Ecological implications of *Cousinia* Cass. (Asteraceae) persistence through the last two glacial–interglacial cycles in the continental Middle East for the Irano-Turanian flora

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Abstract

This study explores the response of the Irano-Turanian flora to Quaternary glacial–interglacial cycles in SW Asia. We use new fossil pollen data to assess variation in abundance of *Cousinia* Cass. (Compositae), a large genus typical for the Irano-Turanian flora, during these cycles. The results are compared with modern topography, tectonic and palaeoclimatic history, and recent phylogenetic data to explain the extremely high speciation rate and level of endemism as well as the modern geographical distribution of the genus. *Cousinia* is consistently well-represented in glacial-age and late-glacial pollen assemblages of NW Iran and E Anatolia. In the ~200,000-year pollen sequence from Lake Urmia, NW Iran, *Cousinia* pollen shows significant values and is nearly continuously represented during both the last glacial (~70 ka to Holocene) and penultimate glacial periods (~190 to 130 ka). In contrast, its pollen is less frequent and occurs only sporadically during the last interglacial period and the Holocene. This pattern suggests that *Cousinia* could not only withstand Quaternary glaciations, but was a significant part of the glacial-age landscapes of the Irano-Turanian territory. We argue that the extremely high rate of speciation and endemism of *Cousinia* is due to (i) the continuous presence of a complex topography in the Middle East and Central Asia since Tertiary times, which created a wide range of environmental niches and facilitated the formation and persistence of isolated populations over long periods, (ii) relatively stable climate during the late Miocene–Pliocene compared to the Quaternary period that caused small species range shifts and gene flow, and (iii) a dampened impact of multiple glacial–interglacial cycles on the mountain regions of SW Asia compared to the higher latitude European mountain ranges. This left an extensive, non-glaciated altitudinal zone for the survival of Irano-Turanian species, there by reducing extinction during glacial periods. During interglacial periods, many *Cousinia* species may have been geographically isolated in high mountain “interglacial refugia” of the Irano-Turanian region. Overall, the combination of the above factors during the Neogene resulted in geographical isolation and reduced gene flow, thereby fostering allopatric speciation in *Cousinia* and probably also in many other speciose Irano-Turanian plant taxa.

Key words: *Cousinia*, Quaternary glaciations, allopatric speciation, isolation, topographical heterogeneity, interglacial refugia, tectonic history, SW Asia

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1. Introduction

The Irano-Turanian area is one of the richest floristic regions of the world. It is located at the contact zone of the Mediterranean (W), Saharo-Sindian (S), and Euro-Siberian (N) floristic regions ([Fig. 1](#)) and is characterized by high species diversity and endemism, particularly in several large taxonomic groups including the genera *Astragalus* L. (Fabaceae), *Cousinia* Cass. (Compositae), *Acantholimon* Boiss. (Plumbaginaceae), and the families Apiaceae, Brassicaceae, and Chenopodiaceae (e.g. Eig, 1931; Davis et al., 1965–1988; Guest and Al-Rawi, 1966; Zohary, 1973; Couvreur et al., 2010). The evolution and persistence of floristic richness in the face of repeated glacial/interglacial climatic cycles is of interest to biogeography and conservation. What role did glacial/interglacial cycles play in amplifying or dampening species richness in the region? Or is the modern floristic richness a legacy of Tertiary speciation events?

Responses of vegetation to the Quaternary glacial–interglacial cycles in the Irano-Turanian realm have been previously described in a number of studies (van Zeist and Bottema, 1977; Bottema, 1986; Wick et al., 2003; Djamali et al., 2008a). However, none specifically examined floristic changes driven by the climatic cycles. We review late Pleistocene–Holocene pollen records from the Irano-Turanian part of the Middle East, and use a recently published long pollen record from Lake Urmia (NW Iran; Djamali et al., 2008a) to examine the responses of the Irano-Turanian flora to climatic changes during the Quaternary period. Lake Urmia is situated in one of the richest sub-regions of the Irano-Turanian phytogeographical region (IT2 according to White and Léonard, 1991 and Irano-Anatolian according to Zohary, 1973; [Fig. 1](#)).

One problem with this approach is that most of the dominant upland Irano-Turanian steppe plants (e.g., *Astragalus*, *Acantholimon*, *Acanthophyllum* Hook & Arn., *Cousinia* Cass., *Heliotropium* L., Zygophyllaceae, etc.) and many steppe-forest trees (*Amygdalus* L., *Prunus* L., *Cerasus* Mill., and *Pyrus* L.) are entomophilous and hence are severely under-represented in the pollen rain (e.g. van Zeist et al., 1970; Moore and Stevenson, 1982; Djamali et al., 2008b). These genera are only sparsely recorded in pollen diagrams. The genus *Cousinia* is, however, more frequently encountered in pollen diagrams of the Irano-Turanian region (e.g. van Zeist and Bottema, 1977; Wick et al., 2003; Djamali et al., 2008a). Further, the modern geographical range of *Cousinia* correlates almost perfectly with the Irano-Turanian floristic region suggesting it as a good representative of the Irano-Turanian flora ([Figs. 1](#) and [2](#)). Chenopodiaceae comprise another characteristic Irano-Turanian group that is well-represented in pollen diagrams. However, this pollen may belong to either littoral lowland or upland species (Djamali et al., 2008c), whereas *Cousinia* spp. most commonly grow in the upland vegetation. This is confirmed by the modern distribution of most *Cousinia* species, which are concentrated in the mountainous areas of Turkey, Iran, Afghanistan, and Central Asia (Knapp, 1987). This suggests that the variation in the pollen curves of *Cousinia* can be used as a proxy to understand how the Irano-Turanian upland flora in general may have responded to the Quaternary glacial–interglacial cycles. Although some studies on the pollen morphology of *Cousinia* exist, (Shtepa, 1976; Saber et al., 2009), current knowledge is insufficient to investigate past changes in species diversity of the genus.

