



The Diaptomidae (Copepoda, Calanoida) of Tunisia and the role of spatial and environmental factors as drivers of their distribution patterns

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Abstract Even in a biodiversity hotspot such as the Mediterranean basin, aspects relating to the distribution of some groups of microcrustaceans still need clarification. In this paper, we critically analyse the available information on diaptomid copepods in Tunisian inland waters and, based on the largest sampling campaign to date carried out in the country, report new data on their distribution. In the frame of this study, 248 crustacean samples were collected from 190 sites, and 10 diaptomid species belonging to 7 genera and 2 subfamilies were found in the

samples. Their distribution follows a climate gradient determined by precipitation, and ecological variables mainly affect diaptomid distribution in the study area, while pure spatial factors are of negligible importance. Diaptomid biodiversity is therefore strongly linked to the diversity of inland waters that characterise the country. This is especially true in the wetlands of the Medjerda alluvial plain, where six diaptomid species co-occurred sympatrically, with up to four or five species coexisting syntopically and synchronically in some sites. Unfortunately, the natural water bodies of this plain are currently strongly threatened by urban expansion and agricultural reclamation, and the risk of local extinction for the species they host is increasingly high.

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Introduction

Our understanding of the ecology, biogeography and natural history of taxa must be necessarily based on the sound identification of the biological units we are dealing with, and on an accurate knowledge of their distribution. In the absence of this information, or it being of inadequate or of uneven quality, any inference is susceptible to important biases (Agapow et al., 2004; Fišer et al., 2018; Marrone et al., 2022). Along with a stable taxonomy based on phylogenetic informative characters, the realisation of accurate faunal surveys is thus pivotal for our understanding of Nature and for its management.

Calanoid copepods are crustaceans mostly linked with lentic water bodies, where they constitute a keystone component of aquatic ecosystems (Hutchinson, 1967; Boxshall & Defaye, 2008). Representatives of the family Diaptomidae dominate the inland water calanoid copepod fauna of Europe, Asia, North America, Africa, and part of South America (Dussart & Defaye, 2001). This copepod family is characterised by a stable taxonomy, a moderate diversity, and by distribution patterns shaped by both ecological and historical factors, being thus an ideal study taxon for investigating diversity patterns in freshwater invertebrates (Leibold et al., 2010; Perbiche-Neves et al., 2014; Henriques-Silva et al., 2016; Marrone et al., 2017, and references therein). In the western Palearctic biogeographical region, 94 native diaptomid species are reported to occur, with a peak in species richness located between 40° and 45° north of latitude, i.e., in the central and northern circum-Mediterranean area (Marrone et al., 2017). However, the accuracy of the information available for different regions within the western Palearctic is uneven, and occurrence and distribution data are not exhaustive for most of the countries located along the southern and eastern shores of the Mediterranean Sea.

The currently available information on diaptomid copepods occurring in the Maghreb is mainly based on papers published in the first half of the twentieth century, summarised by Mouelhi et al. (2000, but see also Hamaidi et al., 2010 and Marrone et al., 2017

for some amendments). For this reason, the need for recent, extensive surveys in these areas has often been stressed. In this frame, the high diversity of Tunisian climate and landscape (Morgan, 1982) and its geographic position at the centre of the Mediterranean basin make Tunisia an extremely interesting study area, where diaptomid faunas with different ecological requirements and biogeographical affinities could converge. The pioneering studies by Gauthier (e.g., 1928, 1933) suggested the presence in the country of different copepod assemblages, whose distribution is mostly determined by the amount of annual precipitation. Such a sharp pattern has been recently tested for other inland water taxa, with somehow controversial results, although the existence of a faunal latitudinal pattern in the country is rather evident (cf. Dumont et al., 1979; Turki and El Abed, 1999; Marrone et al., 2016a, b; Stoch et al., 2016; Marrone et al., 2020a).

Based on the most extensive field survey ever carried out on this crustacean group in Tunisian inland waters, we present here an updated checklist of recent diaptomid copepods from Tunisia and provide data on taxa distribution. In this frame, we analysed the role of spatial and environmental factors as potential drivers of Tunisian diaptomid diversity pattern, attempting to untangle their relative role in explaining species distribution.

Materials and methods

Study area

Tunisia is located in the easternmost part of the Maghreb, between Algeria and Libya (Fig. 1). It encompasses an area of about 164,000 km² between 30° and 37.5° North latitude. The country is characterised by some physiographically and climatically different zones, ranging from Mediterranean to desert landscapes. A detailed description of Tunisian geography and climate can be found in Sicilia et al. (2009) and Marrone et al. (2016a). Gauthier (1928, 1933) stressed the importance of the isohyets of 300 and 500 mm year⁻¹ in determining the composition of the crustacean assemblages in the inland waters of Tunisia and neighbouring Algeria, thus dividing the country in three zones: (1) a rainy zone (“*zone pluvieuse*”), i.e. a humid area with Mediterranean climate and mean annual rainfall > 500 mm; (2) a substeppe zone

