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# A pollen rain-vegetation study along a 3600 m mountain-desert transect in the Irano-Turanian region; implications for the reliability of some pollen ratios as moisture indicators

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## Keywords:

*Chenopodiaceae/Artemisia*  
pollen ratio Desert steppe,  
Iranian flora, Montane steppes,  
Pollen assemblage, Vegetation

## Abstract

A set of 42 modern pollen samples has been investigated to determine the relationship between pollen percent-ages and vegetation composition along a 3600 m elevational mountain-desert transect in central Iran. The studied transect shows three main vegetation groups including a "high altitude zone" (embracing subnival, alpine and montane subzones), a "xerophytic desert steppe zone", and a "halophytic zone", correlated with the groups defined in Correspondence Analysis (CA) of vegetation dataset and Principal Component Analysis (PCA) of pollen dataset. The subnival subzone is characterized by high values of Asteraceae, Brassicaceae and Cyperaceae pollen, while alpine and montane subzones are characterized by the highest pollen diversity with a predominance of grass pollen along the whole transect. The halophytic zone is dominated by Chenopodiaceae pollen while xerophytic desert steppe shows a high occurrence of *Artemisia* pollen. The comparison of pollen percentages with the corresponding vegetation plots shows a high congruency between pollen and vegetation compositions of alpine subzone and undisturbed xerophytic desert steppe but a weak correlation between those of the subnival and montane subzones and human affected xerophytic desert steppe. In addition, pollen representation of frequently encountered or important plant taxa in the Irano-Turanian region is provided. The widely used *Chenopodiaceae/Artemisia* = C/A pollen ratio, as an aridity index, is shown to be unreliable in the Irano-Turanian steppes. Our results suggest that a combined graph of all four indices (C/A pollen ratio,  $Poaceae/Artemisia = P/A$ ,  $Poaceae/Chenopodiaceae = P/C$  and  $(A + C)/P$  ratios) can represent the vegetation and climate relationships more accurately. In conclusion, surface pollen composition can reflect the actual vegetation zones/subzones in Irano-Turanian steppes. Together, P/A and P/C ratios are more confident to differentiate mesic from arid steppes, while C/A and  $(A + C)/P$  ratios provide a useful tool to differentiate halophytic desert vegetation developed in endorheic depressions with saline soils from xerophytic desert steppe developed in well-drained soils.

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## 1. Introduction

A reliable regional calibration scheme of different plant taxa contributing in modern pollen assemblages is essential to correctly interpret fossil pollen spectra. In spite of expanding fossil pollen studies in the Middle Eastern countries since sixties (Wright, 1961; Van Zeist, 1967; Van Zeist and Bottema, 1977; El-Moslimany, 1983; Bottema, 1986; Bottema and Woldring, 1990; Tzedakis, 1994; Ramezani et al., 2008; Djamali et al., 2008, 2009b, 2016), modern surface pollen studies are quite scarce in the region (Wright et al., 1967; El-Moslimany, 1990; Davies and Fall, 2001).

In Iran, only four studies on modern pollen vegetation calibration have been published, two in the Euro-Siberian and two in the Irano-Turanian floristic regions. In the Euro-Siberian floristic region in northern Iran, comparison of surface pollen percentages with vegetation composition along a forest steppe transect in Golestan National Park in north-eastern Iran using descriptive and numerical approaches, helps to distinguish different vegetation types, with the worst correspondence found in transitional zones or ecotones (Djamali et al., 2009a). Ramezani et al. (2013) studied a 20 km long altitudinal transect in the South Caspian region which included only forest communities, providing some data on pollen production and dispersal of common place trees in central Hyrcanian forest in northern Iran.

In the Irano-Turanian region a set of sixty samples along four transects in the Zagros Mountains of western Iran was studied by Wright et al. (1967). This was a first attempt to interpret the fossil pollen data

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obtained from a few sediment cores from lakes Zaribar (also Zeribar) and Mirabad. They found that pollen rain assemblages taken from Mesopotamian steppes and piedmont pseudo-savannas contained high amounts of Plantago pollen, while those of oak woodlands and plateau steppes were characterized by high percentages of *Quercus*, and *Artemisia*, and chenopod pollen, respectively. However, their study suffered from two main limitations including lacking of numerical analysis and poor floristic data which was available at that time. Another study was done 15 years later in an arid region in northeastern corner of Central Iran, as a complementary study to palynological investigation of a late Holocene alluvial sediment core by Moore and Stevensen (1982). They distinguished five vegetation types on limestone outcrops, Ephedra zone, Zygophyllum zone, saline areas and disturbed areas in which 14 plots were taken subjectively, rather than a real transect along an ecological gradient. They showed that pollen of *Artemisia* and Chenopodiaceae dominates the pollen percentages and that C/A ratio is variable in different vegetation types with the highest value in saline areas with dominance of members of Chenopodiaceae. They also noted that arboreal pollen is very scarce in the region with interesting presence of some tree pollen coming from south Caspian temperate forests by long distance dispersal.

Pollen ratios of Chenopodiaceae, *Artemisia* and Poaceae have been widely used as ecological indices in palynological studies (El-Moslimany, 1990; Van Campo and Gasse, 1993; Davis and Fall, 2001; Djamali et al., 2008; Zhao et al., 2008). The Chenopodiaceae/*Artemisia* (C/A) pollen ratio as an aridity index in open vegetation types (El-Moslimany, 1990) has received the highest attention by many authors, although its reliability in different environments has rarely been evaluated (Djamali et al., 2008; Zhao et al., 2012). A semi-quantitative aridity index ((A + C)/P) has also been proposed to determine moisture variability and delimitation of steppe from desert steppe. This palynological index is suggested to be supported as a trustworthy moisture index by sedimentological data and palaeoclimate reconstructions at millennial scale (Fowell et al., 2003).

Presenting a detailed study on quantitative pollen-vegetation relationships in the Irano-Turanian floristic region is the subject matter of this paper. This region forms one of the richest floristic regions of the world with unique and remarkably diversified steppe vegetation covering an area of N6 million km<sup>2</sup>, housing more than 17,000 species in the Middle East and Central Asia (Davis et al., 1994). Here, we will study both vegetation and modern pollen assemblages along an exceptionally long mountain-desert transect of 3600 m elevation range and N150 km horizontal distance from Alborz mountains in northern Iran to the central Iranian deserts crossing a range of vegetation and bioclimatic zones (see Fig. 1B) in the heart of the Irano-Turanian region (sub-region IT2 sensu White and Léonard, 1991). We aim at:

- 1) Determining pollen contribution of different Irano-Turanian floristic elements and vegetation communities in surface samples to provide a calibration scheme for more accurate interpretation of fossil pollen diagrams in the region.

- 2) Verifying the ecological significance of Chenopodiaceae, *Artemisia* and Poaceae pollen values and ratios which are used by palynologists as aridity indices (El-Moslimany, 1983, 1987, 1990; Fowell et al., 2003; Djamali et al., 2008; Zhao et al., 2012).

## 2. Study area

### 2.1. Physical setting

Our study area (Fig. 1) stretches from subnival zone close to upper vegetation limit of Damavand Volcano (35° 56' 0.60"N, 52° 6' 21"E, 4327 m) to Salt Playa Lake (Daryacheh Namak) in western Kavir National Park in central Iran (34° 40' 42"N, 52° 4' 21"E, 835 m). Damavand is a potentially active stratovolcano, located in the Central Alborz Mountains, in 60 km north-east of Tehran. The Damavand peak with 5671 m above sea level elevation is the highest summit in the Middle

East and also the highest volcano in Asia separating interior Iranian deserts from the Caspian Sea. Alborz Mountain Range, 650 km long, separates the south Caspian lowland (down to 26 m below sea level) with montane temperate deciduous forests on the northern flanks (Akhani et al., 2010) from Irano-Turanian mountain steppes on the southern flanks (Akhani et al., 2013). The central Iranian plateau contains the Kavir National Park/Kavir Protected Area with a surface area of 670,000 ha, located in the eastern edge of the Salt Playa Lake, which has been protected since 1964 (Rechinger and Wendelbo, 1976; Firouz, 1976). About 75% of this area which is part of an elevated plateau of 650 to 850 m a.s.l., is almost equally composed of interfingering peneplain surface, saline soils, and salt-encrusted depressions (Krinsley, 1970). While the flanks of Damavand are mainly composed of trachyandesitic lava flows and pyroclastic material with nutrient-rich soils, the Alborz Mountains are of various geological compositions from Tertiary volcanoclastic sediments to Mesozoic limestone and marl formations (Allen et al., 2003; Davidson et al., 2004).

According to regional weather stations along the selected transect (Rineh, Larijan, Abali, Damavand, Garmsar and Siah Kuh), mean annual rainfall decreases steadily towards low elevations, ranging from 548, 538, 373, 117 to 68 mm/year respectively; while mean annual temperature increases in the same direction from 9.89, 9, 13, 19 and 19 accordingly. The meteorological stations along the studied transect as well as the climate diagrams showing the length of dry and humid periods are presented in Fig. 1. There is no meteorological data available for high elevations of our sampling sites but obviously the pattern of temperature and precipitation fluctuations is consistent along the whole transect. Similarly, Khalili (1973) showed that high altitudes of Alborz Mountain Range show strong continentality and that the mean annual precipitation increases with altitude in southern slopes of Alborz. In a bioclimatic point of view, our study transect crosses the Mediterranean Pluviseasonal-Continental, Mediterranean Xeric-Continental, and Mediterranean Desertic-Continental moving from north to south according to Global Bioclimatic Classification System (Djamali et al., 2011). The bioclimate is thus continental everywhere with increasing aridity and longer dry seasons southward.

## 3. Material and methods

### 3.1. Vegetation measurements and surface pollen sampling

#### 3.1.1. Field works

From August to November 2014, an altitudinal study transect was defined along N150 km aerial distance from Damavand Volcano to Salt Playa Lake in central Iran across which the vegetation composition was quantified and the surface pollen samples were collected within 42 plots (Figs. 1A, B and D, and 2). All vegetation plots were of the same size (20 × 20 m) except for samples 14 (10 × 10), 23 (10 × 10), 24 (10 × 10 m) and 35 (10 × 30 m) in which the physical conditions did not permit following exactly the protocol (Table 1). Since the selected transect was cut by roads and residential areas, sampling was done at 50–2000 m distances from the road side to avoid disturbances on the sampled vegetation plots.

#### 3.1.2. Vegetation measurements and zonation

Vegetation measurements were performed following the methodology of Zürich-Montpellier school of plant sociology (Braun-Blanquet, 1964) along elevational gradient from 4327 m to 765 m a.s.l. For each vegetation plot all possible vegetation data were gathered and all taxa were identified based on regional references especially Flora Iranica (Rechinger, 1963–2015). The nomenclature follows mostly the Flora Iranica with updates of family Chenopodiaceae in Akhiani et al. (2007). All 42 plots data were stored in TURBOVEG 2.15 for windows database (Hennekens and Schaminée, 2001). The final table from TURBOVEG was imported to JUICE 7.0.84 software (Tichý, 2002). Using TWINSpan method (Hill, 1979) the halophytic communities are separated from the

