



Unravelling the environmental correlates influencing the seasonal biodiversity of aquatic Heteropteran assemblages in northern Africa

Noura Slimani, Eric Guilbert, James White, Matthew Hill, Paul Wood,
Moncef Boumaïza, Jean Thioulouse

► To cite this version:

Noura Slimani, Eric Guilbert, James White, Matthew Hill, Paul Wood, et al.. Unravelling the environmental correlates influencing the seasonal biodiversity of aquatic Heteropteran assemblages in northern Africa. *Limnologia*, 2022, pp.126021. 10.1016/j.limno.2022.126021 . hal-03778516

HAL Id: hal-03778516

<https://hal.science/hal-03778516>

Submitted on 15 Sep 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

High Heteroptera biodiversity

Low Heteroptera biodiversity

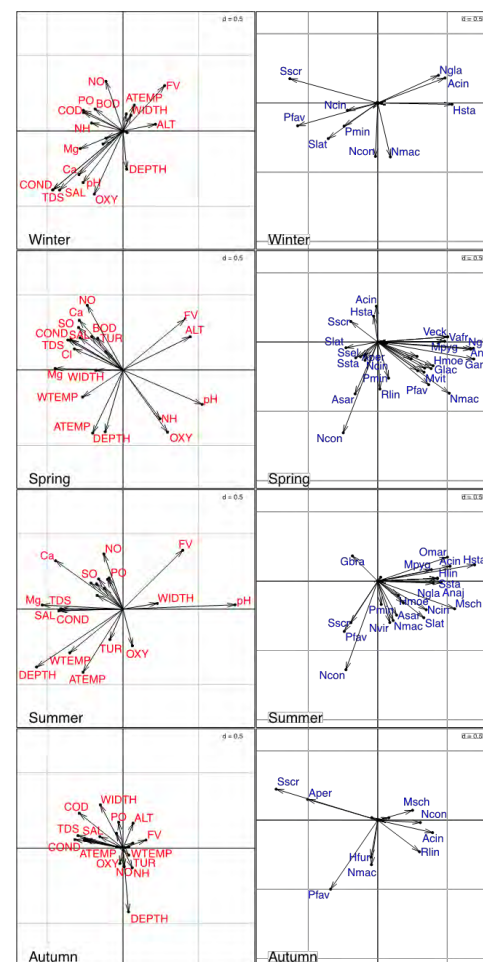
Spring & Summer

Autumn & Winter

Environmental Gradients

Low salinity / conductivity
High dissolved Oxygen

High salinity / conductivity
Low dissolved Oxygen



Headwater
Riparian forest
Aquatic macrophytes

Lowland
Urbanisation
Pollution

**Unravelling the environmental correlates influencing the seasonal biodiversity
of aquatic Heteropteran assemblages in northern Africa**

Noura Slimani^{1,2}, Eric Guilbert¹, James C. White³, Matthew J. Hill⁴, Paul J. Wood⁵, Moncef Boumaïza², Jean Thioulouse⁶

1 UMR7179 CNRS/MNHN, Muséum National d'Histoire Naturelle, CP 50, 57 rue Cuvier, 75005 Paris, France,

2 Université de Carthage, Faculté des Sciences de Bizerte, LR05ES09 Laboratoire des applications de la chimie aux ressources et substances naturelles et à l'environnement (LACREsNE), 7021, Bizerte, Tunisie,

3 River Restoration Centre, Cranfield University, Cranfield, Bedfordshire MK43 0AL, UK

4 School of Applied Sciences, University of Huddersfield, Huddersfield, HD1 3DH, UK

5 Geography and Environment, Loughborough University, Loughborough, Leicestershire, LE11 3TU, UK

6 Université de Lyon, Université Lyon 1, CNRS, Laboratoire de Biométrie et Biologie Evolutive, UMR 5558, 69622 Villeurbanne Cedex, France

Abstract

Heteropteran communities form a key component of aquatic ecosystems but have not been widely studied compared to other freshwater faunal groups. This research examined the environmental parameters influencing the diversity, seasonal distribution and structure of aquatic Heteroptera assemblages in the Mediterranean region of Tunisia, northern Africa. Heteropterans were most abundant during spring and summer, coinciding with the emergence of several species and the most favorable environmental conditions for benthic aquatic fauna. Three-way multivariate analyses (combining community composition data from all sites and seasons) highlighted the longitudinal spatial organization of Heteropteran communities. Headwater regions were dominated by halophobic sensitive taxa, and lowland sites were characterized by high salinity resistant taxa (halophilic taxa). The longitudinal organization was driven by gradients of mineralization (salinity and electrical conductivity) and oxygen (DO, COD and BOD) concentrations. Taxonomic composition differed between river catchments, with significantly higher diversity (taxa richness) in the streams with adjacent riparian forest cover. These sites were characterized by the presence of endemic species, such as *Velia africana* and *Velia eckerleini*, and rare species, *Notonecta meridionalis*, and *Aquarius najas*. Results recorded highlight the importance of aquatic vegetation and water quality in driving the seasonal and spatial variability of Heteropterans, and provide important information to inform the management and conservation of freshwater biodiversity in Northern Africa.

Key words. freshwater ecosystems, water quality, macroinvertebrate, aquatic ecology, Mediterranean.

1 **Introduction**

2 Freshwater ecosystems in the Mediterranean region of North Africa are increasingly recognized as global
3 biodiversity hotspots (Beauchard et al., 2003). However, there remains a fundamental lack of research
4 considering the structure and functioning of north African Mediterranean freshwater ecosystems and in the insect
5 communities they support (Slimani et al., 2019). This limited ecological knowledge currently hinders our
6 scientific understanding of how aquatic ecosystems and their biodiversity will respond to anthropogenic
7 pressures across North Africa in the future (Schilling et al., 2012). The primary threats to the freshwater
8 biodiversity of north Africa, and globally, include excessive freshwater water abstraction (for domestic,
9 agricultural and industrial use) and the construction of engineered infrastructure (e.g. dams, weirs and
10 channelization), which have driven the rapid loss of natural freshwater habitats (Reid et al., 2019).
11 Anthropogenic flow regime modifications and projected climatic change threatens freshwater environments
12 (Döll and Schmied, 2012; Colin et al., 2016), their high biodiversity and the endemic freshwater fauna (including
13 the freshwater insects) they support (García et al., 2010) across North Africa.

14 Heteropterans represent a subgroup of the Hemiptera, an insect order forming an integral part of freshwater
15 ecosystems globally. There are over 4500 Heteropteran species thought to inhabit aquatic environments globally,
16 making a significant contribution to the biodiversity of freshwater ecosystems (Polhemus and Polhemus, 2008).
17 They have been recorded in virtually all aquatic habitats, including surface and subsurface environments
18 associated with lotic (e.g. headwater streams, lowland rivers) and lentic (e.g. pond, lakes, coastal rock pools)
19 waterbodies (Slimani et al., 2015, 2016, 2017). Heteropterans are important for the functioning of aquatic
20 ecosystems as they help regulate fluxes of energy and matter across aquatic food webs, through facilitating
21 nutrient cycling and providing a source of food for higher trophic levels (Brown and McLachlan, 2010; Amaral
22 et al., 2016). Aquatic Heteropteran taxa vary considerably in their ecological requirements (Aukema et al., 2013;
23 De Figueroa et al., 2013; Damgaard and Zettel, 2014; Turić et al., 2015), and many species display specific
24 habitat preferences (Bloechl et al., 2010; Carbonell et al., 2011; Annani et al., 2012; Dudgeon, 2012). As such,
25 Heteropteran communities are widely used as indicators of aquatic ecosystem health and to characterize
26 ecological responses to anthropogenic pressures (e.g., Hershey et al., 2010; Lock et al., 2013; Slimani et al.,
27 2017). In addition, many Heteropteran species are recognized as reliable surrogates for the wider biodiversity of
28 aquatic ecosystems and have been used to support the conservation and restoration of freshwater habitats
29 (Whiteman and Sites, 2008; Cunha and Juen, 2017).