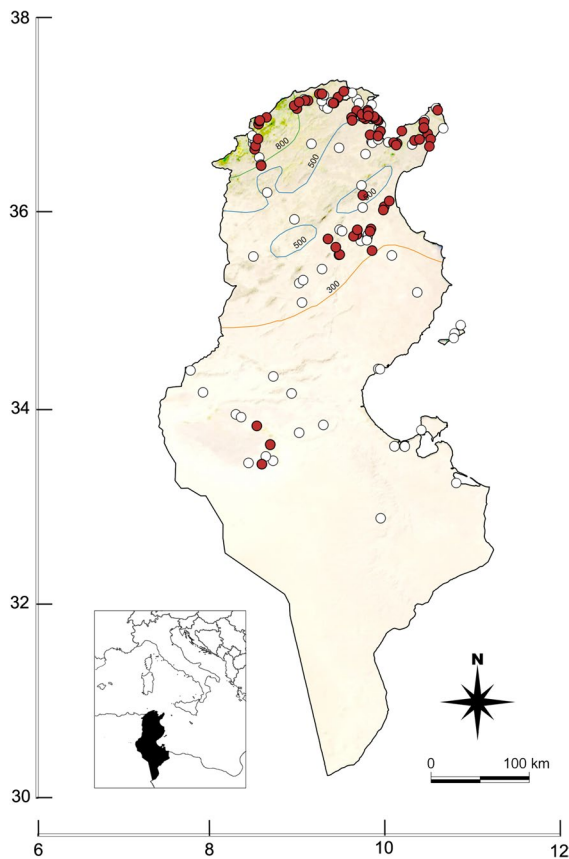


Fig. 1 Location of the sampled sites. Red dots: sites where at least one diaptomid species was collected; white dots: sites where no diaptomids were collected

(“*zone substeppique*”), including the eastern coastal part of the country north of Sfax and the Tell plateau, with mean annual rainfall between 300 and 500 mm, and (3) a steppic zone (“*zone steppique*”), i.e. arid, steppic and semi-desertic areas, with mean annual rainfall below 300 mm. In the south, the Sahara Desert area is characterised by annual mean rainfalls lower than 100 mm.

When mapping the distribution of the sampled sites and collected species, we plotted the 300 mm y^{-1} and 500 mm $year^{-1}$ isohyets proposed by Gauthier (1928, 1933). In addition to these, we further plotted the 800 mm $year^{-1}$ isohyet to consider a “hyper-humid” area, which was not appraised by former authors, within the rainy zone.

Bibliographical review

A database of the papers dealing with Tunisian diaptomid copepods was compiled based on an extensive literature search. In addition, queries on the databases of Google Scholar (<https://scholar.google.it/>) and SCOPUS® (www.scopus.com) were performed using different combinations of the keywords: “*diaptomus”, “diaptomid*”, “Maghreb”, and “tunis*”. Further queries were performed using the binomia of the diaptomid species known to occur in the country and “tunis*”. A comprehensive coverage of the published data was performed, but data published in theses and grey literature may have been overlooked. All obtained occurrence data were critically revised and, when possible, checked through targeted sampling surveys.

Sampling and species identification

Tunisian surface lentic water bodies were investigated from 2002 to 2012. Sampled water bodies ranged from large swamps or coastal lakes to small pools on dirt roads in the rainy, substeppic and steppic areas. Both natural (swamps, pools, and ponds) and man-made (reservoirs) water bodies with different hydroperiods were included in the sampling survey. Some of the sites were repeatedly visited in different months and years to account for the seasonal successions and the possible inter-annual differences of their copepod assemblages. Geographic coordinates of the sampling sites were registered in situ with a Garmin GPS device, and then checked in Google Earth™. Each sampling site was identified by an alphanumeric code consisting of a letter followed by a number. Distribution maps were realised using the QGIS freeware software v. 3.16 (QGIS Development Team, 2020).

Crustacean samples were collected by means of two different nets: a towing net with a mesh size of 125 μm was used in the open waters of larger water bodies, and a hand net with 200 μm mesh size was used for the littoral zone and in shallower water bodies. Collected samples were fixed in situ in 4% buffered formalin (samples collected from 2002 to 2005) or 90% ethanol (from 2006 to 2012). When the water bodies visited were dry, sediment samples were collected and cultured in laboratory following the so-called “Sars’ method” as described in Marrone et al. (2019). All samples are stored in FM’s crustacean

collection at the Department “STEBICEF” (Dip.to di Scienze e Tecnologie Biologiche Chimiche e Farmaceutiche—University of Palermo, Palermo, Italy) and are available for loan on request.

The morphological identification of collected calanoids was based on Dussart (1989), Kiefer (1978), and Rayner (1999). The identity of some *Hemidiaptomus* and *Metadiaptomus* taxa have been also checked through the sequencing of mitochondrial and nuclear DNA markers (see Marrone et al., 2010, 2013, 2016b, 2020b). Diaptomid nomenclature was based on Dussart & Defaye (2002) with the only exception of the genus *Hemidiaptomus*, for which we referred to Marrone et al. (2013).

Sample-based rarefaction curves (Gotelli & Colwell, 2001) were computed to evaluate whether the sampling effort was exhaustive enough to be representative of the diaptomid diversity of the study area. The non-parametric species richness estimators Jackknife1 (first order Jackknife-based estimator), and the bias-corrected formula of Chao2 were calculated. Analyses were done using the routines available in the Primer 6+PERMANOVA software (Anderson et al., 2008).

Statistical analyses

Along with the collection of crustacean samples, selected environmental parameters and variables were measured for each sampling site following the approach described in Stoch et al. (2016): elevation (Elev, m a.s.l.), size (classes), electrical conductivity (Cond, $\mu\text{S}/\text{cm}$), turbidity (Turb, classes), and macrophyte cover (Macr, classes). Three climatic variables were used as predictors of species distribution: actual evapotranspiration (AET), average monthly maximum temperature (T_{max} , $^{\circ}\text{C}$), and average monthly precipitation (Prec, mm). T_{max} and Prec were obtained from the WorldClim database (www.worldclim.org; Hijmans et al., 2005); annual actual evapotranspiration (AET) data were extracted from the map released by Trabucco & Zomer (2010). Both maps had a 30 arc-second resolution. Variables were standardized to zero mean and unit variance to account for their different scales of measurement.