Fig. 1. Phytogeographical map of SW Asia. IT: Irano-Turanian with numbers 1 to 4 designating the four subregions proposed by White and Léonard (1991), ES: Euro-Siberian, M: Mediterranean, SS: Saharo-Sindian, AC: Central Asiatic. The geographical range of *Cousinia* is shown in dark gray. The three lakes referred to in the description of pollen data are indicated: V: Lake Van; U: Lake Urmia; Z: Lake Zeribar.

One problem with this approach is that most of the dominant upland Irano-Turanian steppe plants (e.g., *Astragalus*, *Acantholimon*, *Acanthophyllum* Hook & Arn., *Cousinia* Cass., *Heliotropium* L., Zygophyllaceae, etc.) and many steppe-forest trees (*Amygdalus* L., *Prunus* L., *Cerasus* Mill., and *Pyrus* L.) are entomophilous and hence are severely under-represented in the pollen rain (e.g. van Zeist et al., 1970; Moore and Stevenson, 1982; Djamali et al., 2008b). These genera are only sparsely recorded in pollen diagrams. The genus *Cousinia* is, however, more frequently encountered in pollen diagrams of the Irano-Turanian region (e.g. van Zeist and Bottema, 1977; Wick et al., 2003; Djamali et al., 2008a). Further, the modern geographical range of *Cousinia* correlates almost perfectly with the Irano-Turanian floristic region suggesting it as a good representative of the Irano-Turanian flora (Figs. 1 and 2). Chenopodiaceae comprise another characteristic Irano-Turanian group that is well-represented in pollen diagrams. However, this pollen may belong to either littoral lowland or upland species (Djamali et al., 2008c), whereas *Cousinia* spp. most commonly grow in the upland vegetation. This is confirmed by the modern distribution of most *Cousinia* species, which are concentrated in the mountainous areas of Turkey, Iran, Afghanistan, and Central Asia (Knapp, 1987). This suggests that the variation in the pollen curves of *Cousinia* can be used as a proxy to understand how the Irano-Turanian upland flora in general may have responded to the Quaternary glacial-interglacial cycles. Although some studies on the pollen morphology of *Cousinia* exist, (Shtepa, 1976; Saber et al., 2009), current knowledge is insufficient to investigate past changes in species diversity of the genus.

Fig. 2. A. Map showing the distribution of *Cousinia* species richness in SW Asia (after Knapp, 1987). B. A topographic cross section along the solid line in A (from 40°E, 30°N to 70°E, 40°N). Abbreviations are the major tectono-sedimentary units of Iran and adjacent areas: U.D., Urumieh (Urmia)–Dokhtar volcanic arc; A.D., Allah Dag Mountains; K.D., Kopeh Dag Mountains; C. Iran, Central Iran; S.S., Sanandaj–Sirjan; HZ, High Zagros; FZ, Folded Zagros. The topographical profile is based on GTOPO 30 digital elevation model.

This palaeoecological approach can be complemented by phylogenetic investigations to better reveal plant population changes driven by past climatic changes (e.g. Hu et al., 2008). Recent analyses of the phylogeny and systematic of the *Arctium*–*Cousinia* complex (López-Vinyallonga et al., 2009, 2011) have revealed that within this complex only *Cousinia* subg. *Cousinia* should be treated as a newly defined genus *Cousinia*. All pollen considered here belongs to the *Cousinia*-type characteristic of this lineage. These findings, combined with palaeoecological data, allow us to evaluate the factors driving the diversification of one of the most speciose taxa of the Irano-Turanian flora.

Using *Cousinia* as a representative taxon, this study aims at (i) reconstructing the variation in distribution and abundance of *Cousinia* in the Irano-Turanian landscapes of NW Iran during the two most recent glacial–interglacial cycles, (ii) analyzing the relationships between modern species diversity and distribution patterns in *Cousinia* and the topography of SW Asia, (iii) studying the likely role of the long-term regional tectonic history in shaping this distribution pattern, and (iv) inferring the effects of Quaternary glaciations and pre-Quaternary palaeoclimates in SW Asia on the evolution of the Irano-Turanian flora.

2. Material and methods

To investigate the relationship between the distribution of *Cousinia* species and the topography of the Middle East and Central Asia, we analyzed the topographical heterogeneity of each of the four classes of species diversity (i.e. areas with equal number of species) of *Cousinia* as proposed by Knapp (1987). [Fig. 2A](#) shows the geographical distribution of these diversity areas, and [Fig. 2B](#) shows a topographical transect along with the specific diversity of *Cousinia*. In [Fig. 3](#), the spatial distribution of different elevational levels corresponding to each species diversity classes (1–3 spp., 4–9 spp., 10–29 spp., >30 spp.) is shown.

