005), but has reached most regions including the Arctic (Abbott and Comes, 2004), China (Qiu et al., 2011), the Southern Hemisphere (Beheregaray, 2008) and also the Mediterranean region, where a substantial increase in the number of studies has occurred over the last ten to twelve years.

The present paper reviews the topic of Mediterranean Plant Phylogeography aiming to throw light on the evolutionary history of plants in the Basin, finding clues for its biodiversity richness and complexity, and contributing to understand the whole puzzle of the history of European plants during the last 2–3 Mya. The review has a double focus, on patterns and process, and has been elaborated from studies published in over 130 papers.

A summary of the knowledge concerning a very significant part of the region, i.e., the three southern European peninsulas (Iberia, Italy, Balkans), and the role they have played in European biogeography during the last million years, has been recently published (Hewitt, 2011). The Balkans represent the main biodiversity hotspot and the major source for postglacial colonization of central and northern Europe and it was suggested that such richness