Considering that the mixohaline species *Arctodiaptomus salinus*, present in seven sites (four located along the coast and three in inner saline waters) where it was the only diaptomid present, distorted

the analyses making unclear the scenario depicted using the other species, it was excluded from further analyses. Distance-based Moran’s Eigenvector Maps (dbMEMs: Dray et al., 2012) were used to describe the spatial structure of the dataset. dbMEM eigenvectors were computed using R package *PCNM* (Legendre et al., 2015) from a truncated geodesic distance matrix obtained with R package *fields* (Furrer et al., 2011). The longest distance connecting two ponds in a minimum spanning tree was used as a threshold to truncate the distance matrix. A forward selection procedure with double-stopping performed in R package *packfor* (Dray, 2016) was used to only select dbMEMs that significantly explained the variation in the species composition matrix. This procedure recovered 3 dbMEMs (Fig. S1).

A Mantel’s correlogram (Borcard & Legendre, 2012) was implemented to assess the pattern of spatial autocorrelation of the species similarity matrix (calculated using Sorensen’s index) to obtain the geographical distance threshold above which sites are to be considered no more autocorrelated. The analyses were performed using the R package *ecodist* (Goslee & Urban, 2002).

Relationships between diaptomid assemblages and environmental and spatial variables data were assessed by a distance-based redundancy analysis (dbRDA: Legendre & Anderson 1999). Analyses were implemented in the Primer 6+PERMANOVA software; variation partitioning was applied to dbRDA using the command *varpar* in R package *vegan* (Oksanen et al., 2022).

Results

Bibliographical review

Altogether, 21 studies were found providing original data on the occurrence of Diaptomidae in Tunisia, and 11 reviews based on existing data. The first reference to diaptomid copepods in Tunisia is reported by Gurney (1909), who described three new species from “Oued Tindja”, i.e., *Hemidiaptomus ingens* (Gurney, 1909), *Diaptomus cyanus* Gurney, 1909, and *Copidodiaptomus numidicus* (Gurney, 1909), and reported the occurrence of three further species, *Arctodiaptomus salinus* (Daday, 1885), *A. wierzejskii* (Richard, 1888), and

Mixodiaptomus incrassatus (Sars, 1903). Later, Brehm (1924) described the controversial species *Eudiaptomus ziegelmayeri* (Brehm, 1924) from an unspecified locality in the Sahara (see below), and Roy (1927) described *Hemidiaptomus gurneyi* (Roy, 1927) from a pond near Tabarka. Contributions by Roy & Gauthier (1927a, 1927b) and Gauthier (1928) added the species *Mixodiaptomus lilljeborgi* (Guerne & Richard, 1888) and *Metadiaptomus chevreuxi* (Guerne & Richard, 1894) to the checklist of Tunisian diaptomids, and delineated their regional distribution. Subsequent papers (Dumont et al., 1979; Morgan, 1982; Soholobji et al., 1993; Ramdani et al., 2001; Sellami et al., 2010, 2016; Marrone et al., 2010, 2013, 2016b; Montevago et al., 2020; Rogers et al., 2021) added some further occurrence localities but no new species to the Tunisian fauna, with the exceptions of *Paradiaptomus similis* Van Douwe, 1912 (reported as *P. greeni* (Gurney, 1906) by Turki & El Abed, 1999 and Turki & Turki, 2010) and *Eudiaptomus* sp. (Sellami et al., 2009; 2011). Available synopses including data on Tunisian diaptomid fauna are those by Tollinger, (1911), Roy & Gauthier (1927a), Kiefer (1978), Dussart (1989), Zaouali (1995), Mouelhi et al. (1999, 2000), Dussart & Defaye (2002), and Marrone et al. (2017), although none of these reviews discuss the possible presence of *Eudiaptomus* species in the country. Brtek (1977) and Rayner (1999) reported the occurrence of *Neolovenula alluaudi*

(Guerne & Richard, 1890) in Tunisia, without providing exact localities or any reference supporting this statement. Although the species is known from all other North African countries (Alfonso & Belmonte, 2013), sound evidence about its occurrence in Tunisia is to date lacking; therefore *N. alluaudi* is here excluded from its fauna.

Sampling sites and species diversity

In the frame of this study, 248 crustacean samples were collected from 190 sites. A synopsis of the environmental data and collected copepods for each site and sampling date is reported in Table S1.

Diaptomid copepods were found in 85 (45%) of the surveyed sites. A total of 10 diaptomid species belonging to 7 genera and 2 subfamilies were found in the samples (Table 1). The occurrence sites for each of the recorded species are shown in Fig. 2. With the only exception of *Arctodiaptomus salinus*, collected as far south as 33.4° N latitude, all the diaptomid species in the frame of this survey were found north of 35.5° N latitude.

Rarefaction curves and species richness estimators are reported in Fig. 3. The sample-based rarefaction curve of observed species richness based on the sampling data and the implemented non-parametric species richness estimators (Chao2 and Jackknife1) reached the asymptote for a species richness of 10, thus suggesting that the recorded species richness is

Table 1 Checklist of the Tunisian Diaptomidae and their acronyms

Taxa	Number of sites	Acronyms
Diaptominae		
<i>Arctodiaptomus (Arctodiaptomus) wierzejskii</i> (Richard, 1888)	40	Awie
<i>Arctodiaptomus (Rhabdodiaptomus) salinus</i> (Daday, 1885)	11	Asal
<i>Copiodiaptomus numidicus</i> (Gurney, 1909)	11	Cnum
<i>Diaptomus (Chaetodiaptomus) cyaneus</i> Gurney, 1909	13	Dcya
* <i>Eudiaptomus</i> sp.	0	–
* <i>Eudiaptomus ziegelmayeri</i> (Brehm, 1924)	0	–
<i>Hemidiaptomus (Hemidiaptomus) gurneyi</i> (Roy, 1927)	6	Hgur
<i>Hemidiaptomus (Occidodiaptomus) ingens</i> (Gurney, 1909)	7	Hing
<i>Mixodiaptomus incrassatus</i> (Sars, 1903)	16	Minc
<i>Mixodiaptomus lilljeborgi</i> (Guerne & Richard, 1888)	9	Mlil
Paradiaptominae		
<i>Metadiaptomus chevreuxi</i> (Guerne & Richard, 1894)	16	Mche
<i>Paradiaptomus similis</i> Van Douwe, 1912	2	Psim