We examined the changes in pollen percentages of *Cousinia* s. str. in the available late glacial–Holocene pollen diagrams of the continental Middle East (see [Table 1](#), van Zeist and Bottema, 1977; Bottema and Woldring, 1984; Bottema, 1986; Woldring and Bottema, 2001/2002; Wick et al., 2003; Djamali et al., 2008a). *Cousinia* percentages were calculated based on pollen count data available in European Pollen Database (EPD: <http://www.europeanpollendatabase.net/>). Particular attention was paid to the longest of these pollen records; core BH3 from Lake Urmia, which covers the last two glacial–interglacial cycles (Djamali et al., 2008a). In this core, variations of trees and upland steppe plants (plants growing in well-drained soils including Poaceae but excluding aquatic and halophytic plants such as Cyperaceae, *Typha**Sparganium*, and Chenopodiaceae) were compared to the changes in *Cousinia* ([Fig. 5](#)). The transition from the penultimate glacial to the last interglacial period was studied with higher resolution, compared to the Penultimate Glacial, in order to understand changes in the abundance of *Cousinia* during a typical glacial–interglacial transition (Termination 2). In addition to pollen percentages (calculated in Tilia software and visualized in TGView; Grimm, 2004/2005), pollen concentrations were calculated for BH3 record using *Lycopodium* spores as exotic markers (Stockmarr, 1971). Unfortunately, concentration values could not be calculated for the late-Pleistocene–Holocene records of lakes Zeribar, Urmia and Van based on data available in EPD.

The chronostratigraphy of the studied long pollen record of Lake Urmia is based on correlation with several terrestrial pollen and marine isotope records, together with two radiocarbon ages and one U/Th age (see Djamali et al., 2008a).

To compare the variations of pollen concentration among different plant groups during different climatic stages (Marine Isotope Stages in [Fig. 5](#)), coefficients of variation or CVs ($CV = \sigma/\mu \times 100$, σ =standard deviation and μ =mean) were calculated using R statistical software (R Development Core Team, 2010). The CV values provide an index for the stability of each taxon or plant group during a given interval, so that lower values correlate with higher stability in time during a given period. This can be used as a rough estimate for the persistence of a taxon or plant group in the landscape ([Table 2](#)).

3. Results

The results of our topographical analysis show a direct relationship between the heterogeneity of topography and *Cousinia* species diversity ([Fig. 3](#)). The highest diversity is observed in regions with the widest range of topographical variations and the highest frequency of elevations above 2000 m ([Fig. 3C](#) and [D](#)). This is demonstrated spatially in the topographical cross-section of [Fig. 2](#) showing that the major SW Asian mountain ranges including the Zagros Mts (W Iran), Alborz Mts (N Iran), Kopeh Dagh Mts (NE Iran), and parts of the high plateau of Pamir contain the highest *Cousinia* species richness.

Fig. 3. Histograms showing the distribution of topography in four species diversity zones of *Cousinia* (Fig. 2A) proposed by Knapp (1987). The topography is taken from SRTM grids, aggregated to a 30 arcsecond grid. Frequency denotes the total number of 30 arcsecond grids corresponding to each altitudinal class. Vertical line represents the median.

[Fig. 4](#) shows pollen percentage curves of *Cousinia* versus oak during the late Pleistocene–Holocene in three pollen sites located in NW Iran and SE Turkey (Lake Zeribar, NW Iran: van Zeist and Bottema, 1977; Lake Urmia, NW Iran: Bottema, 1986; Lake Van, SE Turkey: Wick et al., 2003). These diagrams clearly show that *Cousinia* pollen percentages were higher during the last glacial period when regional landscapes were dominated by treeless steppe vegetation, and decreased during the late glacial–Holocene transition, a period characterized by gradual expansion of oak woodlands in NW Iran. The more or less continuous glacial presence of *Cousinia* is replaced by small peaks with very low and increasingly sporadic percentage values during the Holocene.

In [Fig. 5](#), percentage variations of *Cousinia* pollen are compared with trees and upland steppe herbs for the last ca. 200 ka from Lake Urmia core BH3 (Djamali et al., 2008a). Both pollen percentages (gray-filled curves: 0–3.2%) and concentrations (black bars: 0–142 grain/g) are illustrated. As pollen percentages of one taxon may be affected by variations in other taxa, the concentration values provide a more robust view of the temporal variations in *Cousinia* pollen percentages. Comparison of percentage and concentration values provides valuable information about the density of plants in the landscapes. They help to quantify the pollen deposition of a given taxon and are informative in revealing the density of that taxon in the landscape. As shown by [Fig. 5](#),

in the Urmia pollen sequence, glacial intervals are characterized by the dominance of montane steppes with xerophytic upland herbs, and interglacial intervals are characterized by the expansion of trees and shrubs, especially deciduous oak and juniper woodlands. Both upland herbs and trees are considerably more frequent during the interglacial, and to a lesser extent, interstadial intervals. This indicates denser vegetation cover during the interglacial compared to glacial periods. *Cousinia* pollen percentages form an almost continuous curve during both the penultimate glacial (MIS 6) and the last glacial periods (MIS 3 and 4), but *Cousinia* pollen became less frequent to even absent during the last interglacial period (MIS 5e) and the Holocene (gray curve in Fig. 5C). The concentration values of *Cousinia* pollen show a pattern similar to the change of percentages for most of the record with some exceptions (e.g. MIS 5e). The total pollen production of upland herbs was much lower during the glacial compared to interglacial intervals, suggesting that *Cousinia* spp. played a very important role in the plant communities of glacial landscapes in the NW Irano-Turanian region. This is also evident by substantially higher ratio of pollen concentrations of *Cousinia* over upland herbs (Fig. 5F). Less frequent occurrences of *Cousinia* pollen during the interglacial intervals suggest that its role in the interglacial landscapes became less important. Table 2 summarizes the coefficients of variation of *Cousinia* pollen concentration during the climatic stages (glacial/interglacial and stadial/interstadial intervals) of the past ~200 ka. (Fig. 5). *Cousinia* shows the lowest CV values during the glacial/stadial periods, compared to other herbs/trees confirming the stability and persistence of this taxon during the Quaternary cold stages.