Globally, the majority of aquatic Heteropterans belong to one of two major groups: Nepomorpha (water bugs) which largely live below the water surface, and Gerromorpha (water striders) comprising species that inhabit the water surface film (Polhemus and Polhemus, 2008). Both Nepomorpha and Gerromorpha are particularly common within Mediterranean freshwater ecosystems (De Figueroa et al., 2013), including those of northern Africa (Aukema et al., 2013; Slimani et al., 2015, 2016). The distribution and diversity of both subgroups may be influenced by a range of environmental factors, including physicochemical conditions (particularly dissolved solutes and oxygen concentrations), flow conditions (lentic or lotic habitats) and water temperature (Tully et al., 1991; Hufnagel et al., 1999; Barahona et al., 2005; Karaouzas and Gritzalis, 2006; Skern et al., 2010). The size and shape of the water body has been reported to strongly influence their distribution; with clear distinctions between small shallow waterbodies and larger deeper lakes (Macan, 1954; Savage, 1994).

Heteropterans display a range of traits which allow them to survive extreme hydroclimatic conditions, from torrential floods during winter to the severe summer droughts which occur consistently in the Mediterranean region of North Africa (Annani et al., 2012). For example, species from the genus *Notonecta* spp. (Notonectidae) have a prolonged period of development over multiple months and are typically be found in freshwaters at higher altitude during the drier summer months (Annani et al., 2012). While a limited number of studies have explored the taxonomic composition and diversity of aquatic Heteropteran communities in northern Africa (e.g. L'mohdi et al., 2008 -Morocco; Annani et al., 2012 -Algeria; Slimani et al., 2015, 2016 - Tunisia), to our knowledge none have tested their sensitivity to varying environmental conditions beyond individual river basins or seasons.

In order to better understand the key drivers underpinning the spatiotemporal distributions of aquatic Heteropteran assemblages, we examined seasonal variations in community structure and environmental controls across 45 sites within 4 catchments in northern Tunisian. A total of 21 environmental variables, identified as drivers of aquatic Heteroptera assemblages were measured: including salinity, conductivity, dissolved oxygen, water depth, and surface area of open water. The main objectives of the study were to: (i) examine differences in Heteropteran community composition and diversity between the four river catchments examined; and (ii) quantify the environmental correlates driving spatiotemporal variability of Heteropteran communities across the catchments.

Materials and Methods

Study site

This research was undertaken in northern Tunisia (Fig. 1 and Table S.1 in Supplementary Material), a Mediterranean region located in the Maghreb (North Africa) and included 45 sites within four catchments (Medjerda; Kroumirie-Mogods; Ichkeul; and Meliane-Cap Bon).

All sites maintained perennial surface water and encompassed the entire diversity of freshwater habitats preferred by the target group, including streams, springs, ponds and lakes with both lotic/lentic water conditions; comprising 34 lotic and 11 lentic waterbodies (Fig. 1, Table S.1 in Supplementary Material). Substrates within the freshwater habitats were characterized by cobbles, gravel, sand, silt and clay; with some sites appearing muddy and having a loamy character. Sampling sites were established on each catchment longitudinally from upstream to downstream (St 1 to St 45). Site 1 was in the headwaters (upstream) of the Wadi Medjerda in North-West Tunisia, and site 45 was located the furthest downstream on the Wadi Lebna in the North-Eastern extremity of Tunisia in the Cap Bon region (A summary of sites is presented Table 1). The northern area of Tunisia is characterized by a typical Mediterranean climate, ranging from humid to sub-humid and supports a rich floral diversity including *Typha angustifolia* L., *Quercus canariensis* Willd., and *Quercus suber* L. This northern region occupies 17% of the land mass but includes 60% of the national freshwater resource.

Biological data

Aquatic Heteroptera samples were collected on 4 separate occasions: February (spring), May (summer), September (autumn), and December (winter) 2013 from the 45 sites (Fig. 1, Table S.1 in Supplementary Material). The samples were obtained using a combination of both Surber samples (300 µm mesh net with an opening 0.20 m wide and 0.10 m deep) and a kick / sweep net (filet Troubleau). A total of 25 minutes of sampling and searching was undertaken at each site ensuring that the entire habitat heterogeneity was considered at each site. Samples were preserved in 70% ethanol and returned to the laboratory for processing and species level identification. Laboratory identification of fauna was undertaken using available identification keys (Poisson, 1957; Tamanini, 1979; Jansson, 1986; Andersen, 1990; Zimmermann and Scholl, 1993), a binocular microscope, and the Heteroptera collections deposited at the National Museum of Natural History in Paris and the Naturalis Biodiversity Centre in Leiden to verify the identifications with the assistance of three experts.

Environmental parameters

The following environmental parameters were measured in situ at each site at the time of sampling aquatic Heteroptera comprising pH, salinity (SAL), electrical conductivity (COND), total dissolved salt (TDS) and

dissolved oxygen (OXY) with portable probes (WTW, PP350). Air and water temperature (ATEMP, WTEMP) were measured simultaneously in the field using a mercury glass thermometer graduated to 0.1°C. Altitude (ALT) was calculated using a GPS (Garmin etrex 10). Flow velocity (FV) was measured using the time (seconds) taken by a float (cork stopper) to cover a minimum distance of one meter. Visual estimates of percentage substrate composition in shallow water and riparian cover were made at each site (Table S.1 in Supplementary Material). Water samples were collected at each site using 4 L polyethylene bottles and transported on ice back to the “Centre International des Technologies de l'Environnement de Tunis” CITET laboratory for further analyses. Turbidity was measured in the laboratory using a turbidity meter (Hach model 2100A). Major cation and anion concentrations: Calcium (Ca^{2+}) and Magnesium (Mg^{2+}) were measured by inductively coupled plasma optical emission spectrometry (ICP-OES). Chloride (Cl^-), and sulphates (SO_4^{2-}) were measured by liquid chromatography (DX-120 Ion Chromatograph). The concentration of nutrients: nitrates (NO_3^-), nitrite (NO_2^-), ammoniac (NH_4^+), and Orthophosphate (PO_4^{3-}), were measured by spectrophotometry (JASCO V-530 UV/VIS) at 630 nm. Chemical oxygen demand (COD) was measured using the amount of potassium dichromate ($\text{K}_2\text{Cr}_2\text{O}_7$) consumed by the dissolved solids in suspension. Biological Oxygen Demand (BOD_5) was measured by incubation of the water sample in the presence of a solution of phosphate and allyl thiourea in darkness and at 20°C over 5-days. Other parameters, including channel width (WIDT) and water depth (DEPT) were measured in the field at each site. The concentration of NO_2^- was consistently below the device's detection limit (0.4 mg L^{-1}), and therefore were not presented in the results below.

Data analysis

Statistical analyses were undertaken in the R environment (R Core Team, 2018). The STATICO multivariate analysis method (Thioulouse et al., 2004; Thioulouse, 2011) was used to investigate the relationships between aquatic Heteroptera communities and environmental variables (including morpho-dynamic parameters) over the four seasons. The STATICO method is based on the use of two analyses: Co-inertia Analysis (Dolédéc and Chessel, 1994; Dray et al., 2003) and Partial Triadic Analysis (Thioulouse and Chessel, 1987; Thioulouse, 2011). This method allows the simultaneous analyses of three dimensions of the dataset: faunal matrix \times environmental parameters matrix \times four seasons.

Co-inertia analysis was initially performed by building a crossed table between the two datasets: one comprising the 21 environmental parameters and the other for the 36 Heteroptera species. Each of these contained 180 rows, corresponding to the 45 sampling sites over four seasons (spring, summer, autumn and winter). Computations were undertaken on these tables using the *statico* function in the *ade4* package (Slimani et al., 2017; Thioulouse

et al., 2018). Co-inertia analysis computes axes that maximize the covariance between the scores of the rows (sampling sites) of the environmental parameters table, as well as the scores of the rows of the species table.