*Doubtful records (see text)

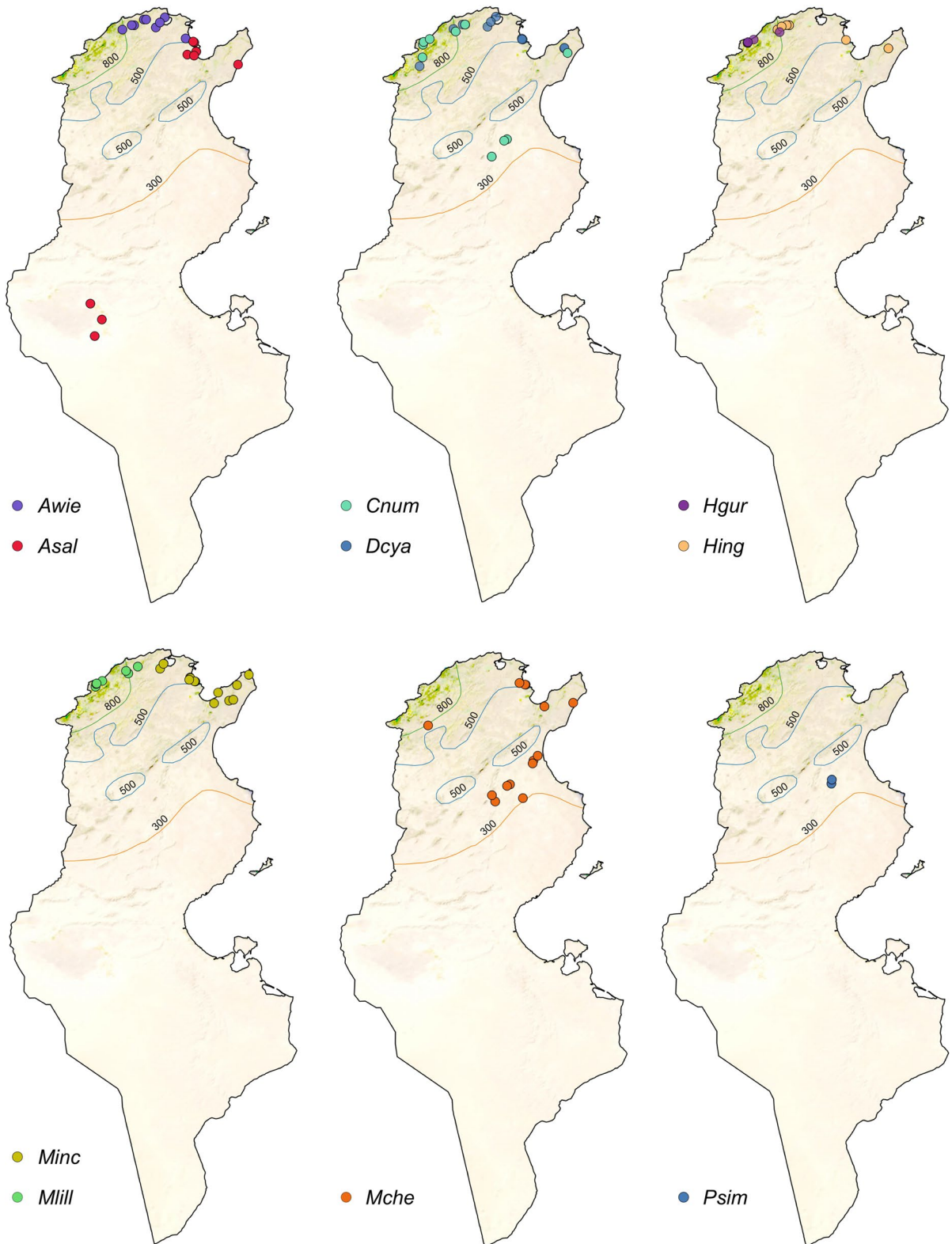
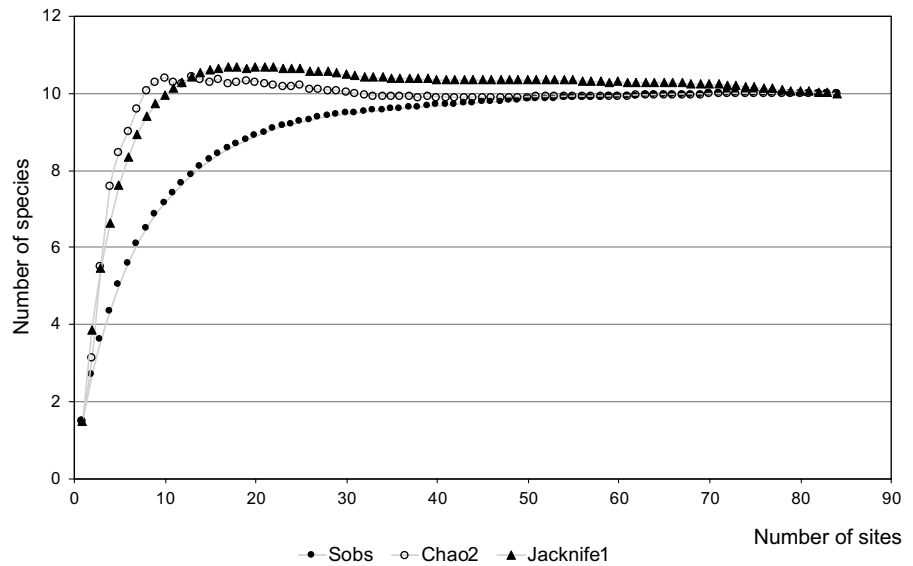