Table 1

Details of examined late-glacial–Holocene pollen sequences of the continental Middle East.

Site	Core	Longitude	Latitude	Altitude	Citation
Lake Eski Acigöl	Eski Acigöl I	34° 32' 41"	38° 33' 01"	1270 m	Woldring and Bottema (2001/2002)
Lake Van	2	42° 42' 24"	38° 28' 20"	1645 m	van Zeist and Woldring (1978)
	13	42° 32' 07"	38° 34' 16"	1645 m	
Lake Van	Van–90–4	42° 34' 48"	38° 36' 04"	1645	Wick et al. (2003)
Lake Urmia	20	45° 26' 52"	37° 35' 31"	1267 m	Bottema (1986)
Lake Urmia	BH3	37° 22' 33"	37° 47' 37"	1265 m	Djamali et al. (2008a, 2008b, 2008c)
Lake Zeribar	1963–J/1970–A	46° 06' 56"	35° 32' 40"	1288 m	van Zeist and Bottema (1977)
Lake Mirabad	1963–B	33° 05' 16"	47° 42' 19"	736 m	van Zeist and Bottema (1977)

Table 2

Coefficients of variation (CV) calculated for pollen concentration values of core BH3 for different depth slices corresponding to different chronological intervals.

	Total land pollen	Herbs	Forbs	Trees	Artemisia	Poaceae	Centaurea	Apiaceae	Cousinia
Late-glacial–Holocene	0.20	0.26	0.22	0.09	0.30	0.29	1.41	0.94	0.34
MIS2–4	0.77	0.74	0.54	1.09	0.51	1.02	1.59	0.90	0.67
MIS5a	0.25	0.29	0.34	0.24	0.53	0.30	0.48	0.83	0.97
MIS5b	0.79	0.77	0.78	0.91	1.11	0.81	0.79	0.75	0.68
MIS5c	0.69	0.50	0.40	1.07	0.44	0.71	0.49	1.19	1.04
MIS5d	0.87	0.90	0.66	0.79	0.47	1.08	0.43	0.48	0.29
MIS5e	0.64	0.63	0.57	0.68	0.58	0.78	0.78	0.84	1.38
MIS6	1.28	0.87	0.84	3.33	0.93	1.05	1.65	1.06	0.78
MIS7a	0.25	0.16	0.06	0.77	0.11	0.36	1.08	0.28	1.49
Glacials	1.11	0.88	0.78	2.61	0.90	1.18	1.50	0.95	0.72
Interglacials	0.74	0.68	0.63	0.89	0.66	0.82	0.91	0.88	1.29

4. Discussion

4.1. Persistence of *Cousinia* in glacial landscapes of the Irano-Turanian region

The *Cousinia*-type pollen recorded in NW Iranian and E Anatolian regions (see pictures in van Zeist and Bottema, 1977) most probably was produced exclusively by species of *Cousinia s.str.* as defined above (see also Shtepa, 1976; Saber et al., 2009). *Cousinia* is both insect- and self-pollinated (Funk et al., 2009; López-Vinyallonga et al., 2009) and is therefore under-represented in the modern pollen rain. Although *Cousinia* is one of the dominant constituents of the Irano-Turanian flora today, its pollen has either not been found (e.g. Wright et al., 1967; van Zeist et al., 1970; Bottema and Barkoudah, 1979; Djamali et al., 2008c) or only been found at extremely low values (b1%) in modern pollen-vegetation studies in Iran and surrounding areas (van Zeist and Bottema, 1977; Moore and Stevenson, 1982). This suggests that this genus formed a major component of the Irano-Turanian glacial steppes in NW Iran during the glacial periods, where *Cousinia* pollen percentages were close to 3%. Further, the quasi-continuous percentage curve, the high concentration values and low CV index of *Cousinia*-type pollen during the last glacial and penultimate glacial periods (Fig. 5, Table 2) provide evidence for the persistence of vegetation with abundant *Cousinia* on upland slopes around Lake Urmia. Note the high values of ratio of *Cousinia* over upland herbs during glacial periods (Fig. 5F) that indicates the higher abundance of *Cousinia* compared to other steppe herbs. Identifying other elements of these glacial plant communities is problematic due to the under-representation of many Irano-Turanian genera. However, the higher glacial-age pollen values of Plumbaginaceae and Fabaceae (see pollen data of cores BH2 and BH3 in European Pollen Database: <http://www.europeanpollendatabase.net/>) may have been mainly produced by *Acantholimon*, *Onobrychis* and *Astragalus*, three important Irano-Turanian steppe taxa.