Partial Triadic Analysis is a K-tables data analytical method. The STATICO analysis consists of computing the four (one for each season) crossed tables (environmental parameters x species) for the four corresponding co-inertia analyses. A Partial Triadic Analysis is then undertaken on the series based on these four crossed tables. The interstructure step computes a weighted mean of the four seasons (the compromise). The compromise step includes a PCA using this table, providing environmental parameter scores and species scores. The intrastructure step computes the scores of the rows (environmental parameters) and columns (species) of the four crossed tables (one for each season) and of the rows of the initial tables (sampling sites of the environmental parameters table and of the species table). The scores computed in the intrastructure step of the STATICO analysis describe the temporal (within and between seasons) and spatial (within and between catchments) variability of the associations between aquatic Heteropteran communities and environmental parameters.

When using the STATICO method, the variable scaling and the row weights must be chosen with great care, as they imply different ecological considerations (Dray et al., 2003). In this study, the separate analysis of each table was performed using a PCA because the species responses to the environmental parameters are approximately linear (verified graphically in preliminary analysis). The table of environmental variables was submitted to a “partial Bouroche standardization”, which means that it was first standardized (i.e. centered and normalized) for the whole dataset (globally), and then standardized within each season. The PCA of species abundance data was performed using $\log_{10}(x+1)$ transformed data to reduce the influence of highly abundant species and also submitted to a partial Bouroche standardization. Sampling site weights were considered uniform because the sampling method was homogeneous throughout the time-series and the taxonomic identification was performed consistently by the same individual.

Results

Environmental characterization

Environmental factors displayed spatial and temporal differences between sampling sites and seasons respectively (Table 1). One-Way Analysis of Variance (ANOVA) indicated significant seasonal differences for the following physicochemical parameters between seasons: pH ($DF = 3$, $F = 25.94$, $P < 0.001$, $R^2 = 0.30$), dissolved oxygen ($DF = 3$, $F = 13.13$, $P < 0.001$, $R^2 = 0.18$), turbidity ($DF = 3$, $F = 9.69$, $P < 0.001$, $R^2 = 0.14$), water temperature ($DF = 3$, $F = 258.35$, $P < 0.001$, $R^2 = 0.81$), air temperature ($DF = 3$, $F = 180.96$, $P < 0.001$, $R^2 = 0.75$), flow velocity ($DF = 3$, $F = 15.32$, $P < 0.001$, $R^2 = 0.20$), nitrate - NO_3^- L^{-1} ($DF = 3$, $F =$

150 9.09, = $P < 0.001$, $R^2 = 0.13$), and ammonia - $\text{NH}_4^+ \text{ L}^{-1}$ (DF = 3, $F = 4.57$, = $P < 0.001$, $R^2 = 0.07$). The PCA of
151 physicochemical data indicated that the first and second axes explained 22.91% and 12.46% of the variance in
152 the dataset, respectively (Fig. 2). PCA-axis 1 primarily reflected a gradient of altitude and mineralization, with
153 high altitude low mineralization samples located on the positive end and low altitude high mineralization
154 (COND, SAL, TDS) samples on the negative side of the axes. PCA-axis 2 reflected a gradient of dissolved
155 oxygen concentrations and pH on the positive side and temperature (air and water) on the negative side.

Differences in Heteropteran communities between catchments

A total of 36 aquatic Heteroptera species representing 19 genera and 13 families were recorded; 23 species belonging to the Nepomorpha subgroup and 13 species representing Gerromorpha. The densities (individuals m²) and percentage (%) contribution to abundance during the study period for all taxa recorded are presented in Table 2.

Nepomorpha contributed 66.54% of the total relative abundance, with *Micronecta scholtzi* (Fieber) representing the most abundant species (22.43%). The Gerromorpha species contributed 33.46% of the total abundance, with *Aquarius cinereus* (Puton) being the most common (17.18%) (Table 2). Species richness and the distribution of Heteroptera varied between catchments, reflecting the variable contribution of different species throughout the study period (Fig. 3). The total density of Heteroptera was greatest at Meliane-Cap Bon (2382 ind/m²) and the highest species richness was recorded at Kroumirie -Mogods (33 species).

The aquatic Heteroptera community compositions varied considerably between catchments (Fig. 3). The Medjerda and Kroumirie-Mogods catchments were dominated by two species *Micronecta scholtzi*, and *Aquarius cinereus*. The Ichkeul catchment was characterized by higher densities of *Micronecta scholtzi*, *Nepa cinerea* L., *Naucoris maculatus conspersus* (Stål). *Nepa cinerea*, *Naucoris maculatus conspersus*, and *Hydrometra stagnorum* L.. *Parasigara favieri* (Poisson), *Sigara scripta* (Rambur), and *Notonecta maculata* (Fabricius) were more abundant at Meliane-Cap Bon.. *M. scholtzi* and *A. cinereus* occurred at all sites at varying abundances. A number of species were relatively rare in the study region: *Ranatra linearis* L., *Ochterus marginatus marginatus* (Latreille), *Corixa panzeri* (Fieber), *Hesperocorixa linnaei* (Fieber), *Hesperocorixa moesta* (Fieber), *Hesperocorixa furtiva* (Horvath), *Sigara stagnalis stagnalis* (Leach), *Sigara selecta* (Fieber), *Sigara nigrolineata nigrolineata* (Fieber), *Notonecta meridionalis* (Poisson), *Hebrus montanus* (Kolenati) and two endemic taxa to Maghreb (Algeria, Tunisia) - *Velia eckerleini* (Tamanini), and *Velia Africana* (Tamanini).

Seasonal community responses to environment variables

Weights obtained from the interstructure process of STATICO were 0.49, 0.50, 0.50, and 0.51 for Winter, Spring, Summer and Autumn, respectively (Fig. 4A). This indicated that the four seasons had equal importance and that the relationships between aquatic Heteropteran communities and environmental parameters could be directly compared between seasons (Fig.4B).

The compromise step of the STATICO method identified the main environmental structures persisting across the four seasons within the PCA. The first PCA-axis reflected the longitudinal gradient from headwater sites (high altitude, high flow velocity, high dissolved oxygen and pH - higher axis values) to lowland sites (high salinity

and conductivity – lower axis values). The second PCA-axis reflected a pollution gradient; with sites with high concentrations of nitrates, phosphates, sulfates, and higher values of BOD₅ and COD in the upper/positive sector of the graph, and deeper sites with high dissolved oxygen levels on the lower/negative part of the graph (Fig.4C). Heteroptera species were ordered along these two gradients reflecting their preferences in relation to the environmental parameters (Fig.4D).

Inter-catchment differences in community responses to different environmental parameters

Within the intrastructure step of the analysis, the environmental parameters and Heteroptera communities were averaged across all four seasons (Fig. 5). The first axis reflected a mineralization gradient with higher values of salinity (SAL), electric conductivity (COND), and total dissolved salts (TDS) on the left, and high altitude (ALT), flow velocity (FS), and pH on the right of the factorial plan. The second axis reflected a nitrate (NO) gradient from the top of the factorial plan and dissolved oxygen (OXY), and depth (Dept) at the bottom of the factorial plan. The structure of the species reflected the environmental gradient on the first axis (Fig. 4), with species displaying saline intolerance (*Aquarius cinereus* (Acin), *Hydrometra stagnorum* (Hysta), and *Notonecta glauca glauca* (Ngla)) located on the low mineralization side of the factorial plan (right) and halophilic species (*Sigara scripta* (Sscr), and *Anisops debilis perplexus* (Aper)) on the high salinity side (left). Nepomorpha and Gerromorpha species were distributed according to their individual salinity affinities. The distribution of the species along the second axis indicated that *Parasigara favieri* (Pfav) *Naucoris maculatus conspersus* (Ncon) and *Notonecta maculata* (Nmac) were associated with high dissolved oxygen concentrations and greater water depth. As a result, the species–environment relationships primarily consisted of a salinity gradient linked to a freshwater - brackish water faunal gradient. *Gerris brasili*, *Gerris maculatus*, *Hydrometra stagnorum*, *Microvelia pygmaea*, *Velia africana*, *Velia eckerleini*, *Hesperocorixa linnaei*, *Hesperocorixa furtiva* and *Notonecta meridionalis* were associated with low mineralization and relatively high altitude and higher flow velocities. In contrast, *Sigara stagnalis*, *Sigara lateralis*, *Sigara selecta*, *Anisops debilis perplexus*, and *Anisops sardeus sardeus* were associated with higher mineralization levels and relatively low altitude and reduced flow velocities. *Parasigara favieri* were associated with high dissolved oxygen concentrations.