Fig. 2 Distribution maps of diaptomid species based on the present survey

Fig. 3 Species accumulation curves for diaptomid copepods in Tunisian water bodies at increasing sample size. Sobs: species rarefaction curve of observed species richness (mean values of 9999 randomizations); Chao 2 and Jackknife 1: estimated species richness using different formulas. The sampling effort yielded all the estimated species (i.e., 10 species)



likely representative of the diaptomid diversity occurring in the study area.

No species new to Tunisia were observed, although the study of Paradiaptominae *Paradiaptomus similis* samples from sites F072 and F247 allowed to amend the identification of the Tunisian *Paradiaptomus* populations, previously ascribed to the morphologically similar *Paradiaptomus greeni* by Turki & El Abed (1999) and Turki & Turki (2010), based on the morphology of male P5 and A1 (Rayner, 1999). This is in agreement with the expectations by Rayner (1999), who hypothesized that all *P. greeni* reports from Africa are in fact likely to be ascribed to *P. similis*.

In this survey, no species belonging to the genus *Eudiaptomus* were collected, thus not confirming its occurrence in the country.

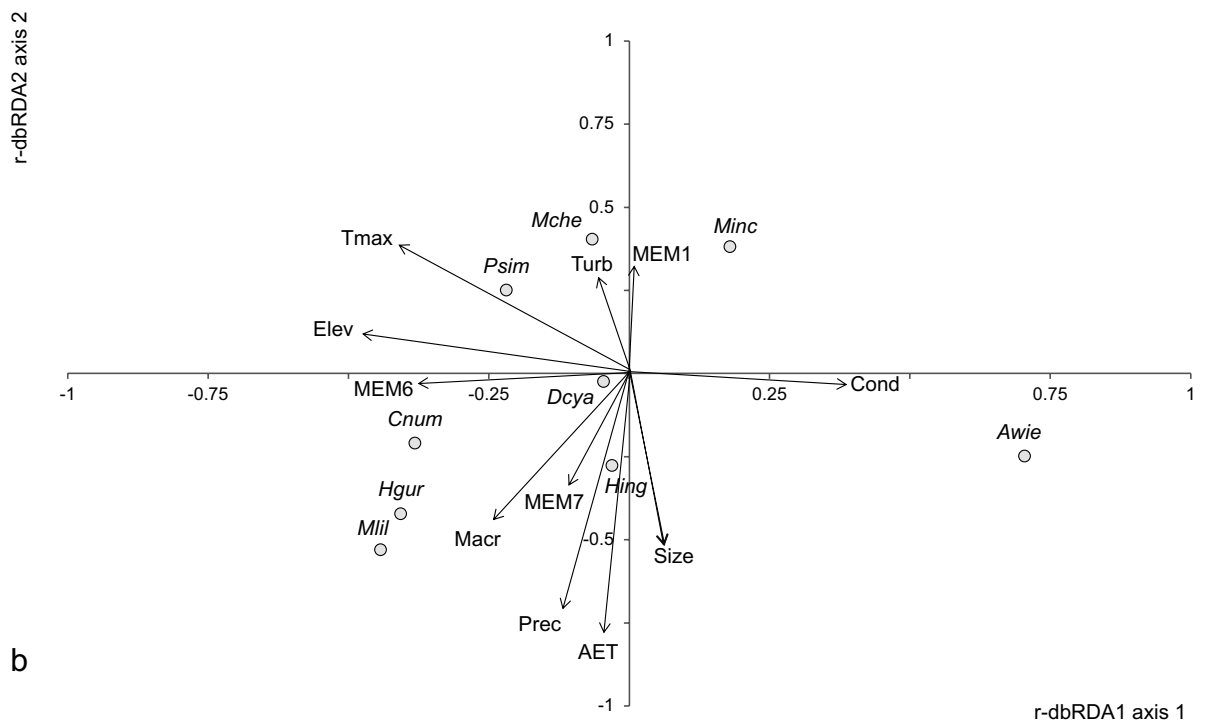
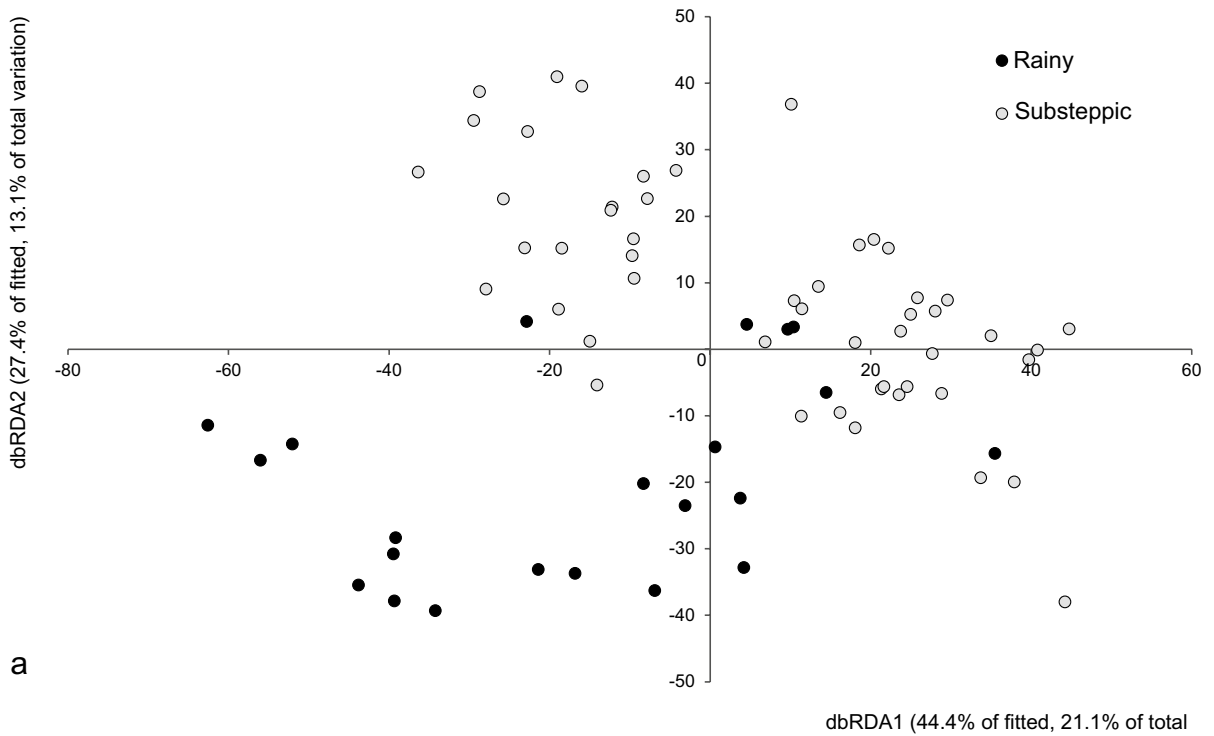
Spatial and environmental drivers of species diversity