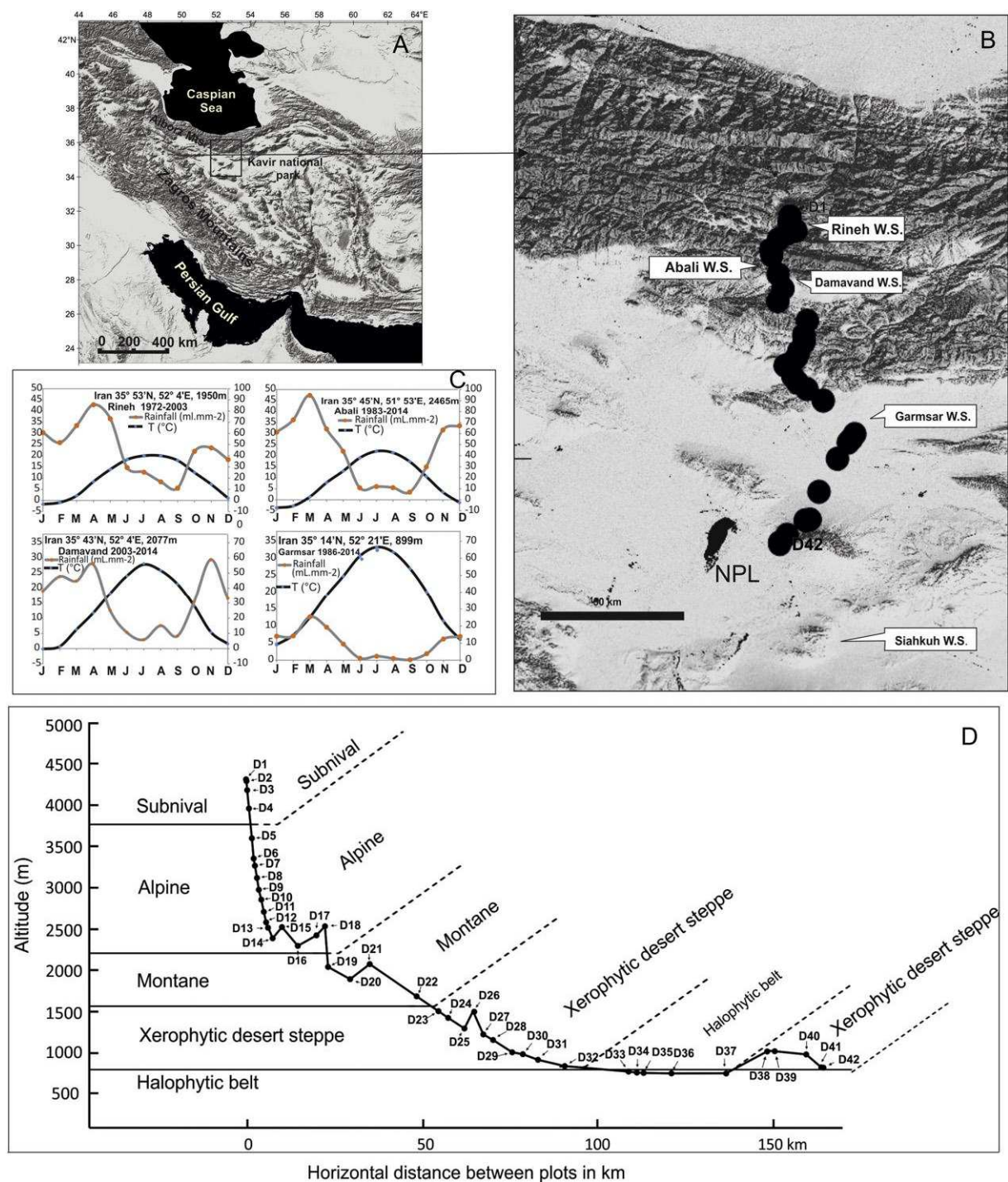


Fig. 1. A. Location of the pollen-vegetation transect from Damavand Volcano to Salt Playa Lake (Daryacheye Namak) in Central Iran. B. Topographic map of the studied transect as well as locations of the meteorological stations along the transect (NPL: Namak Playa Lake). C. Climatic diagrams of meteorological data showing mean monthly temperature and mean monthly precipitation curves as well as the length of dry and humid periods. D. Topographic profile representing the elevational position of each sampling point against the main vegetation belts along the studied transect.

rest of plant communities by cut level 2. The montane to subnival main vegetation groups were subsequently separated from desert steppe plots by cut level 3. We continued clustering up to 9 cut levels and finally determined 5 vegetation zones. Furthermore, in each zone, communities/community groups were separated manually based on dominated and/or characteristic species. Because of the absence of a reliable syntaxonomical system and the fact that our plots could not cover all plant communities existing from the top of Damavand to the lowland desert, we did not classify all plant communities following Braun-Blanquet's nomenclature, but rather we named each community or

community group according to representative dominant and physiognomically important species.

### 3.1.3. Surface pollen sampling

Surface pollen samples were taken randomly at least from 20 points within the vegetation plots, either from moss polsters, plant detritus or soil samples according to the availability of each material. When all materials were present, the priority was given to moss polsters, plant detritus and soil in order of importance. The collected modern pollen



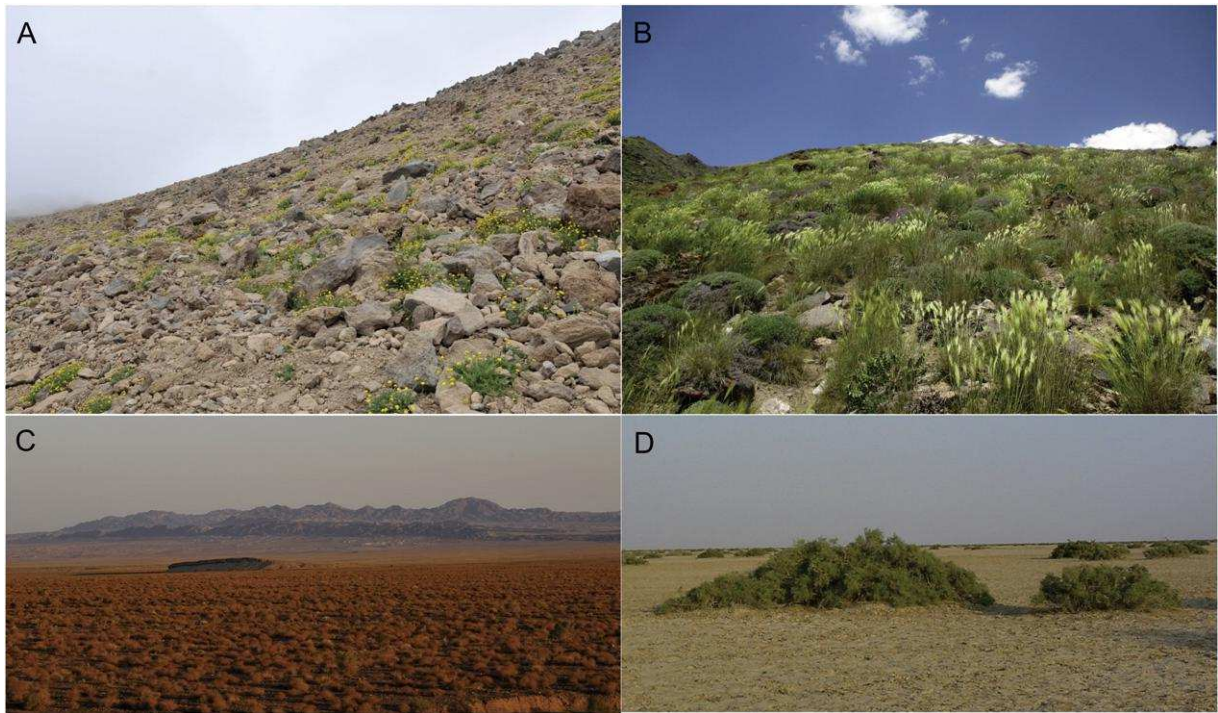


Fig. 2. Photographs of the vegetation belts along the studied transect. A. Subnival community near the peak of Damavand Mt. dominated by *Achillea aucheri* and *Dracocephalum aucheri* (*Dracocephaletum aucheri*). B. Alpine communities dominated by grasses and cushion-like plants. C. *Artemisia* steppe near Ghasre Bahram, Kavir National Park, dominated by *Artemisia inculta*. D. Halophytic community near Mobarakieh dominated by *Halostachys belangeriana* with scattered *Tamarix* shrubs. Photo credit: A, C, D (H. Akhani), B (M. Dehghani).

samples were then thoroughly mixed and kept in paper envelopes for subsequent laboratory treatments.

### 3.2. Pollen analysis of surface samples

Pollen sample preparation followed the modified procedure outlined by Faegri and Iversen (1989) and that of Moore et al. (1991). The samples were treated in 10% NaOH for an hour followed by multiple washing in water, sieving with a 160  $\mu\text{m}$  mesh and treating with 37% HCl for 24 h in room temperature. Subsequently, samples were treated with 40% HF followed by retreatment with 37% HCl. Finally the samples were acetolysed and sieved at 10  $\mu\text{m}$  mesh filter before being mounted between slides and coverslips in glycerol as a mounting medium. Pollen grains were identified and counted using a Nikon Eclipse E200 microscope at a magnification of  $\times 500$ . On the average, 490 pollen grains per sample were tallied including the aquatic plants encountered in a few sampling quadrats (samples 4, 9, 12, 16, 19–20, 25–27). Pollen identifications were performed using the European and Mediterranean pollen collections as well as the “Middle East Pollen Reference Collection” (MEPRC) hosted at Institut Méditerranéen de Biodiversité et d’Ecologie with occasional use of pollen atlases of Europe and North Africa (Moore et al., 1991; Reille, 1992, 1995, 1998; Beug, 2004). Pollen percentages of each pollen taxon were then calculated based on the total pollen sum of terrestrial and aquatic taxa. Undetermined and damaged pollen and fern spores were excluded from the total pollen sum. A pollen diagram was then created (Fig. 4) based on calculated pollen percentages in TILIA-TGView software (Grimm, 2004, 2005).

### 3.3. Multivariate statistical analyses

We applied a number of multivariate analyses to two matrices of pollen and vegetation data. First and second runs of Correspondence Analysis (CA) on vegetation data revealed that samples taken in saline soils (plots D33–37) as well as plot number 14, sampled from an abandoned sand exploitation area, act as outliers and mask proper clustering of other plots (Fig. 1S). However, Principal Component Analysis (PCA) on

pollen data is not congruent with CA graph (Fig. 2S). Therefore, we decided to remove plot numbers D33–37, and D14 from both pollen and vegetation datasets. Finally, the matrix of pollen percentages versus vegetation plots was composed of 61 pollen types and 36 samples. Rare taxa (occur in only one sample) were removed from the analyses. The matrix was square-root transformed in order to stabilize the variance.

The vegetation matrix (72 plant taxa and 36 samples) was composed of plant abundances of Zürich-Montpellier vegetation-scale technique against plot numbers. In our multivariate analyses of vegetation data, we deliberately deleted most species including those with low abundances and those with occurrence in a limited number of plots. In our data matrix we used the same values recorded for Braun-Blanquet cover abundance scales (1, 2, 3, 4 and 5). The value 0 was arbitrarily given to species with less than 1% contribution in the vegetation, which are traditionally shown by a “+” instead of a figure.

PCA and CA were applied to 61 (variables)  $\times$  36 (samples) matrix of pollen and 72 (variables)  $\times$  36 (samples) matrix of vegetation data, respectively, using the “Ade-4” and “factoextra” packages from the R software version 3.2.2 (R Development Core Team, 2012). Co-Inertia Analysis (CoIA) (Dolédéc and Chessel, 1994; Dray et al., 2003) was performed with the same software using Ade-4 package. CoIA allows studying the common structure of a pair of data tables and to measure the adequacy between two data sets. CoIA is very flexible and is suitable for quantitative and/or qualitative or fuzzy environmental variables (Dray et al., 2003). A Monte Carlo permutation test, where the rows of one matrix are randomly permuted followed by a re-computation of the total inertia (Thioulouse et al., 1995) was used to check the significance of the co-structure of this CoIA.

## 4. Results and discussion

### 4.1. Vegetation communities and their floristic composition

A total of 312 plant taxa were encountered and identified (33 species only to generic level) in the 42 vegetation plots along the selected

A summary description of plant communities, location of sampled plots and the materials from which the pollen rain samples were taken. D = Debris, L = Lichen, M = Moss polster, S = Soil. Plots coordination: 1: 35°56'N, 52°62'1"E; 2: 35°55'58"N, 52°62'2"E; 3: 35°55'50"N, 52°62'5"E; 4: 35°53'34"N, 52°62'6"E; 5: 35°55'8"N, 52°61'4"E; 6: 35°54'44"N, 52°61'6"E; 7: 35°54'32"N, 52°61'9"E; 8: 35°54'14"N, 52°62'3"E; 9: 35°53'59"N, 52°63'4"; 10: 35°53'36"N, 52°63'0"E; 11: 35°53'13"N, 52°63'30"E; 12: 35°52'35"N, 52°64'1"E; 13: 35°52'46"N, 52°64'3"E; 14: 35°52'43"N, 52°74'9"E; 15: 35°52'16"N, 52°69'E; 16: 35°50'50"N, 52°34'3"E; 17: 35°48'22"N, 52°15'3"E; 18: 35°47'5"N, 52°29'E; 19: 35°42'43"N, 52°33'9"E; 20: 35°39'25"N, 52°44'8"E; 21: 35°36'31"N, 52°33'6"E; 22: 35°32'5"N, 52°10'38"E; 23: 35°28'47"N, 52°94'7"E; 24: 35°27'17"N, 52°95'5"E; 25: 35°25"N, 52°83'8"E; 26: 35°23'44"N, 52°811'90"E; 27: 35°22'27"N, 52°71'E; 28: 35°21'43"N, 52°52'5"E; 29: 35°19'10"N, 52°71'8"E; 30: 35°17'49"N, 52°82'3"N, E; 31: 35°16'21"N, 52°10'36"E; 32: 35°13'44"N, 52°14'29"E; 33: 35°6'4"N, 52°22'E; 34: 35°4'57"N, 52°21'14"E; 35: 35°4'7"N, 52°20'29"E; 36: 35°0'22"N, 52°17'56"E; 37: 34°52'45"N, 52°13'35"E; 38: 34°46'21"N, 52°11'31"E; 39: 34°46'10"N, 52°10'22"E; 40: 34°42'50"N, 52°65'E; 41: 34°41'2"N, 52°41'9"E; 42: 34°40'42"N, 52°42'1"E.