Inter- and intra-basin variations in communities in relation to different environment controls

The Intrastructure between the two sets of descriptors (environmental parameters - red labels- and aquatic Heteroptera - blue labels) on the PCA of the compromise output for each catchment is presented in Figure 6. For the Medjerda catchment, sites are roughly ordered along an upstream-downstream gradient from right to left along the first axis. This reflects the mineralization and salinity gradient. In all seasons, site 5 appears at the top

of axis 2 due to increased pollution, higher water and air temperature, an absence of precipitation and reduced flow velocities. The low values of dissolved oxygen (OXY) at these sites (0.3 mg/l) are consistent with this interpretation (Fig. 6A). However, aquatic Heteroptera displayed clear seasonal variability mainly because of the differences in the density of species between seasons (Fig. 6B).

For the Kroumirie-Mogods catchment, the environmental parameters clustered on the positive side of axis I, associated with mild mineralization, linked to lithology; the catchment is dominated by clay-sandstone soils and dense vegetation cover (Fig. 6A). The distribution of species from the sampling sites indicated a strong structure, which indicates a good fit between the aquatic Heteroptera (corresponding to a majority to freshwater affinities) and environmental parameters (the arrows were mostly short). In spring and summer, large differences were observed for stations 1 and 9 when higher Heteroptera species richness and/or abundances were recorded (Fig. 6B).

For the Ichkeul catchment, during winter and autumn, environmental trajectories for most sites clustered at the center of the axes. However, during spring and summer sites 11, 14 and 15 were located on the negative side of axis I, reflecting an upstream-downstream gradient and seasonal variation of temperature and salinity (Fig. 6A). Most species were located centrally and / or on the negative part of axis I (Fig. 6B). Environmental and aquatic Heteroptera trajectories followed similar patterns for most seasons.

For the Meliane-Cap Bon catchment, the upstream-downstream gradient was less clear; site 9 was clearly distinguished from other sites due to pollution and higher COD and BOD₅ (Fig. 6A). A poor association between the fauna and the environment parameters was observed (Fig. 6B).

Discussion

Our results provide an important contribution to the study of freshwater communities from the north African Mediterranean region including North Tunisia, which has been identified as a biodiversity hotspot (Marignani et al., 2017; Abdou et al., 2018). This is consistent with previous Mediterranean ecosystem assessment studies, and results that identified macroinvertebrate diversity as contributing disproportionately to ecological knowledge for the North African region (Beauchard et al., 2003; Ball et al., 2013; De Figueroa et al., 2013; Slimani et al., 2019). Benthic macroinvertebrates depend on a wide range of abiotic factors, including climate, water physiochemistry, anthropogenic pressures and riparian habitat availability (White et al., 2019; Ceron et al., 2020) and this study confirms that this is also true for aquatic insects such as Heteroptera. This study also supports the finding of research linking the distribution and abundance of some Aquatic Heteroptera to water physico-

chemistry from other regions (Savage, 1994; Hufnagel et al., 1999). However, there were marked differences in the Heteropteran assemblage in the semiarid Mediterranean study region (Northern Tunisia). The Heteropteran fauna displayed significant differences in species richness and abundance. Richness of Heteroptera declined from 33 species in Kroumirie-Mogods (Northern western) to 19 species in the Meliane-Cap Bon catchment (Northern western), with a similar reduction in the relative density of individuals. This reflects changes in with water quality, with the least impacted sites displaying a positive correlation between good water quality and Heteroptera density for eight of the environmental parameters (out of 21). This indicates a strong link between the faunal functional composition and local in-stream habitats conditions (micro-habitats) rather than the larger-scale environmental conditions (Townsend and Hildrew, 1994).

The aquatic Heteroptera densities recorded in northern Tunisia displayed clear spatial variation reflecting the preference and tolerances of individual species. *Micronecta scholtzi*, *Naucoris maculatus conspersus*, and *Aquarius cinereus* occurred in high numbers highlighting their generalist characteristics in relation to most abiotic, allowing them to thrive in extreme environmental conditions (Carbonell et al., 2011). The reduction in macroinvertebrate densities in the Kroumirie-Mogods catchment may reflect interspecific competition at sites with high species richness (Boumaiza, 1994). However, no species were recorded at all of the sampling sites. This reflects the heterogenous abiotic conditions of the habitats studied as well as the preferences and adaptations (ecological valence) of the individual Heteroptera species.

The results of STATICO analyses indicate that environmental and spatio-temporal gradients were particularly important determinants of community structure in northern Tunisia (providing evidence to support our hypothesis). The distribution of fauna reflected several physicochemical parameters which varied among the four river catchments. The analysis highlights that the distribution of Heteroptera most strongly reflect a mineralization gradient which has been shown to primary factor structuring communities (Verneaux and Tuffery, 1967). Other factors, such as altitude and flow velocity were also strongly correlated with mineralization. This study provides further evidence that mineralization represents one of the principal forces driving heteroptera community composition and distribution a global scale (Tully et al., 1991; Karaouzas and Gritzalis, 2006; Bloechl et al., 2010; Carbonell et al., 2011; Scheibler et al., 2016). Previous studies on inland aquatic systems have shown that richness and diversity decline with increasing mineralization (Sánchez et al., 2006; Kefford et al., 2011; Millán et al., 2011; Slimani et al., 2019; Gutiérrez-Cánovas et al., 2019). In addition, mineralization was reported to be the most important factor influencing the macroinvertebrate community richness of wetland aquatic systems (Kefford et al., 2011; Millán et al., 2011; Cañedo-Argüelles et al., 2012; Velasco et al., 2019).

Our analysis demonstrated aquatic heteroptera diversity decreased downstream with increasing mineralization (Fig.5). The salinity (SAL), electric conductivity (COND), and total dissolved salts (TDS) of stream waters were identified as the primary factor controlling Heteroptera diversity. Many oligo- and mesotrophic taxa, such as Veliidae and Notonectidae, were abundant in streams with low mineralization and higher DO concentrations, but some Corixidae displayed an association with brackish water systems; comparable to results reported in other studies (Slimani et al., 2015, 2016).

The specific richness of Heteroptera displayed a general reduction with increasing salinity from headwaters to downstream (ST1 to ST44), and were absent from sites subject to high pollution stress (ST5 and ST45 - the site with the highest BOD₅ and COD concentrations). This pattern was reflected in the Heteroptera species recorded, with some species more common in freshwater, for example *N. meridionalis*, *V. eckerleini*, *V. africana* and *A. najas* were only recorded in the Kroumirie-Mogods (SAL ≤ 0.23 PSU), where clayey-sandstone soils dominated and riparian woodland occurred (oak - *Quercus canariensis* and cork tree - *Quercus suber*) (Boumaiza, 1994). In the other catchments (SAL ≥ 1 PSU; EC ≥ 1900 µs/cm at 20°C), Heteroptera communities were characterised by *A. cinereus*, *M. scholtzi*, *N. glauca* in the headwaters and *S. scripta*, *S. stagnalis*, *S. lateralis* and *N. conspersus* in the more mineralized sites downstream. Such distributional patterns have also been reported observed in other saline Mediterranean streams (Millán et al., 2011). In particular, some Corixidae appear to be well adapted to osmotic stress and some, such as are *Sigara scripta* are considered halophilic taxa and indicative of hypersaline streams (Savage, 1982, 1990; Millán et al., 2011; Slimani et al., 2015). There is great variation among species regarding salinity tolerance with species-based ecophysiological and metabolically mechanisms enabling them to tolerate such stress (Oren, 2000; Velasco et al., 2006; Elevi Bardavid and Oren, 2008).