A detailed review of the altitudinal range of extant species of *Cousinia* is useful in understanding their response to Quaternary glaciations. Currently, *Cousinia* species grow across a wide range of altitudes. For example, in the Irano-Turanian part of Golestan National Park (NE Iran), the 14 species reported in Akhani (1998) are distributed from 900 to 2200 m. In the Anatolian plateau and adjacent Mesopotamian lowlands, *Cousinia* ranges between 320 and 3450 m (Davis et al., 1965–1988). In the flora of the alpine zone of Iran (3000–4000 m), *Cousinia* constitutes one of the largest genera with more than 20 species, of which 18 are endemic to Iranian high mountain systems (Noroozi et al., 2008). The genus is also represented by many species in the subalpine thorn-cushion vegetation belts of Iran, Iraq and Turkey (Davis et al., 1965–1988; Guest and Al-Rawi, 1966; Klein, 2001). This large altitudinal variation shows that *Cousinia* can grow in a broad range of elevations. However, individual *Cousinia* species commonly have narrow altitudinal ranges. For instance, in Golestan National Park, most of the *Cousinia* species are limited to a narrow (320 m) elevation range (Akhani, 1998).

Fig. 4. Pollen percentage variations of *Cousinia* during the late-glacial–Holocene in lakes Van and Urmia and also the Last Glacial to Holocene in Lake Zeribar. Pollen data are taken from van Zeist et al. (1970), Bottema (1986), and van Zeist and Bottema (1977) available as pollen counts in the website of the European Pollen Database (<http://www.europeanpollenbase.net/>).

In mountain systems, climatic changes lead to vertical rather than horizontal shifts of plant species and communities. These altitudinal range shifts allow species to track their optimal habitats by short-distance migration. However, the location and complexity of the high mountain systems are of critical importance to understand how species ranges shifted, as well as to understand the evolutionary history of mountain species (Alvarez et al., 2009; Schmitt, 2009). For example, in the main range of the Alps, such vertical migrations were difficult if not impossible due to the lowered snowline and the large extension of glaciers covering large parts of mountain slopes (e.g. Kelly et al., 2004). The high number of local endemics in Central European high mountain systems indicates their isolation and survival in non-glaciated areas located in (i) low altitude habitats in peripheral regions and (ii) high altitude “nunataks” (Schönschwetter et al., 2005; Hu et al., 2008; Thiel-Egenter et al., 2008; Schmitt, 2009). In contrast, in the mountainous regions in southern Europe, e.g. the Sierra Nevada in the Iberian Peninsula, the extension of glaciers and snowline descent were less pronounced, leaving vertical space for the survival and vertical migration of many species and having in significant impact on the genetic structure of plant and animal populations (e.g. Gutiérrez Larena et al., 2002; Schmitt, 2009). Major glacial refugia in Europe were located in topographically heterogeneous areas in southern and southeastern Europe (Caucasus region) (Huntley and Birks, 1983; Taberlet and Cheddadi, 2002; Tzedakis et al., 2002; Leroy and Arpe, 2007; Médail and Diadema, 2009; Arpe et al., 2011). By contrast, in the northern Andes of Colombia, another example of low latitude mountain systems (~5°N), the highest vegetation belt kept nearly the same altitudinal extension as today during the LGM, i.e. between 2000 and 3000m (Hooghiemstra et al., 2006).

Fig. 5. Pollen percentage and concentration variations for a selection of taxa from a long pollen record of Lake Urmia (Djamali et al., 2008a). A. chronostratigraphy, B. Marine Isotope Stages, C. *Cousinia* pollen percentages (gray-colored curves) and concentrations (bars). Darker gray show the real percentages and lighter gray show three-fold exaggeration. D. and E. show the pollen percentages (gray-colored curve) and concentrations (bars) of trees and upland herbs. F. Ratio of *Cousinia*/Upland herb concentrations. Note that *Cousinia* displays a more continuous curve during glacial periods and sporadic occurrences during the interglacial periods (C) and its role in the landscape is much less important during the interglacial intervals (F).

In the low latitude mountain ranges of SW Asia, the snowline was considerably higher than in Europe and glacier extension was less developed. The lower extent of glacier advances may have resulted from lower precipitation compared to northern latitudes of Europe in glacial times. Likewise, the vegetation belts of the Irano-Turanian region in the Alborz Mountains lie about 1000 m higher than their equivalent belts in the European Alps (Klein, 2001). In SE Iran, the snowline dropped ~1500–1600m to the altitudes of ~2950–3050 m a.s.l. during the last glacial and penultimate glacial periods, respectively (Kuhle, 2008). The Last Glacial snowline in the Hindu Kush Mountains of Afghanistan, which form a main diversity center for *Cousinia* (Knapp, 1987), dropped about 1000 m and was located between ~4000 and 4600m a.s.l. (Porter, 2004). Therefore, we can assume that during the late Pleistocene glaciations the snowline descent in SW Asia left a wide altitudinal range uncovered by ice which could have been colonized by downward-migrating Irano-Turanian high altitude species including *Cousinia*. The Quaternary climatic oscillations therefore, caused a downward shift rather than elimination of the montane and sub-alpine vegetation belts (“Oro-Irano-Turanian” and “Alti-Irano-Turanian” sensu Klein, 2001). In NW Iran, the snowline descent has been estimated to ~1200 m (Wright, 1961). Lake Urmia, located at an altitude of 1250m a.s.l., would have been surrounded by plants which now grow above 2450 m a.s.l. Today, this vegetation in the Alborz Mountains includes the Lower Alti-Irano-Turanian zone (2500–3200 m a.s.l.), dominated by *Juniperus excelsa* open woodlands, and the Upper Alti-Irano-Turanian zone (>3200m a.s.l.; Klein, 2001). Both

of these zones are dominated by Irano-Turanian thorny cushion plants such as *Astragalus*, *Onobrychis*, *Acantholimon*, and *Cousinia*.