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Table 1 (continued)

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Table 1 (continued)

<i>Acantholimon subnigrum</i> 18; 1; <i>Acantholimon scoparium</i> 18; 1; <i>Acantholimon species</i> 30; 1, 2; 2; <i>Acanthophyllum microcephalum</i> 30; 1, 2; 2; <i>Achillea millefolium</i> 13; 1; <i>Achillea species</i> 23; 3; <i>Achillea vernicularis</i> 17; 2, 19; 1; <i>Acinos graveolens</i> 38; 1, 23; 1; <i>Aethionema species</i> 18; 1; <i>Aikania bracteosa</i> 13; 1; <i>Allium Bungei</i> 31; 1, 37; 1; <i>Allium sibiranum</i> 18; 1; <i>Allium foliosum</i> 28; 1, 39; 1; <i>Alysseum curale</i> 12; 1; <i>Alysseum species</i> 39; 1; <i>Amberboa turanica</i> 32; 1, 23; 1, 37; 1; <i>Androsace telephifolia</i> 38; 1; <i>Androsace namus</i> 20; 2; <i>Anthracanthus polygaloides</i> 22; 3, 23; 1; <i>Artemisia arbuscula</i> 13; 1, 18; 1; <i>Artemisia eriophyllifolia</i> 28; 1; <i>Artemisia species</i> 18; 1; <i>Artemisia species</i> 23; 1; <i>Artemisia fragrans</i> 11; 1, 18; 1; <i>Asperugo procumbens</i> 15; 1; <i>Asperula arvensis</i> 11; 1; <i>Astragalus bracteatus</i> 12; 2; <i>Astragalus suberosus</i> 7; 1; <i>Astragalus species</i> 37; 1, 23; 1, 28; 1, 41; 1; <i>Astragalus tricholobus</i> 18; 1, 32; 1, 38; 1, 40; 1; <i>Astragalus verus</i> 18; 2, 21; 2; <i>Astragalus polygalifolius</i> 13; 1; <i>Astragalus leucomela</i> 25; 1; <i>Astragalus species</i> 17; 1; <i>Baealis eriantha</i> 37; 1; <i>Baealis pilosa</i> 37; 1; <i>Baealis integrifolia</i> 15; 1; <i>Balanites squarrosa</i> 3; 1, 23; 2, 23; 1; <i>Balanites chripodum</i> 18; 1; <i>Balanites species</i> 1; 1; <i>Calamagrostis pseudocymbifolia</i> 8; 1, 12; 1; <i>Calligonum polygonoides</i> 19; 4; 2; <i>Campylodactylis stenialis</i> 8; <i>Cassipourea</i> 1; 1; <i>Cassipourea species</i> 33; 1, 1, 23; 1; <i>Cerastium species</i> 38; 1; <i>Centaurea scutellifolia</i> 13; 2, 12; 1, 13; 1; <i>Centaurea species</i> 40; 1; <i>Cephalanthus microcephalus</i> 13; 1; <i>Cephalanthus thymoides</i> 22; 2; <i>Cerastium dichotomum</i> 17; 1; <i>Cerastium arvensis</i> 14; 2, 22; 1, 37; 1; <i>Cerastophala falcata</i> 19; 2, 21; 1; <i>Chorizanthe orientalis</i> 20; 1, 21; 1; <i>Claudia arbuscula</i> 12; 1; <i>Claudia rugulosa</i> 18; 1; <i>Cousinia cylicandrea</i> 21; 1; <i>Cousinia species</i> 37; 1; <i>Crepis acaulis</i> 18; 1, 12; 1; <i>Crotalaria vavayensis</i> 11; 1; <i>Cuscuta species</i> 18; 1, 13; 1, 17; 1; <i>Cyananthus acutus</i> 23; 1; <i>Cyananthus fragilis</i> 4; 1; <i>Delphinium apiculifolium</i> 12; 1; <i>Descurainia sophia</i> 3; 1, 12; 1, 15; 1; <i>Dicentra hirsuta</i> 22; 1, 39; 1; <i>Draba pulchella</i> 4; 1, 5; 1, 41; 1; <i>Dunalia anethifolia</i> 23; 1; <i>Echinops albusensis</i> 17; 2; <i>Echinops lasiophyllus</i> 22; 1; <i>Echinops pungens</i> 13; 1; <i>Echinops viridescens</i> 15; 1, 21; 2; <i>Echinops species</i> 12; 1; <i>Ephedra intermedia</i> 15; 1; 24; 1; <i>Eremurus persicus</i> 16; 1; <i>Erodium species</i> 27; 1, 23; 1; <i>Euphorbia species</i> 21; 2; <i>Ferula gossypifolia</i> 12; 1; <i>Ferula ovina</i> 13; 2, 15; 1; <i>Ferula persica</i> 9; <i>ferula</i> 13; 1; <i>Galium species</i> 7; 1, 18; 1, 17; 1; <i>Galium suberectum</i> 3; 1; <i>Geranium persicum</i> 3; 1; <i>Geranium tuberosum</i> 17; 1; <i>Glaucium elegans</i> 22; 1, 22; 1; <i>Halimolobos parviflorus</i> 13; 1; <i>Helictotrichum oligoneurum</i> 12; 2, 13; 1; <i>Helictotrichum species</i> 30; 1, 21; 1; <i>Helictotrichum aucheri</i> 37; 1; <i>Helictotrichum dasystachyum</i> 28; 1; <i>Helictotrichum suberosum</i> 7; 1, 41; 1; <i>Helictotrichum species</i> 3; 1; <i>Hemerocallis hirsuta</i> 18; 1; <i>Hemerocallis hirsuta</i> 18; 1; <i>Hippocrepis microcarpa</i> 12; 1; <i>Holcistidium viciifolium</i> 19; 1, 22; 1; <i>Hypochaeris pumilio</i> 23; 1, 39; 1, 37; 1; <i>Tassia capudefuensis</i> 1; 1; 12; 1; <i>Chimelia species</i> 21; 1; <i>Kali tragus</i> 14; 1, 22; 1; <i>Kalimeris tenuifolia</i> 23; 1, 23; 1, 40; 1; <i>Lactuca serriola</i> 14; 1; <i>Lactuca species</i> 38; 1; <i>Lappula platyphallus</i> 30; 1; <i>Lappula tomentosa</i> 1; 1; <i>Lappula barbata</i> 9; <i>barbata</i> 21; 1; <i>Lappula serotina</i> 19; 1; <i>Lappula spinetorum</i> 24; 1, 24; 1; <i>Leontodon asperifolius</i> 8; 1; <i>Leptochloa parviflora</i> 12; 2; <i>Linaria linearis</i> 19; 1, 30; 1; <i>Lelidius ambulator</i> 28; 2; <i>Malcolmia africana</i> 22; 1; <i>Malva neglecta</i> 16; 1; <i>Malva species</i> 8; 1; <i>Matthiola carolina</i> 22; 1; <i>Matthiola officinalis</i> 14; 1; <i>Minuartia hybrida</i> 1; <i>hybrida</i> 17; 1; <i>Minuartia nageri</i> 19; 1, 22; 2, 28; 1; <i>Muscari caucasicum</i> 13; 1, 12; 1, 15; 1; <i>Neotoma linearis</i> 31; 1, 40; 1, 41; 1; <i>Nepeta cyparissia</i> 22; 2; <i>Onchodroma ochradum</i> 1; <i>ochradum</i> 22; 1; <i>Onobrychis aucheri</i> 40; 1; <i>Onopordium acanthium</i> 12; 1; <i>Onopordium dichroanthum</i> 12; 1; <i>Orobancha species</i> 12; 1, 18; 1, 23; 1; <i>Oxytropis lateralis</i> 5; 1, 6; 1; <i>Papaver argemone</i> 20; 1; <i>Papaver matsum</i> 17; 1; <i>Papaver rhoeas</i> 19; 1; <i>Papaver species</i> 38; 1; <i>Perovskia orientalis</i> 24; 1; <i>Perovskia arvensis</i> 12; 1; <i>Phagnalon vifidum</i> 24; 1; <i>Phidolia ulivifolia</i> 18; 1; <i>Picramnia ascarum</i> 22; 1; <i>Picris species</i> 17; 1; <i>Pimpinella trapii</i> 1; <i>depressa</i> 10; 13; 1; <i>Polypoda homocarpica</i> 27; 1, 28; 1; <i>Polygonum alpinum</i> 16; 1; <i>Polygonum amplexicaule</i> 28; 1; <i>Potentilla arguta</i> 3; 1; <i>Potentilla polychaeta</i> 3; 1; <i>Prunella farcta</i> 15; 38; 1; <i>Pseudocymopterus species</i> 37; 1; <i>Pulicaria gnaphalodes</i> 23; 1; <i>Anoda lutea</i> 23; 1; <i>Rachella Bungei</i> 40; 1; <i>Rana carina</i> 11; 13; 1; <i>Rumex species</i> 6; 1; <i>Salvia pygmaea</i> 17; 1; <i>Salvia species</i> 21; 1; <i>Scabiosa argemone</i> 11; 1, 13; 1; <i>Scabiosa species</i> 21; 1; <i>Scandelia stellata</i> 19; 1; <i>Scutellaria arbuscula</i> 17; 4; 2; <i>Scutellaria barbata</i> 32; 1, 23; 1, 28; 1; <i>Schumannia karvinskii</i> 37; 1; <i>Schumannia striata</i> 24; 1; <i>Suaeda iranica</i> 3; 1; <i>Suaeda vermiculata</i> 17; 2; <i>Silene acaulis</i> 9; 1, 11; 1, 13; 2; <i>Silene pallustris</i> 7; 1; <i>Silene species</i> 17; 1; <i>Stachys infesta</i> 30; 1, 22; 1, 24; 1, 28; 1; <i>Stachys species</i> 13; 1; <i>Stegonotus acanthocarpus</i> 18; 1, 38; 1, 37; 1; <i>Stipa capillaris</i> 8; 1, 12; 2; <i>Stipa kobulekiana</i> 13; 1; <i>Taraxacum persica</i> 23; 1; <i>Trigonotis vvedenskii</i> 8; 1, 9; 1; <i>Trigonotis montana</i> 11; 1; <i>Valeriana montana</i> 8; 1, 11; 1; <i>Valeriana dielsii</i> 8; 1; <i>Valerianella species</i> 23; 1, 41; 1; <i>Valerianella moscovitica</i> 28; 1, 38; 1; <i>Viola caucasica</i> 15; 1; <i>Viola occulta</i> 17; 1; <i>Zoegea purpurea</i> 19; 2, 24; 1, 40; 1; <i>Zygophyllum atriplicoides</i> 18; 2; 1, 40; 1; <i>Zygophyllum fabago</i> 22; 1, 25; 1; 2
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transect. The TWINSPLAN clustering resulted in three main vegetation groups including a "high altitude zone" from 1700 to 4400 m a.s.l. (zone A), a "xerophytic desert steppe" from 770 to 1700 m (zone B) and finally a "halophytic zone" from 770 to 800 m (zone C) (Table 1).

Zone A: High altitude zone. This zone includes subnival (plots 1–4, Fig. 2A), alpine (plots 5–18, Fig. 2B) and montane subzones (plots 19–22) and is further divided into 13 communities or 7 community groups: A1) This includes subnival communities (4327–3974 m a.s.l., D1–4) starting from somewhere close to upper vegetation line of Damavand volcano and contains two communities. *Draba siliquosa*-*Erysimum caespitosum* community (A1.1) occupies poor soils largely covered by scree, gravel and rocky substrate. By decreasing altitude, *Carex pseudofetida*-*Astragalus macrosemis* community (A1.2) occurs on slightly developed soil layer. These subnival communities are equivalent to the association *Dracocephalum aucheri* described from the area (Noroozi et al., 2014). A2) The thorny cushion form alpine community group (2970–3613 m. a.s.l., D5–10) is dominated largely by *Onobrychis cornuta* and is divided into two communities of *Cousinia harazensis* and *Astragalus ochroleucus*. A3) The six plots from alpine zone form a group of communities of perennial grasses and perennial herbs with few thorny species on well-developed soil layer containing higher moisture (2437–2722 m, D11–13, 15). This zone is subjected to intensive grazing and is locally harvested for fodder plants. *Galium verum*, *Stachys lavandulifolia*, *Chondrilla juncea* and *Eryngium billardieri* are characteristic species of this community group; the two latter species are indicators of overgrazed habitats. The five communities (A3.1, A3.2, A3.3, A3.4, and A3.5) distinguished in this group reflect the heterogeneity of the area mostly related to slope directions, substrate variability, disturbance and water supply. This group with an average species richness of 37 represents the most diverse zone along the studied transect. A4) Plot No. 16 represents a water tunnel on alpine area and surrounding parts in an elevation of 2310 m, largely covered by the ruderal species *Sophora alopecuroides* on moist soil and species such as *Thymus kotschyana*, *Papaver bracteatum*, *Astragalus microcephalus*, *Elymus hispidus*, and *Marrubium anisodon*. A5) The community of *Dysphania botrys* forms on sandy soils in remnants of a former sand mine with some other ruderal species such as *Heliotropium europaeum* and *Kali tragus* in elevation of 2402 m with very low species richness of 4. A6) Two plots from elevations of 1907 and 2055 (D19–20) are located near the city of Damavand on the hills of montane steppes which have largely been overgrazed. *Taeniatherum caput-medusae*, an invasive annual grass species not favored by herbivores (Clausnitzer et al., 1999), and thorny ruderal species such as *Gundelia tournefortii* and *Cirsium congestum* are indicators of large parts of montane steppes affected by overgrazing and

land degradation. A7) The two plots sampled from elevation of 2089 m and 1699 m (D21–22) are also representative of wastelands in montane steppes which are in verge of vegetation restoration. Therefore, many species are Irano-Turanian indicators of wastelands such as *Echinophora platyloba*, *Cousinia eryngioides*, *Centaurea virgata* and *Scariola orientalis*.