Although Heteroptera are sensitive to anthropogenic pollution of the aquatic ecosystems, their respiratory physiology (air breathing) and mating behavior enable them to persist even when exposed to harsh environmental conditions (Lytle, 2015). However, in the current study Heteroptera were totally absent from the most severely polluted sites at Kasseb and Lebna. These results are consistent with results reported by Zhang et al. (2018) in response to chronic pollution and habitat modification. The ability of Heteroptera to withstand relatively extreme environmental conditions may partially explain the negative correlations between water temperatures, dissolved oxygen, depth and turbidity in this study and resulted in the high species richness recorded during Spring and Summer. These observations support the findings of Slimani et al. (2017) and previous studies in the study area highlighting correlations between aquatic macrophytes (Casagrande &

Boudouresque, 2007), phytoplankton (Casagrande and Boudouresque, 2010) and Coleoptera - water beetles (Touaylia et al., 2013) with temperature and salinity.

The results reported suggest Heteroptera assemblages could be more widely used as indicators of freshwater biodiversity in biomonitoring programs and the conservation of freshwater biodiversity in Mediterranean freshwater ecosystems (Calapez et al., 2018). They have considerable utility for monitoring changes in environmental parameters, as bioindicators of either deteriorating or improving habitat quality that may be related to changing patterns of land use or other anthropogenic stressors (Buchwalter et al., 2003). The data from this study could be used to inform the development of an index of biological richness and aquatic ecosystem health when combined with wider data from the macroinvertebrate community from the region. These measures could be used to provide measures of both biodiversity and wider environmental quality which could be compared to those developed in adjacent regions in Europe and beyond. In addition, Heteroptera may have utility as agents of biological control. With the exception of the omnivorous Corixidae, aquatic Heteroptera are insect predators and have been recorded to help in the regulation of larval populations of the larvae of mosquito vectors of disease (Aditya et al., 2004; Banerjee et al., 2010). Their use in the biocontrol of mosquitoes could be used alongside the targeted application of insecticides to avoid or minimize the effects of chemical contamination on wetland ecosystems.

Future research is needed to combine the results of abiotic factors within a geographical information system (GIS) to track species current and potential future distributions under climate change scenarios and anthropogenic impacts. Many species of aquatic Heteroptera have been reported to be responding to climate change by shifting their distributional ranges, changes in recorded abundances, phenology, voltinism, physiology, behaviour and community structure, thereby serving as particularly good bioindications of climate change (Musolin, 2007). Rabitsch (2008) referred to the process as Mediterraneanization, given that five new species including *Micronecta scholtzi* (Corixidae), *Microvelia buenoi* (Veliidae), *Microvelia pygmaea* (Veliidae), *Notonecta meridionalis* (Notonectidae), *Velia currens* (Veliidae) were recorded in Central Europe as their geographical range expanded from their native Mediterranean region. Similarly, Klementová and Svitok (2014) demonstrated that *Anisops sardeus* (Notonectidae), native to the Sahelo-Sindian area, was actively expanding its geographical range from the Mediterranean and is now expanding its distribution in Central Europe.

Conclusion

This study examined Heteropteran communities inhabiting the understudied Mediterranean region of north Africa. The results presented highlight how different environmental parameters structure Heteropteran communities, principally altitude, mineralization and dissolved oxygen levels. Strong seasonal differences in environmental conditions in the study area resulted in the temporal variability of Heteropteran assemblages. Moreover, intra- and inter-basin variations in environmental conditions associated with both natural and anthropogenic resulted in a strong spatial structuring of Heteropterans. This study represents the first step towards understanding the relationship between ecological factors and biodiversity of true water bugs, knowing that freshwater management will become increasingly pivotal as increasing human populations and projected climatic change threaten freshwater ecosystems. Findings from this study highlighted that some Heteropteran taxa, including *N. conspersus*, *N. maculata*, *A. najas*, *Aquarius cinereus*, and *Micronecta scholtzi*, were indicative of more pristine semi-natural environments and could provide the basis for characterising reference conditions for other sites in the north African Mediterranean region. Our results also provide clear evidence of how aquatic Heteroptera can be used as indicators of different environmental stressors, including water quality issues, and could be used more widely in biomonitoring assessments across northern Africa.

Acknowledgements

This study was funded by the Ministry of High Education and Scientific Research of Tunisia and the CoopInteer CNRS/DGST project n° 15/R 0902. We are grateful to Pierre Moulet (Museum Requien, 67 rue Joseph Vernet, F-84000 Avignon, France), Ping-Ping Chen and Nico Nieser (Terrestrial Zoology, Naturalis Biodiversity Centre, 2300 RA Leiden, The Netherlands) for their helpful in identifying the material. The first author wishes to thank Habib Ayadi and Jannet Elloumi for their help with this study.

References

- Abdou, K., Gascuel, D., Aubin, J., Romdhane, M.S., Lasram, F.B.R., Le Loc'h, F., 2018. Environmental life cycle assessment of seafood production: a case study of trawler catches in Tunisia. *Sci. Total Environ.* 610, 298–307. <https://doi.org/10.1016/j.scitotenv.2017.08.067>.
- Aditya, G., S. Bhattacharya, N., Kundu, G.K., Saha, S.K. Raut., 2004. Predatory efficiency of the water bug *Sphaerodema annulatum* on mosquito larvae (*Culex quinquefasciatus*) and its effect on adult emergence. *Bioresour. Technol.* 95, 169–172. <https://doi.org/10.1016/j.biortech.2004.02.007>.

357 Amaral, D.S., Venzon, M., dos Santos, H.H., Sujii, E.R., Schmidt, J.M., Harwood, J. D., 2016. Non-crop plant
 358 communities conserve spider populations in chili pepper agroecosystems. *Biol Control*. 103, 69–77.
 359 <https://doi.org/10.1016/j.biocontrol.2016.07.007>.

360 Andersen, N.M., 1990. Phylogeny and taxonomy of water striders, genus *Aquarius* Schellenberg (Insecta,
 361 Hemiptera, Gerridae), with a new species from Australia. *Steenstrupia* 16: 37–81.

362 Annani, F., Alfarhan, A.H, Samraoui, B., 2012. Aquatic Hemiptera of northeastern Algeria: distribution,
 363 phenology and conservation. *Rev. Ecol. (Terre Vie)*. 67, 423–435. <http://hdl.handle.net/2042/55933>.

364 Aukema, B., Rieger, C., Rabitsch, W., 2013. Catalogue of the Heteroptera of the Palaearctic Region. Volume 6.
 365 Supplement. The Netherlands Entomological Society, Amsterdam, xxiv + 629, pp.
 366 <https://doi.org/10.1603/RAN13001>.

367 Ball, J.E., Bêche, L.A., Mendez, P.K., Resh, V.H., 2013. Biodiversity in Mediterranean-climate streams of
 368 California. *Hydrobiologia*. 719, 187–213. <https://doi.org/10.1007/s10750-012-1368-6>.

369 Banerjee, S., Aditya, G., Saha, N., Saha, G.K., 2010. An assessment of macroinvertebrate assemblages in
 370 mosquito larval habitats – space and diversity relationship. *Environ. Monit. Assess*. 168, 597–611.
 371 <https://doi.org/10.1007/s10661-009-1137-9>.

372 Barahona, J., Millan, A., Velasco, J., 2005. Population dynamics, growth and production of *Sigara selecta*
 373 (Fieber, 1848) (Hemiptera, Corixidae) in a Mediterranean hypersaline stream. *Freshw. Biol*. 50, 2101–
 374 2113. <https://doi.org/10.1111/j.1365-2427.2005.01463.x>.

375 Beauchard, O., Gagneur, J., Brosse, S., 2003. Macroinvertebrate richness patterns in North African streams. *J.*
 376 *Biogeogr*. 30, 1821–1833. <https://doi.org/10.1111/j.1365-2699.2003.00954.x>.