Taking these factors into consideration, we agree with El-Moslimany's (1987) interpretation of pollen diagrams of NW Iran, in which it was suggested that the upland vegetation of this region during the last two glacial periods had physiognomic similarities to the vegetation of these high-altitude zones. The reduced impact of glaciations in the Irano-Turanian mountains left vast ice-free areas which were inhabited by vegetation currently found at higher elevations, in which *Cousinia* species constituted an important element.

4.2. *Cousinia* species diversity and topographical heterogeneity of SW Asia

In an analysis of the modern geographical distribution of *Cousinia* species in SW Asia, Knapp (1987) made the following observations: (i) The distribution of *Cousinia* is almost perfectly limited to the Irano-Turanian phytogeographical region, a pattern shared with other typical Irano-Turanian genera (e.g., *Astragalus*, *Acantholimon*, *Acanthophyllum*, *Eremostachys*, *Eremurus*; [Fig. 1](#)). (ii) The great majority of *Cousinia* species are found in the mountain regions of Iran, Afghanistan, and Central Asia. The number of *Cousinia* species rapidly decreases towards lower altitudes, and very few species are found in temperate desert areas of Iran and Central Asia ([Figs. 1](#) and [2](#)). (iii) Most of the recorded *Cousinia* species have very restricted distribution ranges and constitute local endemics. The high rate of endemism of *Cousinia* can be exemplified by the high number of narrow endemic species (~110 spp.) of sect. *Cynaroideae* in SE Turkey, N Iraq, and NW Iran (Mehregan, 2008).

Our topographical analysis of *Cousinia* species richness clearly indicates that diversity is highest in areas of higher elevation, but also in those with more variability in elevation ([Figs. 2B](#) and [3](#)). Thus, topography appears to be linked to the spatial distribution of *Cousinia* species diversity. This fact is confirmed by the modern distribution patterns of *Cousinia* spp., which commonly show relatively restricted ranges (Knapp, 1987; see also the maps in Davis et al., 1965–1988; Attar and Ghahreman, 2006; Mehregan, 2008). A high frequency of small-range species and local endemics of *Cousinia* is the result of topographically induced habitat heterogeneity, which permits the adaptation of species to different habitats. This link between topographical heterogeneity and high plant biodiversity, high number of small-range and rare species, and high rate of speciation has previously been demonstrated in many studies (e.g. Qi and Yang, 1999; Coblenz and Riitters, 2004; Ohlemüller et al., 2008). Topography creates spatial and ecogeographic barriers between plant populations and increases the probability of speciation via allopatry (Stebbins, 1950; Rieseberg and Willis, 2007; Hendry, 2009).

Climate change and tectonism are the most important factors that can affect distribution patterns, and ongoing debates center on their relative importance for speciation and endemism (e.g. Kohn and Fremd, 2008; Badgley, 2010; Hoorn et al., 2010). The comparison of estimated ages of speciation/divergence and tectonic phases and climatic oscillations is therefore important to understand the causes of speciation processes. López-Vinyallonga et al. (2009) recently provided a comprehensive study of the phylogeny of the *Arctium*–*Cousinia* complex. On the basis of the phylogenetic signal of two DNA regions and molecular dating approaches, they demonstrated that the *Arctium*–*Cousinia* complex and more particularly *Cousinia* s.str. has undergone a “massive radiation” in recent geological time. The major diversification of this clade, containing about 200 species, most probably occurred after ~7 million years ago (Ma), so that much speciation took place in the late Tertiary and probably the Quaternary. As this time span is contemporaneous with an intensified

interval of tectonic activities in SW Asia, we review here the tectonic evolution of the Turkish–Iranian Plateau to understand how this contributed to the present diversity of the Irano-Turanian flora.

4.3. Role of tectonic evolution of SW Asia for plant diversity

The topography of SW Asia reflects post-Miocene earth-surface processes and tectonic deformations related to the Arabia–Eurasia collisional convergence (e.g. Falcon, 1974; Bozkurt, 2001; Koçyigit et al., 2001; Guest et al., 2007). This plate convergence, which began in the Late Cretaceous (~90 Ma; Şengör and Yılmaz, 1981; Dewey et al., 1986; Dewey et al., 1989), resulted in the progressive closure of the Neotethyan oceanic basins, the amalgamation of the surrounding continental fragments, and the continental collision (e.g. Berberian and King, 1981; Bozkurt, 2001). This led to the subsequent emplacement of the majority of the mountain ranges in the Turkish–Iranian Plateau, including the Anti-Taurus, Zagros, Alborz, and Kopeh Dag ranges. Spatial variation in lithospheric characteristics of the Plateau involved in the continental deformation created a large variety of physiographic domains roughly similar to the present-day configuration. The Arabia–Eurasia collision started at ~35 Ma, with the final closure of the Neo-Tethys at 20 Ma (e.g., Mouthereau and Lacombe, accepted for publication and references therein). The main stages of crustal thickening (~25 Ma) and the uplift of the Iranian Plateau (~15–12 Ma), however, took place between the Late Oligocene and Late Miocene (~25–12 Ma; Dewey and Şengör, 1979; Woodruff and Savin, 1989; McQuarrie et al., 2003; Homke et al., 2004; Fakhari et al., 2007; Verdel et al., 2007). Afterward, a complex sequence of deformation took place leading to further uplift (e.g., Axen et al., 2001; Guest et al., 2007) and tectonic rearrangement (e.g., Ritz et al., 2006; Shabanian et al., 2009 and references therein) of the mountain ranges.