Zone B: Xerophytic desert and semi-desert steppe zone. This zone includes three main vegetation types. The first is the riverine vegetation on saline soils with high water table dominated by *Tamarix* species (B1, B2, plots D25 and D30). These belong to the Irano-Turanian class *Tamaricetea arceuthoidis* (Akhani and Mucina, 2015). The second and third zones comprised characteristic desert and semi-desert *Artemisia* steppe, in which *Artemisia aucheri* and *Artemisia* sp. occur in higher elevations (B3, mostly in 8541520 m, plots D24, D26–29, D31) but *Artemisia inculta* (formerly known in literatures as *Artemisia sieberi*) dominates extreme xerophytic desert steppes of interior Iran (B4, 767–1040 m, plots D37–41, Fig. 2C). The soil type is a major determining factor in formation of plant communities in this area. *Kaviria aucheri* dominates in marly hills (B3.5, plot D23), *Pteropodium aucheri* occurs in dry river bed (B4.1) and *Xylosalsola richteri* on fixed sandy soils (B4.2).

Zone C: Halophytic communities. The halophytic communities occur in two parts of our transect. One is located in a playa near Garmsar and the second near the margin of Salt Playa Lake. The four plots (D33–36, elevations 765–787 m, Fig. 2D) are sampled from hypersaline soils in which *Halocnemum strobilaceum* is present in very species poor communities (species richness of only 2–4). Three community types (C1, C2, and C3) differ by their local habitat changes favoured by species such as *Phragmites australis*, *Halostachys belangeriana*, *Alhagi maurorum*, *Tamarix androssovii* and *Tamarix pycnocarpa*.

#### 4.2. Correspondence Analysis of vegetation data

Fig. 3 illustrates the CA scatter plots of simplified vegetation plots. First tests of CA revealed that samples taken in saline soils (plots D33–37) act as outliers in CA scatter plots due to high coordination among them masking the distinctive patterns among other communities, almost all developed on well drained soils. This group of plots (removed from the CA) encompasses predominantly halophyte taxa of Zone C, described above (Table 1). The grouping of the remaining plots resulted from CA analysis of simplified vegetation data set and TWINSPLAN analysis of complete data set largely matched each other (Fig. 3, Table 1).

By removing the outliers from the vegetation dataset, the resulted CA diagram displays two main groups corresponding to Zones A, and B (Table 1). Three subzones including subnival, alpine and montane groups are less clearly distinguished in CA diagram (Fig. 3). Zone A



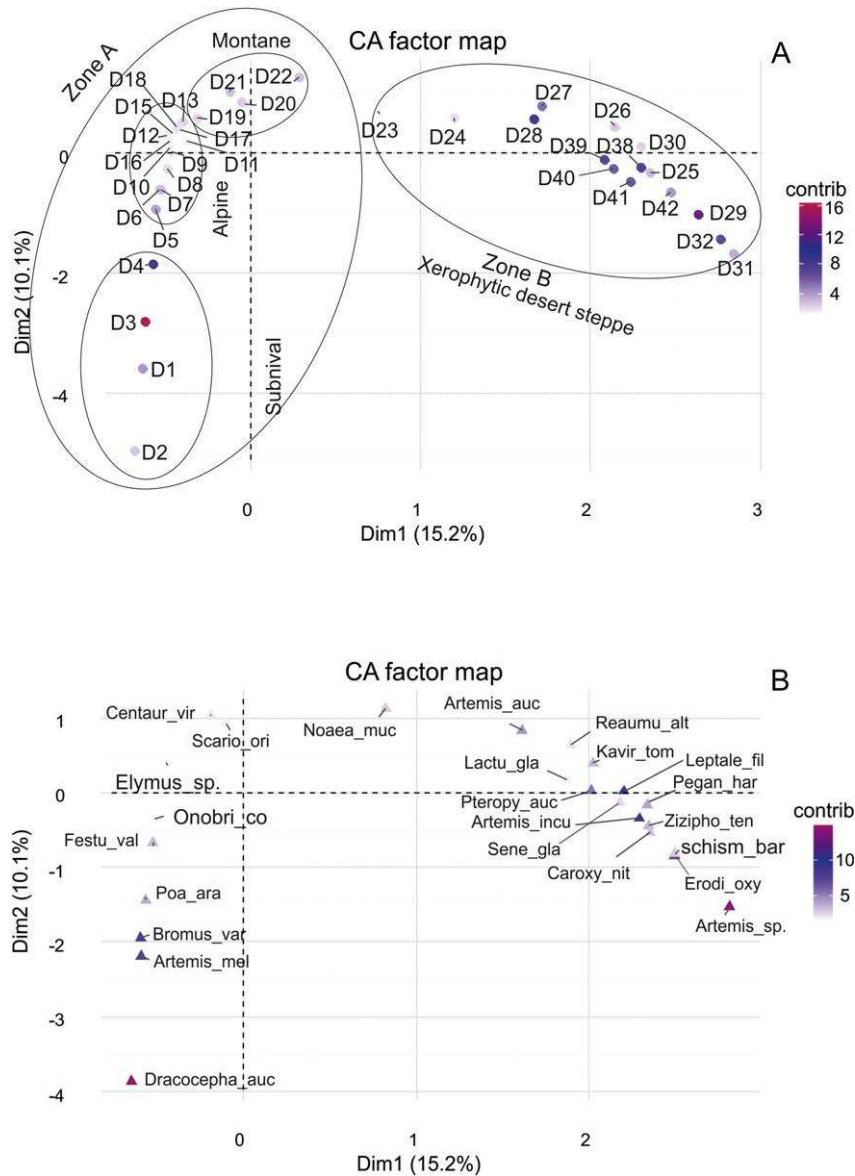


Fig. 3. Correspondence Analysis scatter plots (vegetation data) for both samples and the most contributing plant taxa into the CA axis 1 and CA axis 2. Contrib: contribution color scale of both samples and taxa to the CA-axes 1–2 factorial plan. CA axes 1 and 2 explain respectively 15.2% and 10.1% of the total variance.

includes almost all plots located on negative side of CA Axis 1 (plots D1–22), and Zone B includes samples located far to the positive side of both CA Axis 1 and 2 (plots D23–32 and D38–42). Such repartition shows a clear altitudinal gradient explained by both axes 1 and 2, explaining a visual arch-effect (Guttman effect). The most contributing plant taxa in the CA scatter plot are *Dracocephalum aucheri*, *Artemisia melanolepis* and *Bromus variegatus* in subnival group, *Poa araratica* and *Festuca valesiaca* in alpine group and *Centaurea virgata* and *Scariola orientalis* in montane group of the Zone A shown in Fig. 3B. The most characteristic taxa in Zone B are *Artemisia* spp., various species of Chenopodiaceae, *Leptaleum filifolium*, and *Erodium oxyrhynchum*. In terms of altitudinal distribution, there is a clear separation of Zone A from B, the separation point being located somewhere between sample D22 and D23 in the boundary between montane and xeric desert steppe subzones.

### 4.3. Surface pollen assemblages

#### 4.3.1. Pollen percentage diagram

Altogether 80 pollen types were encountered in the 42 pollen samples of which only 65 types were depicted in a summarized percentage

diagram (Fig. 4). Based on CONISS analysis of pollen percentages verified by visual inspection of the ecologically important taxa, five Pollen Assemblage Zones (PAZ) were recognized:

Pollen assemblage zone A (plots 1–3). This pollen zone, encompassing samples taken from high elevations of subnival zone (N4100 m; Fig. 1D) is characterized by high values of *Achillea/Matricaria*-type pollen (up to 65%). These high values are not very surprising as *Achillea aucheri* is the dominant plant in the vegetation community around plots 1 and 2 (Table 1, Fig. 2A). Pollen percentages of *Artemisia*, Poaceae, and Amaranthaceae/Chenopodiaceae remain low throughout the zone except for spectrum 3 with values of up to 43.5% of *Artemisia* have been encountered, produced by *Artemisia melanolepis* (Table 1). Other noticeable pollen types in this narrow zone especially in spectrum 3 belong to Cyperaceae (*Carex pseudofretida*) and Brassicaceae (*Draba siliquosa*, *Erysimum caespitosum*) (Table 1). There is no significant amount of tree pollen including the cultivated trees with the exception of *Pinus* pollen which keeps almost the same values all along the transect. In summary, in this zone only few taxa are present but with very sporadically high pollen values with herbaceous pollen predominating the spectra.

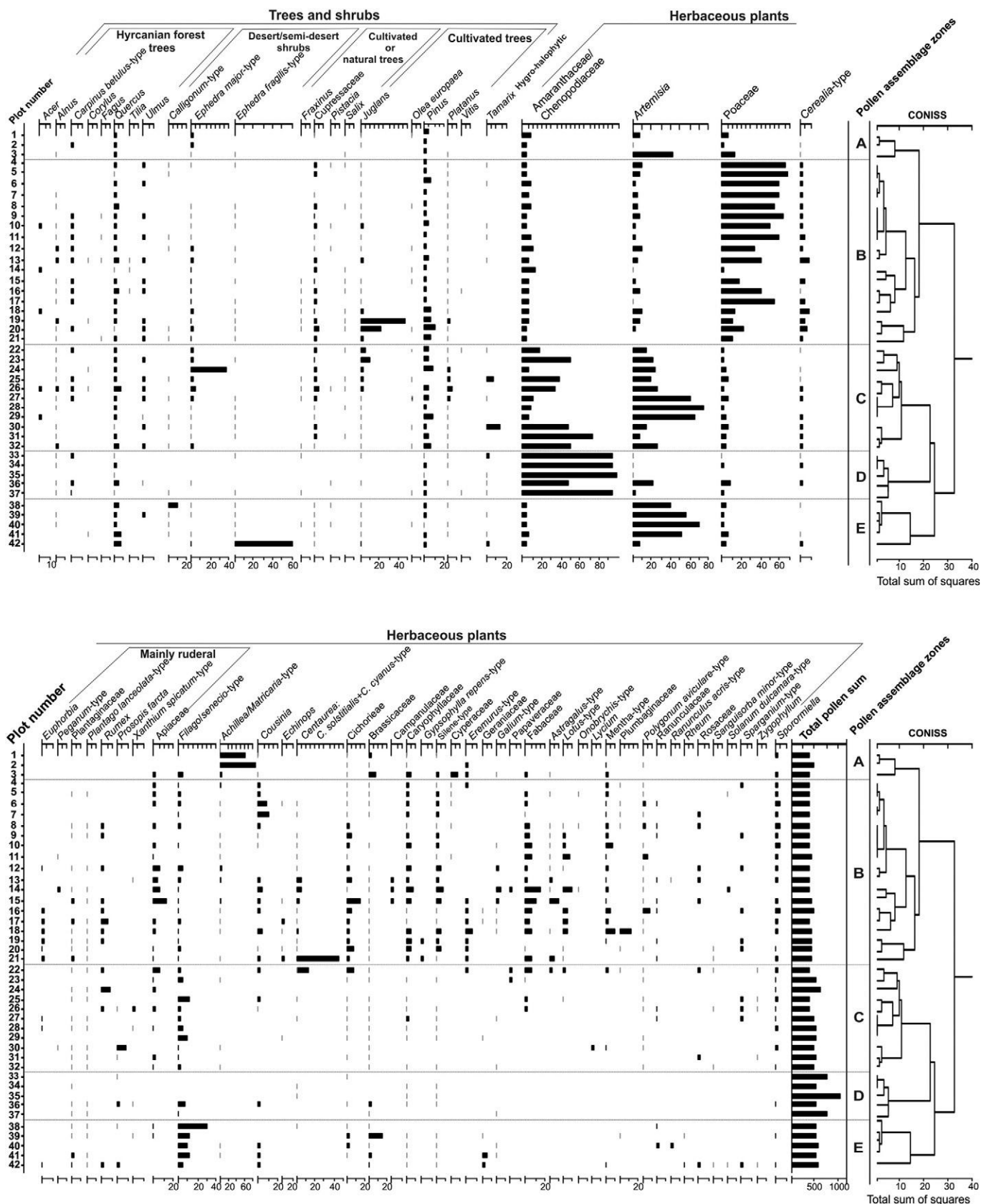


Fig. 4. Pollen percentages diagram of a selection of pollen types encountered along the studied transect.