377 Bloechl, A., Koenemann, S., Philippi, B., Melber, A., 2010. Abundance, diversity and succession of aquatic
 378 Coleoptera and Heteroptera in a cluster of artificial ponds in the North German Lowlands. *Limnologica*. 3,
 379 215–225. <https://doi.org/10.1016/j.limno.2009.08.001>.

380 Boumaiza, M., 1994. Recherches sur les eaux courantes de la Tunisie. Faunistique, Ecologie et Biogéographie.
 381 Thèse de doctorat d'état, Fac. Sc. Tunis, pp. 429.

382 Brown, A.C., McLachlan, A., 2010. The ecology of sandy shores. Elsevier.

383 Buchwalter, D.B., Jenkins, J.J., Curtis, L.R., 2003. Temperature influences on water
 384 permeability and chlorpyrifos uptake in aquatic insects with differing respiratory strategies. *Environ. Toxicol.*
 385 *Chem*. 22, 2806e2812. <https://doi.org/10.1897/02-350>.

386 Calapez, A.R., Serra, S.R.Q., Santos, J.M., Branco, P., Ferreira, T., Hein, T., Brito A.G., Feio, M.J., 2018. The
 387 effect of hypoxia and flow decrease in macroinvertebrate functional responses: A trait-based approach to
 388 multiple-stressors in mesocosms. *Sci. Total Environ.* 637, 647–656.
 389 <https://doi.org/10.1016/j.scitotenv.2018.05.071>.
 390 Cañedo-Argüelles, M., Grantham, T.E., Perrée, I., Rieradevall, M., Céspedes-Sánchez, R., Prat, N., 2012.
 391 Response of stream invertebrates to short-term salinization: a mesocosm approach. *Environ. Pollut.* 166,
 392 144–151. <http://dx.doi.org/10.1016/j.envpol.2012.03.027>.
 393 Carbonell, J.A., Gutiérrez-Cánovas, C., Bruno, D., Abellán, P., Velasco, J., Millán, A., 2011. Ecological factors
 394 determining the distribution and assemblages of the aquatic Hemiptera (Gerromorpha & Nepomorpha) in
 395 the Segura River basin (Spain). *Limnetica*. 30, 59–70. <http://dx.doi.org/10.23818/limn.30.06>
 396 Casagrande, C., Boudouresque C.F., 2007. Biomass of *Ruppia cirrhosa* and *Potamogeton pectinatus* in a
 397 Mediterranean brackish lagoon, Lake Ichkeul, Tunisia. *Fund. Appl. Limnol.* 163, 243–255.
 398 Casagrande, C., Boudouresque, C.F., 2010. A first quantification of the overall biomass, from phytoplankton to
 399 birds, of a Mediterranean brackish lagoon: revisiting the ecosystem of Lake Ichkeul (Tunisia).
 400 *Hydrobiologia*. 637, 73–85. <https://doi.org/10.1007/s10750-009-9986-3>.
 401 Ceron, K., Santana, D.J., Lucas, E.M., Zocche, J.J., Provete, D.B., 2020. Climatic variables influence the
 402 temporal dynamics of an anuran metacommunity in a nonstationary way. *Ecol. Evol.* 10, 4630–4639.
 403 <https://doi.org/10.1002/ece3.6217>.
 404 Colin, N., Porte, C., Fernandes, D., Barata, C., Padrós, F., Carrassón, M., Monroy, M., Cano-Rocabayera, O., de
 405 Sostoa, A., Piña, B., Maceda-Veiga, A., 2016. Ecological relevance of biomarkers in monitoring studies of
 406 macro-invertebrates and fish in Mediterranean rivers. *Sci. Total Environ.* 540, 307–323.
 407 <https://doi.org/10.1016/j.scitotenv.2015.06.099>.
 408 Cunha, E.J., Juen, L., 2017. Impacts of oil palm plantations on changes in environmental heterogeneity and
 409 Heteroptera (Gerromorpha and Nepomorpha) diversity. *J. Insect Conserv.* 1–9. <https://doi.org/10.1007/s10841-017-9959-1>.
 410
 411 Damgaard, J., Zettel, H., 2014. The water bugs (HemipteraHeteroptera: Gerromorpha & Nepomorpha) of New
 412 Caledonia: Diversity, ecology and biogeographical significance. In: Guilbert E, Robillard T, Jourdan H,
 413 Grandcolas P (eds) *Zoologia Neocaledonica* 8. Biodiversity Studies in New Caledonia, pp 219–238.
 414 Muséum national d'Histoire naturelle, Paris.

415 De Figueroa, J.M.T., López-Rodríguez, M.J., Fenoglio, S., Sánchez-Castillo, P., Fochetti, R., 2013. Freshwater
 416 biodiversity in the rivers of the Mediterranean Basin. *Hydrobiologia*. 719, 137–186
 417 <https://doi.org/10.1007/s10750-012-1281-z>.

418 Dolédec, S., Chessel, D., 1994. Co-inertia analysis: an alternative method for studying species–environment
 419 relationships. *Freshw. Biol.* 31, 277–294. <https://doi.org/10.1111/j.1365-2427.1994.tb01741.x>.

420 Döll, P., Schmied, H.M., 2012. How is the impact of climate change on river flow regimes related to the impact
 421 on mean annual runoff? A global-scale analysis. *Environ. Res. Lett.* 7, 014037. [http://dx.doi.org/](http://dx.doi.org/10.1088/1748-9326/7/1/014037)
 422 [10.1088/1748-9326/7/1/014037](http://dx.doi.org/10.1088/1748-9326/7/1/014037).

423 Dray, S., Chessel, D., Thioulouse, J., 2003. Co-inertia analysis and the linking of ecological data tables. *Ecology*.
 424 84, 3078–3089. <https://doi.org/10.1890/03-0178>.

425 Dudgeon, D., 2012. Responses of benthic macroinvertebrate communities to altitude and geology in tributaries
 426 of the Sepik River (Papua New Guinea): the influence of taxonomic resolution on the detection of
 427 environmental gradients. *Freshw. Biol.* 57, 1794–1812. <https://doi.org/10.1111/j.1365-2427.2012.02839.x>.

428 Elevi Bardavid, R., Oren, A., 2008. Dihydroxyacetone metabolism in *Salinibacter ruber* and in *Haloquadratum*
 429 *walsbyi*. *Extremophiles*. 12, 125–131. <https://doi.org/10.1007/s00792-007-0114-x>.

430 García, N., Cuttelod, A., Malak, D.A., 2010. The status and distribution of freshwater biodiversity in Northern
 431 Africa. IUCN. Gland, Switzerland, Cambridge, UK, and Malaga, Spain : IUCN, pp 141.

432 Gutiérrez-Cánovas, C., Sánchez-Fernández, D., Cañedo-Argüelles, M., Millán, A., Velasco, J., Acosta, R.,
 433 Fortuño, P., Otero, N., Soler, A., Bonada, N., 2019. Do all roads lead to Rome? Exploring community
 434 trajectories in response to anthropogenic salinization and dilution of rivers. *Philos. Trans. R. Soc. B Biol.*
 435 *Sci* 374, 20180009. <https://doi.org/10.1098/rstb.2018.0009>.

436 Hershey, A.E., Lamberti, G.A., Chaloner D.T., Northington, R.M., 2010. Aquatic insect ecology. Chapter 17.
 437 In: Thorp JH and Covich AP editors. *Ecology and classification of North American freshwater*
 438 *invertebrates*. Elsevier Press, p. 659–694. <https://doi.org/10.1016/B978-0-12-374855-3.00017-0>.

439 Hufnagel, L., Bakonyi, G., Vásárhelyi, T., 1999. New approach for habitat characterization based on species lists
 440 of aquatic and semiaquatic bugs. *Environ. Monit. Assess.* 58, 305–316.
 441 <https://doi.org/10.1023/A:1006047130545>.