The first two axes of dbRDA (Fig. 4) explained 71.8% of constrained variation (and 34.2% of total variation), indicating that the correlation between predictor variables and species distribution was quite high. The plot of sampling sites (Fig. 4a) clearly showed that ponds grouped into the two ecological zones defined for the Tunisian territory are clearly separated by the diaptomid assemblages. The first axis represented an elevational gradient, paralleled by maximum temperature and dbMEM6 (Fig. 4b), while conductivity was negatively correlated with these variables. The

second axis represented a precipitation gradient, paralleled by actual evapotranspiration (AET) and, to a minor extent, pond size and macrophyte cover. The contribution of the other parameters was quite small (Fig. 4b), indicating that the remaining variables have a low explanatory power in the analysis.

Diaptomid species projected on the plane defined by the first two dbRDA axes (Fig. 4b) showed that *Arctodiaptomus wierzejskii* is present in sites with higher conductivity, lower elevation, and lower maximum temperatures, while the other species prefer lower conductivity. Its distribution was not correlated with precipitation and AET. While *Mixodiaptomus incrassatus*, *Metadiaptomus chevreuxi* and *Paradiaptomus similis* preferred areas with lower precipitation and AET in the substeppic zone, *Mixodiaptomus lilljeborgi*, *Hemidiaptomus gurneyi* and *H. ingens* were found mainly in the rainy zone. In the same zone, also *Diaptomus cyaneus* and *Copidodiaptomus numidicus* were found, albeit these last two species showed to be less influenced by precipitation than the other ones.

Variation partitioning (Fig. S2, explained variance 29.3%), showed that mainly ecological variables affected diaptomid distribution in Tunisia (24.6% of pure influence), while spatial structure was a poor predictor of their distribution (0.2%). Joint variation was consequently quite low as well, accounting for 4.5% of total variation only.



◀**Fig. 4** Map of the results of distance-based redundancy analysis (dbRDA) using the first two axes (explained constrained variation 71.8%): sites (a) and variables (b). Vectors representing spatial and environmental variables are superimposed on the maps of species (b) using the Spearman's correlation coefficients (r) with canonical axes. Species acronyms are listed in Tab. 1. For the variables acronyms see text

The Mantel's correlogram of the species distribution similarity matrix (Fig. S3) revealed that diaptomid species composition showed significant, positive spatial autocorrelation up to around 30 km distance. This fact indicates abrupt changes in species composition with geographical distance increasing over this limit. Comparing this output with the results of the dbRDA analysis and variation partitioning confirms that the explanatory power of ecological variables was generally decoupled from spatial structures; accordingly, space is a poor predictor of diaptomid assemblages.

Discussion

The diaptomid fauna of Tunisia

The updated checklist of Tunisian diaptomids includes 12 taxa, although two of them, both belonging to the genus *Eudiaptomus*, could not be collected in the frame of present survey (Table 1).

E. ziegelmayeri was erroneously reported for Morocco by Mouelhi et al. (2000) and Dussart & Defaye (2002) whereas, based on the “confused note by Brehm (1924)” (Dumont et al., 1979) the species could have been collected everywhere between Tunisia, Algeria, and Libya. In fact, *E. ziegelmayeri* was described for an unspecified locality in the Sahara, within a radius of 1200 km from Sfax (Tunisia), perhaps in a southerly direction (“Die von Herrn Professor Dr. Brehm aufgeführten Arten sind das Ergebnis der Untersuchungen einer Reihe von Oasenzisternen, welche sich von der kleinen Syrte vom Golf vom Gabès quer durch die Erg oder El Areg, das Sandmeer der Sahara, auf einer Strecke von ungefähr 1200 km, also bis auf mittelfrikanisches Gebiet erstrecken” Brehm, 1924, pag. 311). Therefore, the species may have been collected in Tunisia, Algeria, or Libya, but not in Morocco. Moreover, this species was originally described as *Diaptomus ziegelmayeri*, never collected again after its original description,

and moved to the genus *Eudiaptomus* by Kiefer (1932a, 1932b, 1968). However, the sketchy drawings provided by Brehm (1924) are not accurate and the morphology of the male P5 and A1 shown in that paper could be compatible with that of *Copidodiaptomus numidicus*, a species known to occur in Algeria and Tunisia. Only the description of the length of the endopodite of female P5, of which there are no drawings, seems to provide evidence that it might belong to the genus *Eudiaptomus* (“Der fünfte fuss tragt einen Innenast, der gut so lang ist wie das erste Aussenastglied; das dritte Aussenastglied ist gut entwickelt”, Brehm, 1924, pag. 310). Lacking sufficient data about the identity and distribution of this taxon, we here propose to consider *E. ziegelmayeri* as *species inquirenda*.