The timing of the formation of all mountain ranges was, however, not synchronous, either within the Plateau or between the Plateau and Central Asia. For instance, the region presently occupied by the central axis of the Alborz Mountains already separated the Caspian basin from central Iran by the Eocene (Stöcklin, 1974; Berberian, 1983; Brunet et al., 2003), whereas the formation of the western Alborz mountains started only in the late middle Miocene (~12 Ma; e.g., Guest et al., 2007). In the fold-and-thrust belt of Zagros ([Fig. 2B](#)), the main regional shortening has been suggested to have taken place since the late Miocene and during the Pliocene (Falcon, 1974; Haynes and McQuillan, 1974; Stoneley, 1981; Hessami et al., 2001; Sherkati and Letouzey, 2004).

This description suggests that despite the lack of regional synchronicity, the geological age estimates for the main orogenic belts of the Turkish–Iranian Plateau predates the age estimated for the rapid radiation of *Cousinia* at ~7 Ma (López-Vinylallonga et al., 2009). A similar relationship has been observed between the estimated age of a huge monophyletic group of *Lupinus* in the Western Hemisphere (~1.18–1.76 Ma) and the major uplift of the Andes that started ~3–5 Ma and continues to the present (Hughes and Eastwood, 2006). The floristic evaluation of long palaeoecological records in the basin of Bogotá (2550 m; Eastern Cordillera, Colombia) has shown that the late Cenozoic Andean uplift has played a major role in the evolution and distribution of the flora of the northern Andes (Hooghiemstra et al., 2006). In case of *Cousinia*, speciation would have taken place in a region in which the topography was already varied. The effect of topographical features on diversity is most evident in the Zagros Mountains where different stages of topographical evolution can be observed (e.g., Hessami et al., 2001). For instance, the southwestern frontal part of the Zagros Mountains (FZ; [Fig. 2B](#)), which is clearly younger (<12 Ma) than its axial part (>20 Ma), harbors the lowest species diversity whereas the adjacent older mountain systems, with almost the same topographical conditions, show highest species diversity. This raises the possibility that

the continuing rapid uplift of the southern Zagros will favor the propagation of the Irano-Turanian flora into the Saharo-Sindian region.

4.4. Climatic oscillations and evolution of the Irano-Turanian flora; inferences from the palaeoecology and phylogeny of Cousinia as a system model

The ecological and evolutionary responses of flora and fauna to Quaternary climatic instability have long been a matter of debate. Several ecological responses of species to Milankovitch oscillations can be recognized: persistence *in situ*, moderate shifts in habitat, migration, and extinction (Jackson and Overpeck, 2000; Bennett, 2004). Some authors have suggested that 'extinction' and, to a lesser extent, 'persistence' probably were the dominant modes of response to these climatic oscillations, especially during the glacial periods (Bennett, 2004; Willis and Niklas, 2004), but others have demonstrated that the migration of plant populations was the most common biotic response (e.g. Huntley and Webb, 1989; Jackson et al., 1997; Brewer et al., 2002). From an evolutionary point of view, it has also been suggested that the multiple glacial-interglacial cycles did affect the genetic diversity of plant populations (e.g. Petit et al., 2003) but did not profoundly influence speciation rates (e.g. Bennett, 1990; Dynesius and Jansson, 2000; Bennett, 2004; Willis and Niklas, 2004; Barnosky, 2005; Lemmon et al., 2007). This has been attributed to the relatively short duration of isolation during glacial periods and gene flow in the short interglacial intervals which inhibited the formation of reproductive barriers (Dynesius and Jansson, 2000; Willis and Niklas, 2004). However, the steady accumulation of dated molecular phylogenies has shown that the Quaternary, instead, was a period of rapid speciation in ecologically and climatically different environments suggesting a link between climate and diversification (Richardson et al., 2001; von Hagen and Kadereit, 2001; Kadereit and Comes, 2004; Hughes and Eastwood, 2006; Zhang et al., 2007; Brochmann and Brysting, 2008; Bittkau and Comes, 2009; Janssens et al., 2009; Valente et al., 2010).