442 Jansson, A., 1986. The Corixidae (Heteroptera) of Europe and some adjacent regions. *Acta Entomol. Fennica*.
 443 47, 1–94.

444 Karaouzas, I., Gritzalis, K.C., 2006. Local and regional factors determining aquatic and semi-aquatic bug
 445 (Heteroptera) assemblages in rivers and streams of Greece. *Hydrobiologia*. 573, 199–212.
 446 <https://doi.org/10.1007/s10750-006-0274-1>.

447 Kefford, B.J., Marchant, R., Schäfer, R.B., Metzeling, L., Dunlop, J.E., Choy, S.C., Goonan, P., 2011. The
 448 definition of species richness used by species sensitivity distributions approximates observed effects of
 449 salinity on stream macroinvertebrates. *Environ. Pollut.* 159, 302–310.
 450 <https://doi.org/10.1016/j.envpol.2010.08.025>.

451 Klementová, B., Svitok, M., 2014. *Anisops sardeus* (Heteroptera): A new expansive species in Central Europe.
 452 *Biologia*. 69, 676–680. <https://doi.org/10.2478/s11756-014-0354-z>.

453 L'Mohdi, O., EL Haissoufi, M., Bennis, N., Millán, A., 2008. Contribution à la connaissance des Hétéroptères
 454 aquatiques du bassin versant Laou. *Travaux de l'Institut Scientifique, Rabat*. 5, 67–74.

455 Lock, K., Adriaens, T., Van De Meutter, F., Goethals, P., 2013. Effect of water quality on waterbugs
 456 (Hemiptera: Gerromorpha & Nepomorpha) in Flanders (Belgium): results from a large-scale field survey.
 457 *Ann. Limnol. –Int. J. Limnol.* 49, 121–128. <https://doi.org/10.1051/limn/2013047>.

458 Lytle, D.A., 2015. Chapter 37—order Hemiptera. In: Rogers, J.H.T.C. (Ed.), *Thorp and Covich's Freshwater*
 459 *Invertebrates, Ecology and General Biology*, vol. 4. Academic Press, Boston, pp. 951–963.
 460 <https://doi.org/10.1016/B978-0-12-385026-3.00037-1>.

461 Macan, T.T., 1954. A contribution to the study of the ecology of Corixidae (Hemiptera). *J. Anim.Ecol.* 23, 115–
 462 141.

463 Marignani, M., Bruschi, D., Garcia, D.A., Frondoni, R., Carli, E., Pinna, M.S., Cumo, F., Gugliermetti, F.,
 464 Saatkamp, A., Doxa, A., Queller, E.M., Chaieb, M., Bou Dagher-Kharrat, M., El Zein, R., El Jeitani, S.,
 465 Khater, C., Mansour, S., Al-Shami, A., Harik, G., Alameddine, I., El-Fadel, M., Blasi, C., 2017.
 466 Identification and prioritization of areas with high environmental risk in Mediterranean coastal areas: A
 467 flexible approach. *Sci. Total Environ.* 590, 566–578. <https://doi.org/10.1016/j.scitotenv.2017.02.221>.

468 Millán, A., Velasco, J., Gutiérrez-Cánovas, C., Arribas, P., Picazo, F., SánchezFernández, D., Abellán, P., 2011.
 469 Mediterranean saline streams in southeast Spain: what do we know? *J. Arid Environ.* 75, 1352–1359.
 470 <https://doi.org/10.1016/j.jaridenv.2010.12.010>.

471 Musolin, D.H., 2007. Insects in a warmer world: ecological, physiological and life history responses of true bugs
 472 (Heteroptera) to climate change. *Glob. Change Biol.* 13, 1565–1585. <https://doi.org/10.1111/j.1365-2486.2007.01395.x>.

474 Oren, A., 2000. Life at High Salt Concentrations: Possibilities and Limitations. In: Seckbach J. (eds) Journey to
 475 Diverse Microbial Worlds. Cellular Origin and Life in Extreme Habitats, vol 2. Springer, Dordrecht.
 476 https://doi.org/10.1007/978-94-011-4269-4_16.
 477 Poisson, R., 1957. Hétéroptères aquatiques. Faune de France. Vol. 61. Fédération Française des Sociétés de
 478 Sciences Naturelles, Paris, 263 pp.
 479 Polhemus, J.T., Polhemus, D.A., 2008. Global diversity of true bugs (Heteroptera; Insecta) in freshwater.
 480 Hydrobiologia. 595, 379–391. https://doi.org/10.1007/978-1-4020-8259-7_40.
 481 R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical
 482 Computing, Vienna, Austria. URL. <https://www.R-project.org/>. 2018.
 483 Rabitsch, W., 2008. The times they are a-changin': driving forces of recent additions to the Heteroptera fauna of
 484 Austria. In: Grozeva S, Simov N (eds) Advances in Heteroptera research. Festschrift in honour of 80th
 485 anniversary of Michail Josifov. PenSoft, Moscow, Sofia, pp 309–326.
 486 Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J., Kidd, K.A., MacCormack, T.J.,
 487 Olden, J.D., Ormerod, S.J., Smol, J.P., Taylor, W.W., Tockner, K., Vermaire, J.C., Dudgeon, D., Cooke,
 488 S.J., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biol. Rev.
 489 94, 849–873. <https://doi.org/10.1111/brv.12480>.
 490 Sánchez-Fernández, D., Abellán, P., Mellado, A., Velasco, J., Millán, A., 2006. Are water beetles good
 491 indicators of biodiversity in Mediterranean aquatic ecosystems? The case of the Segura river basin (SE
 492 Spain). Biodivers. Conserv. 15, 4507–4520. <https://doi.org/10.1007/s10531-005-5101-x>.
 493 Savage, A.A., 1982. Use of water boatmen (Corixidae) in the classification of lakes. Biol. Conserv. 23, 55–70.
 494 Savage, A.A., 1990. The distribution of Corixidae in lakes and the ecological status of the north-west Midlands
 495 meres. Field Studies. 7, 516–530.
 496 Savage, A.A., 1994. The distribution of Corixidae in relation to the water quality of British lakes: a monitoring
 497 model. Freshw. Forum 4, 32–61.
 498 Skern, M., Zweimüller, I., Schiemer, F., 2010. Water bugs as indicators for terrestrialization of floodplain
 499 habitats. Limnologica. 40, 241–250. <https://doi.org/10.1016/j.limno.2009.09.002>.
 500 Scheibler, E.E., Melo, M.C., Montemayor, S.I., Scollo, A.M., 2016. Abundance, richness, seasonal and
 501 altitudinal dynamics of aquatic true bugs (Heteroptera) in mountain wetlands of Argentina. Wetlands. 36,
 502 265–274. <https://doi.org/10.1007/s13157-016-0735-x>.