Sellami et al. (2009, 2011) reported the occurrence of *Eudiaptomus* sp. coexisting with *Copidodiaptomus numidicus* in some reservoirs located in central and northern Tunisia. Unfortunately, no information about the possible identity of these populations were provided by these authors, and no drawings are available. Accordingly, “*Eudiaptomus* sp.” is here reported dubitatively as part of the diaptomid fauna of the country.

According to Marrone et al. (2010, 2013), a complex of closely related species is currently lumped within the binomen *Hemidiaptomus ingens*. Based on available evidence (see also Kiefer, 1954, 1973), only *Hemidiaptomus ingens* s.str. is to date known to occur in Tunisia. This species is distinguished from the other taxa belonging to *H. ingens* s.l. based on the occurrence of apical setae on the endopod of left male fifth legs and based on mitochondrial and nuclear DNA sequences.

The occurrence of a mixed crustacean fauna characterised by different chorotypes has often been stressed for Tunisia (e.g., Dumont et al., 1979; Turki & Turki, 2010), and the pattern is confirmed in this paper. Five major groups of species with different origin and distribution ranges can be singled out among the Tunisian diaptomids. A first group includes species with an alleged Palearctic-wide distribution (*M. incrassatus*, *A. wierzejskii* and *A. salinus*), although the broad distribution of these taxa might be due to the occurrence of cryptic and/or pseudo-cryptic species currently lumped under these binomia (e.g., Montevago et al., 2020). A second group includes species with a primarily west-Mediterranean distribution,

including *H. ingens*, *D. cyaneus*, *M. lilljeborgi*, and *C. numidicus*. The Mediterranean-Turanian species *M. chevreuxi* represents a third group, whereas *Paradiaptomus similis* is the only Afrotropical element of the Tunisian fauna, although the conspecificity of its populations present north and south of the Sahara deserves to be better investigated. Finally, *Hemidiaptomus gurneyi* seems to have colonised the eastern Maghreb from the Balkan area during the Pleistocene (Marrone et al., 2009), being the only taxon with a north-eastern origin within Tunisian diaptomid fauna. Unfortunately, to date nothing can be said about the status and chorology of the controversial *Eudiaptomus* species reported for the country.

Based on the available data, Tunisian diaptomid fauna is similar to the Algerian one, from which it differs only for (i) the absence of the two Paradiaptominae *Neolovenula alluaudi* and *Metadiaptomus mauretanicus* Kiefer & Roy, 1942, which are reported for the Ahaggar and Tassili n'Ajjer in the Algerian Sahara (Kiefer, 1958; Dumont, 1979), (ii) the controversial reports of *Eudiaptomus* spp. in Tunisia (but *E. ziegelmayeri* could have been actually collected in Algeria, see above), and (iii) the recent finding of a few specimens of *Tropodiaptomus incognitus* in northern Algeria (Hamaidi et al., 2010). Moreover, two vicariant but closely related taxa ascribed to *Hemidiaptomus ingens* s.l. occur in the two countries (see Marrone et al., 2013). Accordingly, apart from those taxa with controversial or sporadic occurrence, the difference between the diaptomid fauna of these two countries is only imputable to the paradiaptomine copepod fauna of the Ahaggar and Tassili n'Ajjer areas, in Algeria, whereas the central and northern parts of Algeria and Tunisia are inhabited by very similar diaptomid assemblages (cf. also Gauthier, 1928; Mouelhi et al., 2000). However, it must be stressed that some calanoid taxa known from Tassili n'Ajjer also occurs in the more arid parts of Tunisia (i.e., *M. chevreuxi* and *P. similis*) so that further surveys carried out in the southernmost Tunisian areas are required. In sharp contrast with the similarity between Algerian and Tunisian diaptomid faunas, the Moroccan one is characterised by the occurrence of several taxa which are absent in central and eastern Maghreb (e.g., *Diaptomus castaneti* Burckhardt, 1920, *D. kenitraensis* Kiefer, 1926, *D. cyaneus admotus* Kiefer, 1974, *Mixodiaptomus laciniatus* s.l., *Eudiaptomus chappuisi* (Kiefer, 1926), and

Hemidiaptomus maroccanus Kiefer, 1954), and by the absence of some taxa which are common in Algeria and Tunisia (e.g., *Hemidiaptomus gurneyi*, *Mixodiaptomus lilljeborgi* and *Copiodiaptomus numidicus*). This confirms a general biogeographical pattern which finds a clear east–west divide for both terrestrial and freshwater faunas in the Maghreb (e.g., Beddek et al., 2018; Marrone et al., 2017, 2020a, b, c).