Pollen assemblage zone B (plots 4–21). This pollen zone constitutes the widest segment of the transect corresponding to alpine subzone (4100–2500 m; Fig. 1D, Table 1) and montane subzone (2500–

1800 m; Fig. 1D). This PAZ remarkably displays the most diversified pollen assemblage along the whole transect. The most significant feature of this zone is the predominance of grass pollen (Poaceae) with values

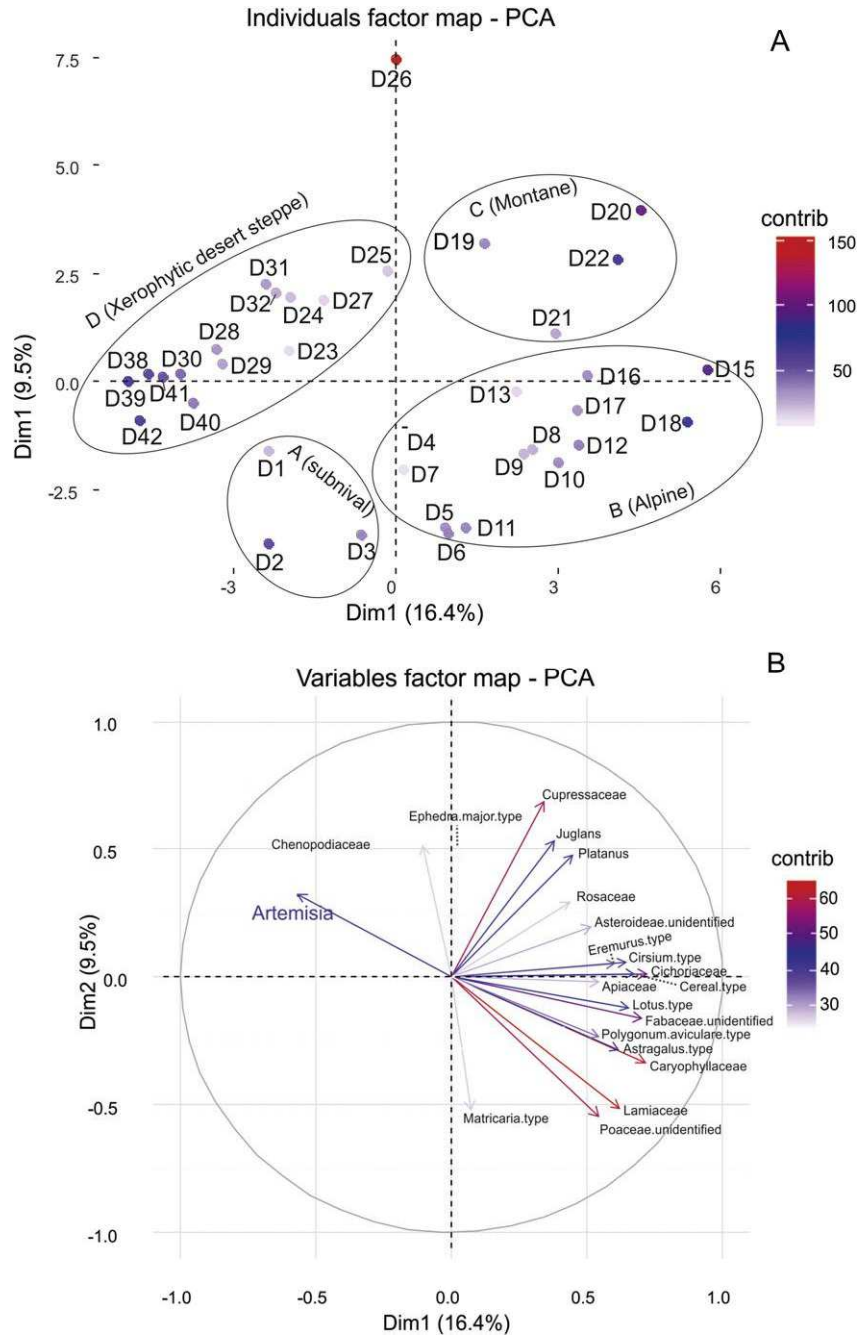


Fig. 5. PCA scatter plots (pollen data) for both samples and the most contributing pollen taxa into the PCA axis 1 and PCA axis 2. PCA axes 1 and 2 explain respectively 16.4% and 9.5% of the total variance.

ranging from 9.2% to 68.8%. Family-level pollen types of Fabaceae, Caryophyllaceae, Asteraceae-Cichorieae, Apiaceae, and Lamiaceae (Mentha-type) and to some extent Polygonaceae (*Polygonum aviculare*-type) are also well represented with highest values at the transition of alpine to montane Irano-Turanian zones (~2500 m). The dung-associated spores of *Sporormiella* show a constant presence with their highest values all along the zone suggesting a strong grazing pressure. Once, the cultivated/cultivation-associated plants (e.g. Cereal-type and *Centaurea solstitialis*-type) and ruderal species (*Plantago*, *Rumex*, Cichorieae, and *Euphorbia*) are also taken into account, the whole zone indicates the strong human activities in the form of agro-pastoralism. This agro-pastoral pressure is more visible in lower part of the zone corresponding to montane Irano-Turanian subzone (2500–1800 m). To the lower part of the zone we also note the increasing

values of cultivated trees (*Juglans*, *Platanus*, *Pinus*, and possibly *Cupressus/Thuja* (Cupressaceae)) showing the proximity of permanent habitations in villages and small towns and artificial plantations in nearby areas. *Cousinia* pollen is also well present in the zone but is more frequent in the spectra corresponding to upper alpine subzone. Of particular interest is the presence of *Eremurus*-type (or *Sisyrinchium*-type) pollen which was already present in subnival (samples D1–3) but reappears in the lower alpine and montane Irano-Turanian sub-zone (samples D15–22). The absence of producers of this pollen in our plots shows that this pollen type has a good production and dispersal in these two vegetation belts (most probably belonging to different species) since some *Eremurus* species are widely distributed in southern slopes of Alborz mountains (Wendelbo, 1982). Exceptionally high values of Plumbaginaceae and *Mentha*-type in spectrum 18 as well as

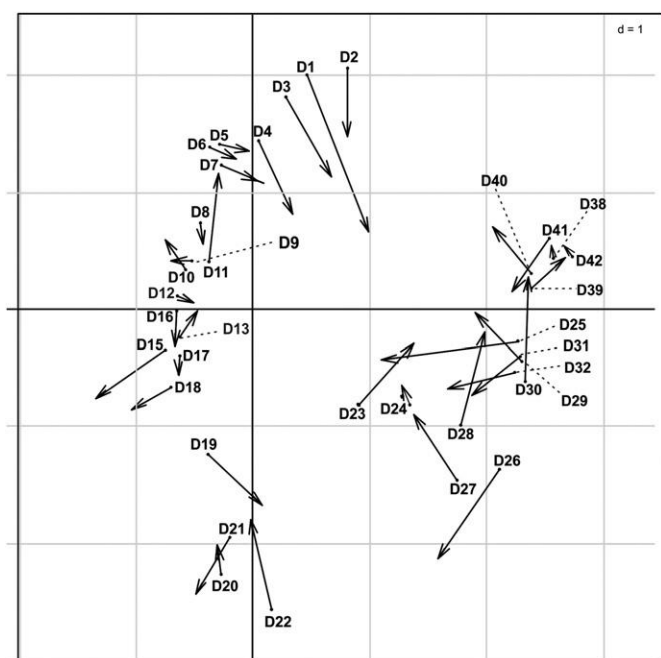


Fig. 6. Co-inertia scatter plots displaying the degree of correlation between vegetation and pollen data. Shorter arrows show stronger similarities between vegetation and pollen assemblages.

*C. solstitialis*-type in spectrum 21 can be attributed to high values of *Acantholimon erinaceum* (~30%), *Thymus kotschyanus* (~20%), and *Centaurea virgata* (~30%), respectively, in the vegetation community surrounding them. The latter comes from an abandoned farmland. Samples 19 and 20 are taken from a zone, well-known for walnut cultivation, namely Damavand, Tehran.

Pollen assemblage zone C (plots 22–32). This pollen zone covers the submontane Irano-Turanian xerophytic steppe (Fig. 1D). In this PAZ, grass pollen decreases drastically down to 0.8% (sample 26) while *Artemisia* and *Amaranthaceae*/*Chenopodiaceae* pollen percentages increase so that one or the other takes advantage in different spectra depending on their contributions in corresponding sampled vegetations. In general, this zone is characterized by dominating presence of *Artemisia aucheri* and different species of *Chenopodiaceae* (e.g. *Kaviria aucheri*, *Haloxylon ammodendron*, *Noaea mucronata*, *Salsola rosmarinus*, *Halothamnus subaphyllus* and so on) in the sampling points (Table 1). There are also high values of *Filago/Senecio*-type pollen and a significant presence of *Apiaceae*. Dominance of plants belonging to *Asteraceae* subfamily *Asteroideae* (e.g. *Senecio glaucus* L. and *Pulicaria gnaphaloides*) explains the increased values of *Filago/Senecio*-type pollen. *Sporormiella* spores exist in the whole zone although with lower values compared to PAZ-B, showing the grazing activities throughout the zone. Lower values of *Cerealia*-type pollen suggest that pastoral activities are more important than cereal cultivation. Cultivated trees (*Juglans*, *Platanus*, and possibly *Cupressus/Thuja*) also indicates the proximity of urban zones and habitations. Exceptionally high pollen percentages of *Ephedra distachyate* (sample

24) and *Tamarix* (samples 25 and 30) can be explained by presence of *Ephedra* and abundant shrubs of *Tamarix*, respectively, in the surrounding vegetation communities (Table 1).

Pollen assemblage zone D (plots 33–37). This pollen zone falls within halophytic vegetation zone but inside a relatively endorheic depression (Fig. 1D). *Chenopodiaceae* pollen predominates the pollen spectra of PAZ-D at expense of *Artemisia* and grass pollen. This zone has the least pollen diversity over the study transect. Predominance of *Chenopodiaceae* can be explained by dominance and high representation of species such as *Halocnemum strobilaceum*, *Halostachys*

*belangeriana*, and *Salsola rosmarinus* developed on saline soils and mud flats (Fig. 2D).

Pollen assemblage zone E (plots 38–42). Like PAZ-D, this zone falls within xerophytic desert steppe zone but on well drained soils (Fig. 1D). *Chenopodiaceae* pollen falls instantly from 94.7% down to 4.9% while *Artemisia* pollen increases abruptly up to 71.8% except for the last spectrum (sample 42) in which high amount of *Ephedra* pollen illustratively compresses the frequency of *Artemisia* pollen since the sample was taken in an *Ephedra strobilacea* community. As for two previous PAZs, grass pollen remains low while the pollen percentages of *Asteroideae* and *Brassicaceae* increase. High amount of *Calligonum*-type pollen in spectrum 38 reflects the major role of *Pteropryum aucheri* in the vegetation community inside and outside the sampled plot (Table 1). Considerable amounts of *Filago/Senecio* pollen type in this PAZ comes most likely from the annual desertic species of *Senecio glaucus* which grows in the region. Likewise, the PAZ-D, *Sporormiella* spores are almost absent from most of the spectra in this pollen assemblage zone indicating low grazing and fairly absence of livestock due to long term conservation and remoteness of the region.

#### 4.4. PCA of pollen data

Fig. 5 presents the PCA scatter plots for both samples (plots) and the most contributing plant taxa into the PCA axis 1 and PCA axis 2, in which the contributions of axes 1 and 2 to the total variance are 16.4% and 9.5% respectively.

PCA analysis of pollen data set, delimits four distinct groups. Group A (plots 1–3) includes subnival samples which are located in negative sides of both PCA axes (Fig. 5A, D1–D3). The most important pollen types in group A are *Asteraceae* and *Cyperaceae* (Table 1, Fig. 4).

Group B (plots 4–18), with highest pollen diversity along the transect is located in negative side of PCA axis 1 and positive side of PCA axis 2 corresponding with well diversified mesic elevation steppes dominated by thorny cushion taxa and *Poaceae*. The most characteristic pollen types in forming group B are *Poaceae*, *Caryophyllaceae*, *Lamiaceae*, *Fabaceae* and *Cichorieae*, yet the role of *Polygonum aviculare*-type pollen is of secondary importance comparing the afore-mentioned taxa.

Group C (plots 19–22) comprises four samples sitting in positive side of both PCA axes. This group of samples has been taken in vicinity of residential places and contains pollen of cultivated taxa or pollen indicating human activities including that of *Juglans regia*, *Centaurea virgata* (*Centaurea solstitialis*-type), *Pinus*, *Euphorbia* and *Rosaceae*. (Not all shown in Fig. 5).

Group D (plots 23–32 and 38–42) lies mostly on negative side of PCA axis 2, entailing samples taken in *Artemisia* dominated thermo-xerophytic steppes. The most characteristic pollen types of group B are *Artemisia*, *Chenopodiaceae*, *Ephedra* and *Filago* (partly shown in Fig. 5).

The anomalous positions of plot 26 in the scatter plot (Fig. 5) which loads highly on PCA axis 1, is due to vegetation composition coming from a barren gypsum substrate near a village where only less than 1 % of the quadrat was occupied by plant taxa. This plot is dominated by *Artemisia*, *Chenopodiaceae* and tree pollen types (Fig. 4).