In case of *Cousinia*, it seems that the late Tertiary orogenic movements in SW Asia, rather than Quaternary climatic oscillations, account for most of the speciation in the genus. The late Tertiary (b20 Ma) corresponds to the onset of severe continental conditions (high range of daily and seasonal temperature variations) in SW Asia (Strömberg et al., 2007) which developed after the retreat of the Oligo-Miocene seas from vast areas of SW Asia (Bosboom et al., 2011). Increased continentality has been proposed by Knapp (1987) as the main bioclimatic factor controlling the geographic range of *Cousinia*. Despite the lack of a synthesis treating the palaeoclimatic history of SW Asia during the Tertiary time, the presence of very thick Mio-Pliocene clastic red beds over large areas of Iran provides evidence of such prevailing continental conditions (Berberian and King, 1981; Amini, 1997). A recent sedimentological and geochemical study of this formation in north-central Iran suggested some variation in the intensity of aridity during the mid- to late Miocene period that seems to be a result mainly of the uplift of the Alborz Mts in northern Iran and to lesser extent of perturbations in atmospheric circulation patterns (Ballato et al., 2010). However, the general climate of the region remained semi-arid in spite of this variation. At a global scale, temperatures during the early to mid-Miocene (~24–13 Ma) were significantly higher than in the Quaternary period (Fig. 6) and started to decrease after the 'Mid-Miocene Climatic Optimum', the onset of the East Antarctic ice-sheet formation (Zachos et al., 2001). Hence, during the early to mid-Miocene, global climate was relatively stable with no large-scale cooling/warming events (Fig. 6). During the Late Miocene–Pliocene, although the climate showed some degree of oscillation affecting the terrestrial vegetation, the contrasts between cold and warm stages were not as severe as in the Quaternary (e.g. Leroy and Dupont, 1994; see also Fig. 2 in Zachos et al., 2001). In summary, the climatic conditions during the Miocene–Pliocene time

interval would not have caused significant range shifts favoring allopatric speciation in *Cousinia*.

Fig. 6. Synthetic picture to compare the tectonic history, global climate, and the diversification ages of the Arctium–Cousinia complex. Climatic information are derived from Zachos et al. (2001) (Fig. 2). The solid line corresponds to the smoothed raw oxygen isotope data obtained from a compilation of several DSDP and ODP sites mainly measured on two benthic taxa (*Cibicidoides* and *Nuttallides*). Phylogenetic tree is re-drawn from Fig. 5 in López-Vinyallonga et al. (2009). Note that the most important diversification event in *Cousinia* occurred after the uplift of the Turkish–Iranian Plateau and the formation of the mountain ranges.

The Quaternary glacial–interglacial cycles, which started ~2.6 Ma at the beginning of the Quaternary (Gibbard et al., 2009), became intensified during the “Mid-Pleistocene Revolution” at ~1 to ~0.6 Ma (Maslin, 2009), and their effects on terrestrial vegetation became significantly stronger during this climatic transition (e.g. de Beaulieu et al., 2005). This time is, by far, younger than the estimated age for major speciation events in *Cousinia*, which predate the Quaternary glaciations (López-Vinyallonga et al., 2009). Therefore, we suggest that the Quaternary climatic oscillations would not have had an important impact on speciation in *Cousinia* and other large Irano-Turanian plant taxa. The few speciation events of *Cousinia* during the glacial–interglacial cycles are likely to have mainly occurred in high-altitude “interglacial refugia” (Bennett and Provan, 2008). These are the deglaciated high-elevation mountain areas re-colonized by upward-migrating xeric and cold-adapted species during the interglacial periods. Presence of such high-altitude “interglacial refugia” in the NW Irano-Turanian region has already been demonstrated based on the presence of sub-fossil remains of boreal-arctic relict species (Djamali, 2008; Kürschner and Djamali, 2008). Restriction to these refugia can potentially cause genetic differentiation during the interglacial intervals. This hypothesis of speciation in “interglacial refugia” has important implications, as it suggests that the evolutionary response of plant taxa to climatic oscillations may vary considerably between mountain systems of high versus low latitudes. Hence, in contrast to the Alps where speciation has been suggested to have taken place in geographically isolated low-altitude “glacial refugia” (e.g. Kadereit et al., 2004), in the southern Irano-Turanian mountain systems diversification would have been concentrated in geographically isolated high-altitude “interglacial refugia”.

5. Conclusion

Our current knowledge of the diversification and palaeoecology of the Irano-Turanian flora is very scanty and the hypotheses proposed in this study remain to be tested in future studies. However, longterm variation in *Cousinia* pollen records from the Irano-Turanian region help to understand the general response of the flora of similar ecology

and geographical distribution (e.g. *Astragalus*, *Acantholimon*, *Acanthophyllum*) of this region to Quaternary glaciations. The available palaeoecological records show that *Cousinia* was present and more abundant during glacial periods, suggesting that the Irano-Turanian flora not only survived the Quaternary glaciations, but that *Cousinia* as well as probably several other important Irano-Turanian taxa were more widespread in glacial-age landscapes than they are today. According to a dated molecular phylogeny of *Cousinia* (López-Vinyallonga et al., 2009), the major radiation of this genus dates to long before the beginning of the Quaternary climatic instability. Hence, it is likely that the continued presence of the heterogeneous topography of SW Asia since the late Tertiary, coupled with a relatively stable continental climate, caused long-term uninterrupted isolation, leading to high rates of allopatric speciation (Fig. 6), and adaptation to spatially restricted ecological niches. The climatic instability of the Quaternary had only a minor impact on isolation, and populations of endemic species persisted in their native regions. Further diversification (e.g. allopatric or sympatric speciation) during the Quaternary glacial–interglacial cycles probably took place during interglacials in high-altitude “interglacial refugia”.

6. Uncited references

Akhani, 2007
 Al-Nafie, 2008
 Coblentz, 2005
 Jackson et al., 2005
 Jonsson and Dynesius, 2002
 Léonard, 1981–1989
 Léonard, 1993
 Magyari et al., 2008

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