Quite unexpectedly, the diaptomid fauna of Tunisia is quite different from that of Sicily, an island which is geographically very close and climatically similar to northern Tunisia. The diaptomid faunas of these two areas are differentiated by the paucity of “Balkan” and “European” elements in the fauna of Tunisia, and, especially, by the puzzling absence in Sicily of some relatively euryecious and widespread taxa as *Mixodiaptomus incrassatus*, *M. lilljeborgi*, and *Arctodiaptomus wierzejskii* (Marrone et al., 2009), which are common in north-eastern Tunisia and also known to occur in neighbouring regions as Malta, Sardinia, and southern Peninsular Italy (see Alfonso et al., 2021). Unfortunately, our knowledge of the diaptomid fauna of Libya is to date largely incomplete (cf. Dusart & Defaye, 2002; Marrone et al., 2017), so that any inference about its relationship and affinity with Tunisian one is currently impossible.

Due to its climatic range, from Mediterranean to desert climate, most natural lentic water bodies in Tunisia are characterized by a temporary hydroperiod. It is therefore not surprising that seven out of 10 diaptomid species observed in the present survey are closely linked to this habitat type, and the other three (i.e., *A. wierzejskii*, *C. numidicus* and *M. incrassatus*) were observed both in temporary and permanent water bodies (mainly man-made reservoirs). Based on both literature and novel data, diaptomids therefore seem to be scarce or absent in Tunisian natural permanent water bodies, where they are replaced by representatives of the calanoid families Acartiidae, Pseudodiaptomidae and Temoridae (cf. Gurney, 1909; Pesce et al., 1981; Morgan, 1982; Turki & Turki, 2010).

Drivers of biodiversity patterns

In the frame of this survey, only *Arctodiaptomus salinus* was observed in areas with average annual precipitation values lower than 300 mm. i.e., in the steppic zone. However, this species was observed over a wide

latitudinal range, i.e., from the Chott El Djerid (F204) in the south to the Sebkha El Ariana (F043, F082 & F083) in the north, its occurrence being related to the availability of saline water bodies, as also confirmed by its wide global distribution range encompassing different climate belts in the whole Palearctic region (Dussart & Defaye, 2002).

Conversely, the distribution of the other Tunisian diaptomid species follows a climatic gradient determined by precipitation and actual evapotranspiration, with *Hemidiaptomus gurneyi* and *Mixodiaptomus lilljeborgi* strictly linked to areas with annual precipitation values higher than 800 mm (i.e., the “hyperhumid area”), *H. ingens* and *Diaptomus cyaneus* mostly occurring in areas with annual rainfall between 500 and 800 mm (rainy zone), *M. incrassatus* and *A. wierzejskii* observed mainly in areas with precipitation between 300 and 800 mm year⁻¹ (i.e., both in rainy and substeppic zones, but not in the hyperhumid area), and the paradiaptomine *Metadiaptomus chevreuxi* and *Paradiaptomus similis* mostly occurring in the substeppic zone, characterized by precipitation values between 300 and 500 mm year⁻¹. In this survey, *Copidodiaptomus numidicus* was observed to occur from the substeppic zone to the hyperhumid area, both in permanent and temporary water bodies with different salinity, thus proving to be the most euryecious diaptomid occurring in Tunisia.

In brief, these observations agree with those of Gauthier (1928), Dumont et al. (1979), and Turki & El Abed (1999), although some occurrence sites were found in allegedly unsuitable zones for the species. This suggests a scenario where the current distribution of Tunisian diaptomids is strongly influenced but not strictly determined by the annual precipitation pattern, probably due to local ecological factors, as also supported by the results of the dbRDA analysis (Fig. 4b). Moreover, variation partitioning suggested that mainly ecological variables affected diaptomid distribution in the study area, while pure spatial factors are of negligible importance. Mantel’s correlogram suggests a spatial autocorrelation of diaptomid similarity matrix (excluding *Arctodiaptomus salinus*) at short distance, and further supports the hypothesis that local ecological factors finely tune the diaptomid distribution in Tunisian water bodies, as already observed for other biogeographical regions (e.g., Perbiche-Neves et al., 2019).

In a previous paper (Stoch et al., 2016), it was observed that Tunisian large branchiopod distribution was determined mainly by species response to spatially structured environmental gradients. Space accounted for 15% of total variation in dbRDA analysis and sampling sites closer than about 100 km were significantly autocorrelated. This difference is mostly explained by the presence of a quite diverse branchiopod assemblage in the large arid zone of central and southern Tunisia, where diaptomids are substantially absent (except for *A. salinus* in saline sites). Comparing the Mantel’s autocorrelograms of the same areas (rainy and steppic zones), autocorrelation values for diaptomids and large branchiopods are indeed similar, indicating that local ecological drivers determine both crustacean assemblages in these northern zones.

In the wetlands of the Medjerda alluvial plain, close to the river mouth, six diaptomid species co-occur sympatrically, with up to four or five species coexisting syntopically and synchronically in some sites (e.g., F037, F084; Tab S1). The same observation was reported for large branchiopods as well (Stoch et al. 2016; Marrone et al. 2016a, b), with up to 7 species co-occurring syntopically in some sites. This area thus confirms its role as a biodiversity hotspot for Tunisian inland water fauna, in agreement with Marrone et al. (2020a) for ostracods, and Sicilia et al. (2009) for amphibians. This high biological diversity is likely due to the geographical location of the flood plain, at the boundary of the rainy and substeppic zones, and to the existence of a local patchwork of water bodies with different hydroperiod and electrical conductivity. This aspect has also been noted for large branchiopods in the Chaouia plain in Morocco (Thiéry, 1991). Unfortunately, natural water bodies in these plains are nowadays heavily threatened by urban expansion and agricultural reclamation and many sites that hosted diaptomids have disappeared in the last years. The risk of local extinction for these species is therefore increasingly high and conservation plans aimed at investigating and safeguarding biodiversity in southern Mediterranean countries should be supported and increased.

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Data availability The data that support the findings of this study are available from the corresponding author, [FM], upon reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical approval N.a.

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