#### 4.5. Pollen-vegetation relationships

##### 4.5.1. Co-inertia analysis of pollen and vegetation data

Co-inertia analysis was done to reveal the amount of similarities between vegetation composition data and corresponding pollen percentages. The shorter arrows indicate higher correlation between vegetation composition and pollen data sets (Fig. 6). The best correlation between pollen and vegetation data sets was found in plots 5–10, 12–13, 16–18, 21, 24, 38–39, and 42 whereas the least correlation was obtained between pollen and vegetation data sets in plots 1–4, 11, 15, 19–20, 22–23, 25–30 (Fig. 6).



The weak correlation between the vegetation and pollen assemblages of plots 1–4 (subnival communities), is due to low pollen production of many plant species in this zone and a significant contribution of background long-distance transport pollen originating from a vast region. The vegetation in this altitude is mostly open and the area is exposed to strong multidirectional winds. With the exception of plots numbers 11, 15 dominated by *Astragalus* spp. and *Chaerophyllum macrospermum* (both are extremely underrepresented in pollen assemblages), the remaining alpine plots show good correlation between vegetation and pollen assemblages. In contrast, most plots found in montane zone and higher elevations of xerophytic desert steppe zone show a weak correlation between plant and pollen assemblages. This is mainly a reflection of human activities (e.g. mining, agriculture, animal husbandry and planting economical and ornamental plants) and higher diversity in vegetation resulted from habitat heterogeneity. More detailed studies are necessary to look for actual vegetation composition and its mirror in pollen assemblages.

In the lowest elevations of xerophytic desert steppe zone, there is a relatively good correlation between plant and pollen assemblages (Figs. 1D and 6). As the samples from saline environments in the depressions are excluded from the analyses (see above), the Co-Inertia could not help testing the correlation of pollen assemblages and vegetation composition in this zone.

The final results of co-inertia analysis is based on maximally covariant co-inertia axes which are derived from principal components analysis (PCA) or correspondence analysis (CA) methods. Since the co-inertia axes in this paper were derived from CA approach, the clustering of samples in co-inertia diagram follows the same pattern as that of CA in Fig. 3.

#### 4.5.2. Pollen representation of plant taxa

4.5.2.1. Trees. Although the studied transect was almost free of trees and large shrubs within and around quadrats (except for *Tamarix* and also *Juglans regia* in vicinity), arboreal pollen transported in by wind was often found but rarely represented in a significant amount (Fig. 4). A well-represented case is the *Alnus* pollen, coming from Hyrcanian forests indicating its high pollen production and dispersal (Djamali et al., 2009a). Other well dispersed arboreal pollen grains are those of *Quercus*, *Carpinus*, and *Platanus*. *Tamarix* seems to be a moderately dispersed under-represented taxon, supplying only 6–13% of pollen assemblages where it comprises about 50% of the coverage (plots 25 and 30). The anemophilous cultivated tree, *Juglans regia* shows over-representation and effective dispersion. According to our findings where *Juglans regia* proportion in fossil pollen reaches 10%, one can conclude that walnut cultivation has taken place in the vicinity of the region, while extensive walnut cultivation can lead to up to 48% pollen representation in fossil pollen diagrams in Irano-Turanian region (see plots 19, 20 and 23). *Pinus* pollen is found in almost all plots along the studied transect but its frequency rises in the vicinity of cities and residential areas (Fig. 4). The application of our finding for interpretation of fossil pollen spectra is that representation of *Pinus* pollen from 6 to 11% shows its occurrence in the original vegetation and below 6% is more likely originates from remote dispersal. In spite of the absence of *Pinus* trees in natural vegetation of Iran, some species (e.g. *P. eldarica*) are widely cultivated as ornamental and artificial forestation in most parts of Iran in particular residential areas in southern and northern slopes of Alborz mountains (Djamali et al., 2016; Akhiani et al., 2013).

4.5.2.2. Shrubs. Ephedra shows by far, the highest pollen production and dispersal among shrubby species and was found with significant amounts in almost all plots (Fig. 4). This extreme pollen production and dispersal has previously been shown by some authors (Welten, 1957; Bortenschlager, 1967; Yuecong et al., 2005; Zhao and Herzschuh, 2009). When *Ephedra* is present within the sampling site, its pollen dominates the pollen spectra (Fig. 4, plots 24 and 42).

*Prosopis farcta* is a ruderal species and a good indicator of severely overgrazed areas of the xerophytic desert zone which displays a moderate representation in modern pollen rain. This pollen type, found exclusively in xeric steppes, is encountered in small numbers in the absence of the parent plant (Fig. 4). When the plant is present in considerable amount inside or around the sampled plots (less than 5%), *P. farcta* pollen can reach up to 7.6% of pollen sum (Fig. 4, plot 30).

*Lycium* has about six species in Iran of which only *Lycium ruthenicum* was found in our transect, inhabiting river beds, roadsides and well-drained to saline soils. Our pollen data suggests that *Lycium* pollen is poorly dispersed and relatively under-represented in modern pollen rain. *Lycium* pollen is found only in plot 30 where it produces 1.1% of total pollen while the parent plant comprises about 7% of the corresponding vegetation (Fig. 4, plot 30).

*Pteropyrum* species are desert shrubs growing often along seasonal river and water runnels in desertic areas or gypsum hills of the southern parts of Iran, showing low to slightly moderate pollen representation. When *Pteropyrum* is present in the sampling vegetation, its pollen largely contributes to the pollen sum (e.g. Fig. 4, plot 38) otherwise its proportion in pollen assemblages is negligible (Fig. 4, compare plot 38 with the rest).

4.5.2.3. Herbs and dwarf Shrubs. Entomophilous taxa of highlands including Apiaceae, *Astragalus*, *Onobrychis*, *Thymus*, *Verbascum* and Plumbaginaceae which alternatively play fundamental roles in high elevation vegetation only contribute meagre percentages in modern pollen assemblages (see Fig. 4).

The family Fabaceae, as the largest family of the Iranian flora (Akhiani, 2006), is poorly represented in modern vegetation as well as in modern pollen assemblages from the desert steppes along our transect (Fig. 4, plots 27–42). However, they are well represented in vegetation of the montane to alpine steppes in which their role in pollen rain is highly insignificant (Fig. 4, e. g. plots 3–13 and 15–16). For instance, in several cases when *Onobrychis cornuta* forms more than 30% coverage in the vegetation, its contribution to modern pollen assemblage varies only between zero and around 1% (Fig. 4, plots 6–9). In the case of *Astragalus* spp. even the coverage percentage of up to 80% in the sampled vegetation represented very low pollen percentages (e.g. 0.2% in plot 11 and 9.5% in plot 15 (Table 1 and Fig. 4)).

Apiaceae is also highly under-represented in studied transect. In a local stand of *Chaerophyllum macrospermum* with above 80% coverage, only 13% of total pollen belongs to Apiaceae (Fig. 4, plot 15). However, pollen contribution of Apiaceae in dry steppes dominated by *Artemisia*-Chenopodiaceae is still far more insignificant than that of high elevation steppes (see Apiaceae pollen percentages in Fig. 4).

*Achillea aucheri* subsp. *aucheri* an endemic taxon in high altitude of central Alborz produces *Matricaria*-type pollen. Although encountered sporadically throughout the studied transect, this pollen type is highly represented (90% of pollen percentages in plots with 20% vegetation cover) in subnival plots dominated by *Achillea aucheri* subsp. *aucheri* (Fig. 4, plots 1–2). Apparently, this over-represented plant in pollen assemblages has a limited range of dispersal since its pollen suddenly vanishes in adjacent plots without individuals of the species.

Several species of *Cousinia* grow along the transect including *Cousinia harazensis*, an endemic to Damavand Mt., *Cousinia pterocaulis*, *Cousinia multiloba*, *Cousinia eryngioides* and *Cousinia cylindracea*. *Cousinia* pollen is found in small amounts along the transect but it can reach up to 11% where producing plant forms about 20% coverage (Fig. 4, plot 7). Apparently, *Cousinia* pollen dispersal is limited. This can be critically important since different species of *Cousinia* are rather geographically distinct, therefore pollen identification to species level will help climate interpretation in fossil pollen sequences (Djamali et al., 2012).

Euphorbia represents around 74 species in Iran (Pahlevani et al., 2015), growing in various habitats. Only *Euphorbia cheiradenia* was found in our transect which occupies disturbed or overgrazed areas.

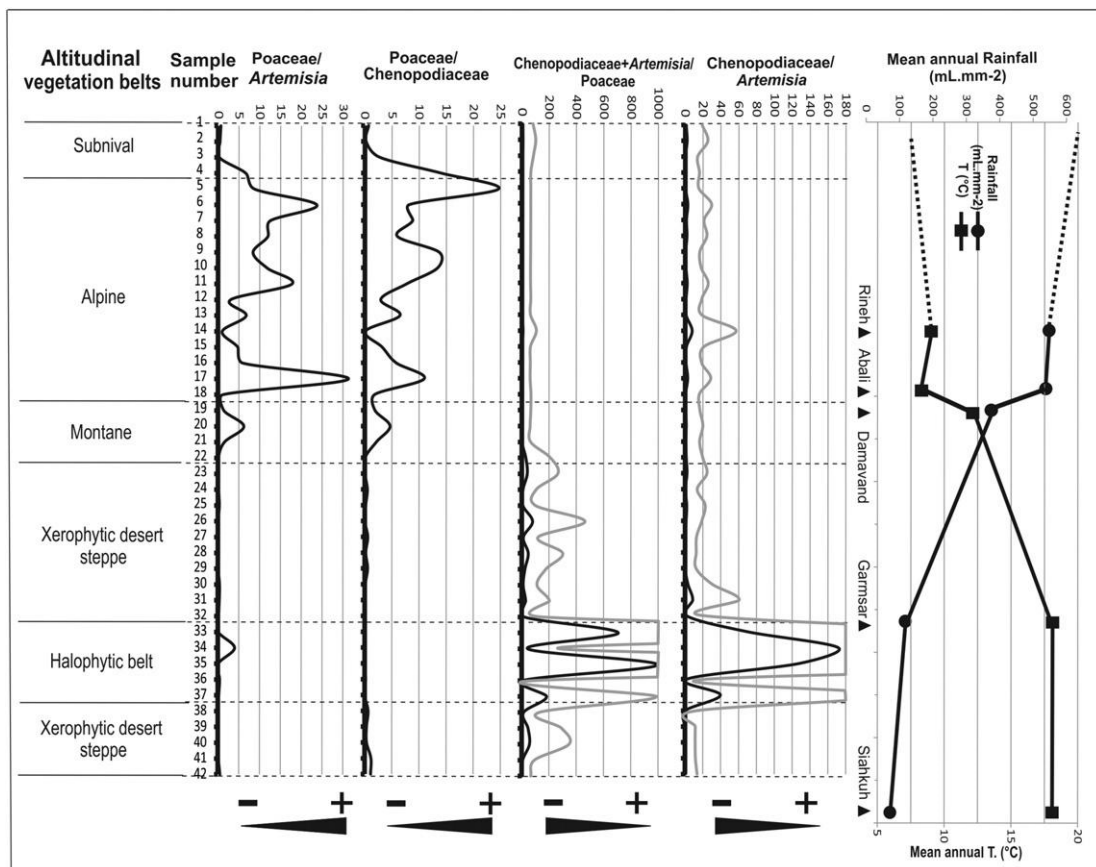


Fig. 7. Comparison of pollen ratios of *Artemisia*, Chenopodiaceae and Poaceae in different vegetation zones of a 3600 m elevational transect in central Iran, along with a climatic curve showing the changes of mean annual temperature and precipitation of five meteorological stations along the studied transect. Arrows beside each index indicate moisture correlation with respective index.

The results of our study propose that *Euphorbia cheiradenia* is highly under-represented and its pollen never exceeds 2% even in samples in which the plant coverage is over 20% (Fig. 4, plot 19).

Pollen of Poaceae is found in all plots except one (Fig. 4, plot 35), reflecting the ubiquity of this diversified family. At present, pollen identification is not feasible to determine lower taxonomic ranks in grasses. Supposedly, different taxa show different abilities in pollen production making it difficult to speculate about their pollen representation. For instance in plot 34 where *Phragmites australis* covers more than 70% of the area, only 1.7% of pollen sum belongs to Poaceae (Fig. 4). This may be partly due to intensive grazing or unsuitable conditions diminishing flowering of reed plants in the area. In plots 18 and 21, in spite of relative dominance of Poaceae, only 10% of total pollen is produced while in plots 4, 5 and 9 with almost the same coverage,

a range of 63–68% of total pollen belongs to Poaceae (see Fig. 4). We suggest that not only in Poaceae but also in other taxa (including *Artemisia* and Chenopodiaceae), different species have different pollen production and dispersal. Furthermore, associated species could affect the amount of pollen representation in pollen rain assemblages.

#### 4.6. Chenopodiaceae/*Artemisia* pollen ratio application

The recent classification of Angiosperm Phylogeny Group, APG VI (Chase et al., 2016) suggested inclusion of Chenopodiaceae into a wide sense Amaranthaceae. The similarity of pollen grains of some groups of Amaranthaceae (Amaranthoideae) with traditional Chenopodiaceae and their distinctiveness from other groups (Gomphrenoideae) has been known in literatures (Borsch, 1998; Borsch and Barthlott, 1998). In this study, we preferred to keep the

name of Chenopodiaceae not only following most of the recent classifications of Caryophyllales (such as Hernández-Ledesma et al., 2015), but also because of the rarity of Amaranthaceae s. str. in Irano-Turanian flora.

Pollen of *Artemisia* and Chenopodiaceae is found in all studied plots which proves their high pollen production and good pollen dispersal, already noticed by many authors (e.g. Wright et al., 1967; Moore and Stevensen, 1982; El-Moslimany, 1990; Djamali et al., 2009c; Zhao et al., 2012). Regardless of high pollen production and dispersal, the *Artemisia* and Chenopodiaceae pollen frequencies in pollen rain spectra seem well reflecting their abundance in sampled locations (Fig. 4, Table 1). The high elevation belt (Zone A including subnival, alpine and montane parts of our transect) is represented by a rather uniform low average percentage of 6.8% of chenopod pollen, in spite of the fact that species of this family are absent or rarely occur in the vegetation. The *Artemisia* shows similar pattern in terms of pollen percentage (7.9%) but in contrary to chenopods, several species of *Artemisia* are associated with different plant communities in the high altitude vegetation. An interesting pattern we found in *Artemisia* pollen diagram is its higher pollen percentages in desert steppes than in high altitude plant communities even in plots with similar coverage. This might represent different pollen production and dispersal capacities of lowland versus highland species of *Artemisia* or the masking of *Artemisia* by the pollen of adjacent plants in the higher altitude vegetation.

Another interesting result in our study is the different patterns of pollen percentages of Chenopodiaceae in xeric and halophytic zones. The extraordinarily high pollen production in euhalophytic chenopods compared to species in the ruderal or xeric habitats might be interpreted as a result of different pollen production rates in different

taxonomic groups. Our own field observations show that usually species of Salicornioideae, as the dominant species in hygrohalophytic communities, produce large amounts of pollen. The available data from a few coastal Mediterranean species belonging to the genera *Atriplex* and *Halimione* (Chenopodiaceae), *Sarcocornia* and *Arthrocnemum* (Salicornioideae), *Suaeda vera* (Suaedoideae) and *Salsola vermiculata* (Salsoloideae) show a complex pattern that can't be used to explain the pollen representation of halophytic communities in the Irano-Turanian inland areas (Fernández-Illescas et al., 2010).

Inspection of pollen count datasets reveals that three pollen types are constantly present in plots including Poaceae, *Artemisia* and Chenopodiaceae, offering the possibility to use them as ecological indicators. El-Moslimany (1990) introduced Chenopodiaceae/*Artemisia* pollen ratio as an index of aridity in open habitats based on the hypothesis that *Artemisia* species require higher moisture than those of chenopods. In spite of the wide use of this ratio in palynological studies (El-Moslimany, 1990; Davies and Fall, 2001; Zhao et al., 2008; Van Campo and Gasse, 1993; Zhao and Herzschuh, 2009), some authors doubted its reliability (Yasuda et al., 2000; Herzschuh, 2007; Djamali et al., 2008; Zhao et al., 2012). Based on the analysis of large data sets by Zhao et al. (2012), the C/A ratio corresponds with annual precipitation only in steppe areas with annual precipitation of 450–500 mm. Additionally, they insisted on the requirement of careful pollen-vegetation-climate relationships prior to applying this index. In studies on fossil pollen from hypersaline lakes in NW and SW Iran, Djamali et al. (2008, 2009a), doubted the reliability of C/A ratio in reconstruction of climate because they found that *Artemisia* and Chenopodiaceae can coexist in the same region. They mentioned the importance of local edaphic conditions particularly soil moisture and salinity and local human effects in the formation of halophytic or ruderal communities of Chenopodiaceae which are not related to macro-climatic conditions. Furthermore, chenopod-dominated communities are important features of many coastal halophytic vegetation and some cultivated plants like Sugar Beet (*Beta vulgaris*), Spinach (*Spinacia oleracea*) or many weedy species of the genus *Chenopodium* s.l. are indicators of crop cultivation. In such cases high amounts of chenopod pollen is by no means an index of aridity. Therefore, some authors suggest the applicability of Poaceae/*Artemisia* pollen ratio as a better index of moisture availability against C/A (Liu et al., 2006; Djamali et al., 2009a). The C/A index has further been criticized in *Artemisia* dominated hyperarid deserts of Badain Jaran, Taklamakan and Tengger in western China (Yang and Scuderi, 2010).

Our study shows that in plots in which *Artemisia* and Chenopods are absent, we can still see small amounts of their pollen in the pollen assemblages, but the C/A ratio in such plots does not show a particular pattern and changes randomly. However, in those plots in which *Artemisia* or Chenopodiaceae are dominated, the pollen assemblages and the C/A ratios of surface samples reflect their relative contribution to actual vegetation (Figs. 4 and 7, Table 1). In Fig. 7 ratios of C/A, P/C (Poaceae/Chenopodiaceae), P/A (Poaceae/*Artemisia*) and (A + C)/P ((*Artemisia* + Chenopodiaceae)/Poaceae) are compared. The C/A and (A + C)/P ratios in xerophytic desert steppes are much lower than that of neighbouring halophytic vegetation despite the fact that macro-climatic conditions of both communities are similar. Further, the soil moisture of halophytic communities is much higher than that of xerophytic desert steppes. It is important to note that soil moisture in halophytic communities could not necessarily be interpreted as higher precipitation. The water table in low endorheic depressions and playa environments is usually high due to the intersection of regional groundwater with ground surface. The (A + C)/P aridity index was proposed by Fowell et al. (2003) to differentiate steppes from desert steppes. Based on this index values above 5 are considered as an indication of arid conditions while values below 5 are interpreted as indications of relatively moist steppes or forest steppes. Contrary to C/A ratio, (A + C)/P aridity index well distinguishes the highland mesic steppes from the lowland xerophytic and halophytic steppes in studied

transect (Fig. 7). Similar to C/A ratio, high values of (A + C)/P index corresponds to the halophytic formations, rather than indicating drier conditions as previously interpreted by other authors (Fowell et al., 2003; Zhao and Herzschuh, 2009, see also Fig. 7). We suggest that C/A ratio is more confident as an index to distinct the halophytic from non-halophytic desert vegetation, comparing to (A + C)/P (compare plot No 34 in C/A and (A + C)/P graphs in Fig. 7).

We suggest to depict pollen ratios of all the three ubiquitous pollen types (Poaceae, *Artemisia* and Chenopodiaceae) in a combined graph as a better tool to reflect vegetation and moisture. Fig. 7 shows that higher P/A and P/C ratios are good indications of high elevation mesic steppes, while higher C/A and (A + C)/P ratios are good indicators of xerophytic desert steppes and chenopod dominated saline soils. The subnival subzone is particularly of interest because it indicates low P/A and P/C values but variable C/A ratios and (A + C)/P values around 5. The poor grass vegetation and occurrence of alpine species of *Artemisia* (*Artemisia melanolepis* and *Artemisia chamaelifolia*) and orophilous chenopod species (*Blitum virgatum*) well explain this deviation. This finding is of great interest to locate this vegetation zone in the fossil pollen diagram from the Irano-Turanian mountain regions. It also shows that very local floristic conditions may change the general trends in the palynological ratios used as aridity or moisture indices.

## 5. Conclusions

Along the 3600 m elevational gradient transect from Damavand Mountain to Salt Playa Lake located in Irano-Turanian desert of Dashte Kavir we found:

1. The pollen assemblage of subnival vegetation belt is characterized by an assemblage of *Achillea*/*Matricaria*-type pollen followed by *Artemisia*, Cyperaceae and Brassicaceae showing a weak correlation with the local vegetation. This might be due to different representation of plant taxa in pollen assemblages and significant contribution of background long-distance transport pollen coming by strong winds in the region.
2. The alpine and montane vegetation subzones (1800–4100 m) show the highest pollen diversity along the whole transect and are characterized by predominance of grass pollen. Pollen types of Fabaceae, Caryophyllaceae, Asteraceae-Cichorioideae, Apiaceae, and Lamiaceae (*Mentha*-type) are also well represented. The stronger correlation between modern vegetation and pollen assemblages in the alpine subzone decreases in the heavily disturbed places, in particular in the montane subzone.
3. The xerophytic desert steppe vegetation zone is well characterized by drastic reduction of grass pollen and a conspicuous increase of *Artemisia* and Chenopodiaceae pollen percentages, well correspond with the actual vegetation. The human activities in non-protected parts of the transect have weakened the correlation between surface pollen assemblage and actual vegetation evidently due to agropastoral activities.
4. The halophytic vegetation zone, showing the lowest species richness and the least pollen diversity over the entire transect, is characterized by absolute dominance of Chenopodiaceae pollen because of dominant chenopod vegetation.
- 5.
6. Entomophilous shrubs encountered in the studied transect including *Prosopis farcta*, *Lycium ruthenicum*, *Pteropryum aucheri* and *Tamarix* spp. were poorly to moderately presented in pollen assemblages. Members of the families Apiaceae, Lamiaceae, Scrophulariaceae, Plumbaginaceae and Fabaceae which dominate the high elevations are very under-represented in modern pollen samples in Irano-Turanian region.
7. The C/A pollen ratio, which has widely been used as an aridity index in open vegetations, is less reliable in the Irano-Turanian region. This ratio is informative to show the contribution of these



two taxa in the parent vegetation only when their pollen percentages are high, otherwise it shows neither the parent vegetation composition nor the moisture conditions. We found depicting and comparing the combined graphs of all four indices (C/A, P/A, P/C and (A + C)/P) better represent the vegetation and climate relationships. In summary, P/A and P/C ratios are more confident to differentiate mesic from arid steppes while C/A and (A + C)/P ratios provide useful tools to distinguish halophytic and non-halophytic desert vegetation.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2017.08.004>.

## References

- Akhani, H., 2006. *Flora Iranica: facts and figures and a list of publications by KH Rechinger on Iran and adjacent areas*. Rostaniha 7 (Suppl. 2), 19–61.
- Akhani, H., Mucina, L., 2015. The Tamaricetea arceuthoidis: a new class for the continental riparian thickets of the Middle East, Central Asia and the subarid regions of the Lower Volga valley. *Lazarova* 36, 61–66.
- Akhani, H., Edwards, G., Roalson, E.H., 2007. Diversification of the old world Salsoleae s.l. (Chenopodiaceae): molecular phylogenetic analysis of nuclear and chloroplast data sets and a revised classification. *Int. J. Plant Sci.* 168 (6), 931–956.
- Akhani, H., Djmal, M., Ghorbanalizadeh, A., Ramezani, E., 2010. Plant biodiversity of Hyrcanian relict forests, N Iran: an overview of the flora, vegetation, palaeoecology and conservation. *Pak. J. Bot.* 42 (Special Issue), 231–258.
- Akhani, H., Mahdavi, P., Noroozi, J., Zarrinpour, V., 2013. Vegetation patterns of the Irano-Turanian steppe along a 3,000 m altitudinal gradient in the Alborz mountains of northern Iran. *Folia Geobotanica* 48 (2), 229–255.
- Allen, M.B., Ghassemi, M.R., Shahrabi, M., Qorashi, M., 2003. Accommodation of late Cenozoic oblique shortening in the Alborz range, northern Iran. *J. Struct. Geol.* 25 (5), 659–672.
- Beug, H.J., 2004. *Leitfaden der Pollenbestimmung für Mitteleuropa und Angrenzende Gebiete*. Friedrich Pfeil, München.
- Borsch, T., 1998. Pollen types in the Amaranthaceae. Morphology and evolutionary significance. *Grana* 37 (3), 129–142.
- Borsch, T., Barthlott, W., 1998. Structure and evolution of metareticulate pollen. *Grana* 37 (2), 68–78.
- Bortenschlager, S., 1967. Pollenanalytische Ergebnisse einer Firnprofiluntersuchung am Kesselwandferner (3240 m, Ötztal, Tirol). *Grana* 7 (1), 261–269.
- Bottema, S., 1986. A late Quaternary pollen diagram from Lake Urmia (northwestern Iran). *Rev. Palaeobot. Palynol.* 47, 241–261.
- Bottema, S., Woldring, H., 1990. Anthropogenic indicators in the pollen diagrams of the Eastern Mediterranean. In: Bottema, S., Entjes-Nieborg, G., van Zeist, W. (Eds.), *Man's Role in the Shaping of the Eastern Mediterranean Landscape*. Balkema, Rotterdam, pp. 231–264.
- Braun-Blanquet, J., 1964. *Pflanzensoziologie. Grundzüge der Vegetationskunde*. Neu bearb. Aufl. 3. Springer, Berlin (865 pp.).
- Chase, M.W., Christenhusz, M.J.M., Fay, M.F., Byng, J.W., Judd, W.S., Soltis, D.E., Mabblerley, D.J., Sennikov, A.N., Soltis, P.S., Stevens, P.F., 2016. An update of the Angiosperm Phylogeny Classification for the orders and families of flowering plants: APG IV. *Bot. J. Linn. Soc.* 181 (1), 1–20.
- Clausnitzer, D.W., Borman, M.M., Johnson, D.E., 1999. Competition between *Elymus elymoides* and *Taeniatherum caput-medusae*. *Weed Sci.* 47, 720–728.
- Davidson, J., Hassanzadeh, J., Berzins, R., Stockli, D.F., Bashukoo, B., Turrin, B., Pandamouz, A., 2004. The geology of Damavand volcano, Alborz Mountains, northern Iran. *Geology* 116, 16–29.
- Davies, C.P., Fall, P.L., 2001. Modern pollen precipitation from an elevational transect in central Jordan and its relationship to vegetation. *J. Biogeogr.* 28 (10), 1195–1210.
- Davis, S.D., Heywood, V.H., Hamilton, A.C., 1994. *Centres of Plant Diversity*. IUCN Publications Unit, Cambridge.
- Djmal, M., de Beaulieu, J.-L., Shah-Hosseini, M., Andrieu-Ponel, V., Amini, A., Akhane, H., Leroy, S.A.G., Stevens, L., Alizadeh, H., Ponel, P., Brewer, S., 2008. An Upper Pleistocene long pollen record from the Near East, the 100 m-long sequence of Lake Urmia, NW Iran. *Quat. Res.* 69, 413–420.
- Djmal, M., de Beaulieu, J.-L., Campagne, P., Akhane, H., Andrieu-Ponel, V., Ponel, P., Leroy, S.A.G., 2009a. Modern pollen rain – vegetation relationships along a forest – steppe transect in the Golestan National Park, NE Iran. *Rev. Palaeobot. Palynol.* 153, 272–281.
- Djmal, M., de Beaulieu, J.-L., Miller, N., Andrieu-Ponel, V., Berberian, M., Gandouin, E., Lahijani, H., Ponel, P., Salimian, M., Guiter, F., 2009b. A late Holocene pollen record from Lake Almalou in NW Iran: evidence for changing land-use in relation to some historical events during the last 3700 years. *J. Archaeol. Sci.* 36, 1346–1375.
- Djmal, M., De Beaulieu, J.L., Miller, N.F., Andrieu-Ponel, V., Ponel, P., Lak, R., Sadeddin, N., Akhane, H., Fazeli, H., 2009c. Vegetation history of the SE section of the Zagros Mountains during the last five millennia; a pollen record from the Maharlou Lake, Fars Province, Iran. *Veg. Hist. Archaeobotany* 18 (2), 123–136.
- Djmal, M., Akhane, H., Khoshravesh, R., Andrieu-Ponel, V., Ponel, P., Brewer, S., 2011. Application of the global bioclimatic classification to Iran: implications for understanding the modern vegetation and biogeography. *Ecol. Mediterr.* 37, 91–114.
- Djmal, M., Baumel, A., Brewer, S., Jackson, S.T., Kadereit, J.W., López-Vinallonga, S., Mehregan, I., Shabanian, E., Simakova, A., 2012. Ecological implications of Cousinia Cass. (Asteraceae) persistence through the last two glacial–interglacial cycles in the continental Middle East for the Irano-Turanian flora. *Rev. Palaeobot. Palynol.* 172, 10–20.
- Djmal, M., Jones, M.D., Migliore, J., Balatti, S., Fader, M., Contreras, D., Gondet, S., Hosseini, Z., Lahijani, H., Naderi, A., Shumilovskikh, L.S., 2016. Olive cultivation in the heart of the Persian Achaemenid Empire: new insights into agricultural practices and environmental changes reflected in a late Holocene pollen record from Lake Parishan, SW Iran. *Veg. Hist. Archaeobotany* 25 (3), 255–269.
- Dolédéc, S., Chessel, D., 1994. Co-inertia analysis: an alternative method for studying species–environment relationships. *Freshw. Biol.* 31 (3), 277–294.
- Dray, S., Chessel, D., Thioulouse, J., 2003. Co-inertia analysis and the linking of ecological data tables. *Ecology* 84 (11), 3078–3089.
- El-Moslimany, A.P., 1983. History of Climate and Vegetation in the Eastern Mediterranean and the Middle East from the Pleniglacial to the Mid-Holocene. (Ph.D. Thesis). University of Washington, Seattle.
- El-Moslimany, A.P., 1987. The late Pleistocene climates of the Lake Zeribar region (Kurdistan, western Iran) deduced from the ecology and pollen production of nonarborescent vegetation. *Plant Ecol.* 72 (3), 131–139.
- El-Moslimany, A.P., 1990. Ecological significance of common nonarborescent pollen: examples from drylands of the Middle East. *Rev. Palaeobot. Palynol.* 64 (1–4), 343–350.
- Fægri, K., Iversen, J., 1989. *Textbook of Pollen Analysis*. 4th Edition. Wiley, Chichester.
- Fernández-Illascales, F., Nieva, F.J.J., Silva, I., Tormo, R., Muñoz, A.F., 2010. Pollen production of Chenopodiaceae species at habitat and landscape scale in Mediterranean salt marshes: an ecological and phenological study. *Rev. Palaeobot. Palynol.* 161 (3), 127–136.
- Firouz, E., 1976. Environmental and nature conservation in Iran. *Environ. Conserv.* 3 (01), 33–42.
- Fowell, S.J., Hansen, B.C., Peck, J.A., Khosbayan, P., Ganbold, E., 2003. Mid to late Holocene climate evolution of the Lake Telmen Basin, North Central Mongolia, based on palynological data. *Quat. Res.* 59 (3), 353–363.
- Grimm, E.C., 2004. *TILIA and TGView software*. Ver 2.0.2. Illinois State University, Springfield, 2005.
- Hennekens, S.M., Schaminée, J.H., 2001. TURBOVEG, a comprehensive data base management system for vegetation data. *J. Veg. Sci.* 12 (4), 589–591.
- Hernández-Ledesma, P., Berendsohn, W.G., Borsch, Th., von Mering, S., Akhane, H., Arias, S., Castañeda-Noa, I., Eggli, U., Eriksson, R., Flores-Olvera, H., Fuentes-Bazán, S., Kadereit, G., Klak, C., Korotkova, N., Nyffeler, R., Ocampo, G., Ochoterena, H., Oxelman, B., Rabaler, R.K., Sanchez, A., Schlumberger, B.O., Uotila, P., 2015. A taxonomic backbone for the global synthesis of species diversity in the angiosperm order Caryophyllales. *Willdenowia* 45 (3), 281–383.
- Herzschuh, U., 2007. Reliability of pollen ratios for environmental reconstructions on the Tibetan Plateau. *J. Biogeogr.* 34 (7), 1265–1273.
- Hill, M.O., 1979. TWINSpan: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Section of Ecology and Systematics, Cornell University.
- Khalili, A., 1973. Precipitation patterns of central Elburz. *Theor. Appl. Climatol.* 21 (2), 215–232.
- Krinsley, D.B., 1970. *A Geomorphological and Paleoclimatological Study of the Playas of Iran*. U.S. Government Printing Office, Washington, D. C.
- Liu, H., Wang, Y., Tian, Y., Zhu, J., Wang, H., 2006. Climatic and anthropogenic control of surface pollen assemblages in East Asian steppes. *Rev. Palaeobot. Palynol.* 138 (3), 281–289.
- Moore, P.D., Stevens, A.C., 1982. Pollen studies in dry environments. In: Spooner, B., Mann, H.S. (Eds.), *Desertification and Development, Dryland Ecology in Social Perspective*. Academic Press, London, pp. 249–267.
- Moore, P.D., Webb, J.A., Collinson, M.E., 1991. *Pollen Analysis*. 2nd ed. Blackwell Scientific Publications, Oxford (216 pp.).
- Noroozi, J., Willner, W., Pauli, H., Grabherr, G., 2014. Phytosociology and ecology of the high-alpine to subalpine scree vegetation of N and NW Iran (Alborz and Azerbaijan Mts.). *Appl. Veg. Sci.* 17 (1), 142–161.
- Pahlevani, A.H., Liede-Schumann, S., Akhane, H., 2015. Seed and capsule morphology of Iranian perennial species of Euphorbia (Euphorbiaceae) and its phylogenetic application. *Bot. J. Linn. Soc.* 177 (3), 335–377.
- R Development Core Team, 2012. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria (URL, <http://www.R-project.org>).
- Ramezani, E., Marvie Mohadjer, M.R., Knapp, H.D., Ahmadi, H., Joosten, H., 2008. The late-Holocene vegetation history of the Central Caspian (Hyrcanian) forests of northern Iran. *The Holocene* 18 (2), 307–321.



- Ramezani, E., Mohadjer, M.R.M., Knapp, H.D., Theuerkauf, M., Manthey, M., Joosten, H., 2013. Pollen–vegetation relationships in the central Caspian (Hyrcanian) forests of northern Iran. *Rev. Palaeobot. Palynol.* 189, 38–49.
- Rechinger, K.H. (Ed.), 1963–2015. *Flora Iranica*, Vols 1–178. Akademische Druck-u. Verlagsanstalt, Graz, Naturhistorisches Museum, Wien.
- Rechinger, K.H., Wendelbo, P., 1976. Plants of the Kavir Protected Region, Iran. *Iran. J. Bot.* 1, 23–56.
- Reille, M., 1992. Pollen et Spores d'Europe et d'Afrique du Nord. Laboratoire de botanique historique et de palynologie, Marseille (520 pp.).
- Reille, M., 1995. Pollen et Spores d'Europe et d'Afrique du Nord, Supplément 1. Laboratoire de botanique historique et de palynologie, Marseille (327 pp.).
- Reille, M., 1998. Pollen et Spores d'Europe et d'Afrique du Nord, Supplément 2. Laboratoire de botanique historique et de palynologie, Marseille (536 pp.).
- Thioulouse, J., Cadet, P., Albrecht, A., 1995. The use of permutation tests in co-inertia analysis: application to the study of nematode-soil relationships. In: Randall, J.H. (Ed.), *Fourth Meeting of the East, Central and Southern African Network of the International Biometric Society: Proceedings*. University of Stellenbosch, Stellenbosch, pp. 144–152.
- Tichý, L., 2002. JUICE, software for vegetation classification. *J. Veg. Sci.* 13 (3), 451–453.
- Tzedakis, P.C., 1994. Vegetation change through glacial–interglacial cycles: a long pollen sequence perspective. *Philos. Trans. R. Soc. Lond. B* 345, 403–432.
- Van Campo, E., Gasse, F., 1993. Pollen-and diatom-inferred climatic and hydrological changes in Sumxi Co Basin (Western Tibet) since 13,000 yr BP. *Quat. Res.* 39 (3), 300–313.
- Van Zeist, W., 1967. Late Quaternary vegetation history of western Iran. *Rev. Palaeobot. Palynol.* 2 (1–4), 301–311.
- Van Zeist, W., Bottema, S., 1977. Palynological investigations in western Iran. *Palaeohistoria* 19, 19–85.
- Welten, M., 1957. Über das glaziale und spätglaziale Vorkommen von *Ephedra* am nordwestlichen Alpenrand.- *Berichte der Schweizerischen Botanischen Gesellschaft*. 67 pp. 33–54.
- Wendelbo, P., 1982. *Liliaceae* I. In: Rechinger, K.H. (Ed.), *Flora Iranica*, 151 Akademische Druck u. Verlagsanstalt, Graz, p. 31.
- White, F., Léonard, J., 1991. Phytogeographical links between Africa and Southwest Asia. *Flora Vegetatio Mundi* 9, 229–246.
- Wright, H.E., 1961. Pleistocene glaciation in Kurdistan. *Eiszeit. Gegenw.* 12, 131–164.
- Wright Jr., H.E., McAndrews, J.H., van Zeist, W., 1967. Modern pollen rain in western Iran, and its relation to plant geography and Quaternary vegetational history. *J. Ecol.* 415–443.
- Yang, X., Scuderi, L.A., 2010. Hydrological and climatic changes in deserts of China since the late Pleistocene. *Quat. Res.* 73 (1), 1–9.
- Yasuda, Y., Kitagawa, H., Nakagawa, T., 2000. The earliest record of major anthropogenic deforestation in the Ghab Valley, northwest Syria: a palynological study. *Quat. Int.* 73, 127–136.
- Yuecong, L., Qinghai, X., Yingkui, Z., Xiaolan, Y., Jule, X., Hui, C., Xinmiao, L., 2005. Pollen indication to source plants in the eastern desert of China. *Chin. Sci. Bull.* 50 (15), 1632–1641.
- Zhao, Y., Herzschuh, U., 2009. Modern pollen representation of source vegetation in the Qaidam Basin and surrounding mountains, north-eastern Tibetan Plateau. *Veg. Hist. Archaeobotany* 18 (3), 245–260.
- Zhao, Y., Yu, Z., Chen, F., Liu, X., Ito, E., 2008. Sensitive response of desert vegetation to moisture change based on a near-annual resolution pollen record from Gahai Lake in the Qaidam Basin, northwest China. *Glob. Planet. Chang.* 62 (1), 107–114.
- Zhao, Y., Liu, H., Li, F., Huang, X., Sun, J., Zhao, W., Herzschuh, U., Tang, Y., 2012. Application and limitations of the *Chenopodiaceae/Artemisia* pollen ratio in arid and semi-arid China. *The Holocene* 22 (12), 1385–1392.