503 Schilling, J., Freier, K.P., Hertig, E., Scheffran, J., 2012. Climate change, vulnerability and adaptation in North
 504 Africa with focus on Morocco. *Agric. Ecosyst. Environ.* 156, 12–26.
 505 <http://dx.doi.org/10.1016/j.agee.2012.04.021>.
 506 Slimani, N., Moulet, P., Chen, P.P., Nieser, N., Pluot-Sigwalt, D., Boumaïza, M., Guilbert, E., 2015. Checklist,
 507 distribution, and a new record of Nepomorphan water bugs (Hemiptera, Heteroptera) in northern Tunisia.
 508 *Zootaxa*. 3981, 151–176. <https://doi.org/10.11646/zootaxa.3981.2.1>.
 509 Slimani, N., Chen, P.P., Nieser, N., Moulet, P., Inacio Ribeiro, J.R., Boumaïza, M., Guilbert, E., 2016.
 510 Annotated check-list of semi-aquatic bugs (Hemiptera: Heteroptera: Gerromorpha) of Tunisia, with detailed
 511 faunistic survey of North Tunisia. *Entomol. Am.* 122, 55–71. <http://dx.doi.org/10.1664/15-RA-059>.
 512 Slimani, N., Guilbert, E., El Ayni, F., Jrad, A., Boumaiza, M., Thioulouse, J., 2017. The use of STATICO and
 513 COSTATIS, two exploratory three-ways analysis methods - An application to the ecology of water bugs in
 514 the Medjerda watershed (Tunisia). *Environ. Ecol. Stat.* 24, 269–295. [https://doi.org/10.1007/s10651-017-](https://doi.org/10.1007/s10651-017-0370-6)
 515 [0370-6](https://doi.org/10.1007/s10651-017-0370-6).
 516 Slimani, N., Sánchez-Fernández, D., Guilbert, E., Boumaïza, M., Guareschi, S., Thioulouse, J., 2019. Assessing
 517 potential surrogates of macroinvertebrate diversity in NorthAfrican Mediterranean aquatic ecosystems.
 518 *Ecol. Ind.* 101, 324–329. <https://doi.org/10.1016/j.ecolind.2019.01.017>.
 519 Tamanini, L., 1979. Guide per il riconoscimento delle specie animali delle acque interne italiane. 6. Eterotteri
 520 acquatici (Heteroptera: Gerromorpha, Nepomorpha). Consiglio Nazionale delle Ricerche, Verona, 106 pp.
 521 Touaylia, S., Garrido, J., Boumaiza, M., 2013. Abundance and diversity of the aquatic beetles in a
 522 Mediterranean stream system (Northern Tunisia). *Annales de la Société entomologique de France (N.S.)*.
 523 *Int. J. Entomol.* 49, 172–180. <https://doi.org/10.1080/00379271.2013.815033>.
 524 Thioulouse, J., 2011. Simultaneous analysis of a sequence of paired ecological tables: A comparison of several
 525 methods. *Ann. Appl. Stat.* 5, 2300–2325. <http://dx.doi.org/10.1214/10-AOAS372>.
 526 Thioulouse, J., Chessel, D., 1987. Les analyses multitableaux en écologie factorielle. I: De la typologie d'état à la
 527 typologie de fonctionnement par l'analyse triadique. *Acta Oecol.* 8, 463–480.
 528 Thioulouse, J., Dray, S., Dufour, A.B., Siberchicot, A., Jombart, T., Pavoine, S., 2018. Multivariate Analysis of
 529 Ecological Data with ade4. New York, NY: Springer-Verlag New York. [https://doi.org/10.1007/978-1-](https://doi.org/10.1007/978-1-4939-8850-1)
 530 [4939-8850-1](https://doi.org/10.1007/978-1-4939-8850-1).
 531 Thioulouse, J., Simier, M., Chessel, D., 2004. Simultaneous analysis of a sequence of paired ecological tables.
 532 *Ecology*. 85, 272–283.

533 Townsend, C.R., Hildrew, A.G., 1994. Species traits in relation to a habitat templet for river systems. *Freshw.*
534 *Biol.* 31(3), 265–275. <https://doi.org/10.1111/j.1365-2427.1994.tb01740.x>.

535 Tully, O., McCarthy, T.K., O'Donnell, D., 1991. The ecology of the Corixidae (Hemiptera: Heteroptera) in the
536 Corrib catchment, Ireland. *Hydrobiologia.* 210, 161–169. <https://doi.org/10.1007/BF00034674>.

537 Turić, N., Temunović, M., Radović, A., Vignjević, G., Sudarić Bogojević, M., Merdić, E., 2015. Flood pulses
538 drive the temporal dynamics of assemblages of aquatic insects (Heteroptera and Coleoptera) in a temperate
539 floodplain. *Freshw. Biol.* 60, 2051–2065. <https://doi.org/10.1111/fwb.12629>.

540 Velasco, J., Millán, A., Hernández, J., Gutiérrez, C., Abellán, P., Sánchez, D., Ruiz, M., 2006. Response of
541 biotic communities to salinity changes in a Mediterranean hypersaline stream. *Saline Syst.* 2, 12.
542 <https://doi.org/10.1186/1746-1448-2-12>.

543 Velasco, J., Gutiérrez-Cánovas, C., Botella-Cruz, M., Sánchez-Fernández, D., Arribas, P., Carbonell, J.A.,
544 Millán, A., Pallarés, S., 2019. Effects of salinity changes on aquatic organisms in a multiple stressor
545 context. *Philos. Trans. R. Soc. B* 374, 20180011. <https://doi.org/10.1098/RSTB.2018.0011>.

546 Verneaux, J., Tuffery, G., 1967. Une méthode zoologique pratique de détermination de la qualité biologique des
547 eaux courantes. Indices biotiques. *Annales Scientifiques de l'Université de Besançon, Zoologiques* 3, 79-
548 90.

549 White, J.C., Krajenbrink, H.J., Hill, M.J., Hannah, D.M., House, A., Wood, P.J., 2019. Habitat-specific
550 invertebrate responses to hydrological variability, anthropogenic flow alterations, and hydraulic
551 conditions. *Freshw. Biol.* 64, 555–576. <https://doi.org/10.1111/fwb.13242>.

552 Whiteman, N. K., Sites, R.W., 2008. Aquatic insects as umbrella species for ecosystem protection in Death
553 Valley National Park. *J. Insect Conserv.* 12(5), 499–509. <https://doi.org/10.1007/s10841-007-9090-9>.

554 Zhang, M., Muñoz-Mas, R., Martínez-Capel, F., Qu, X., Zhang, H., Peng, W., Liu, X., 2018. Determining the
555 macroinvertebrate community indicators and relevant environmental predictors of the Hun-Tai River Basin
556 (Northeast China): A study based on community patterning. *Sci. Total Environ.* 634, 749–759.
557 <https://doi.org/10.1016/j.scitotenv.2018.04.021>.

558 Zimmermann, M., Scholl, A., 1993. Specific status of *Aquarius cinereus* (Puton) and *A. najas* (De Geer)
559 (Hemiptera: Gerridae) and the extent of hybridization in the Mediterranean region. *Insect Syst. Evol.* 24,
560 197–210.

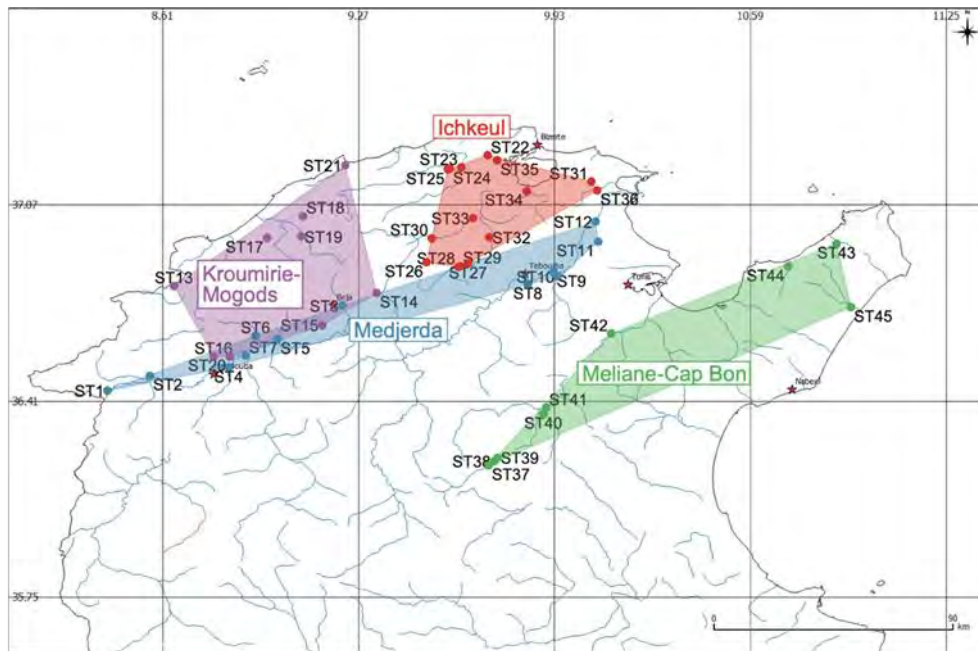


Figure 1.

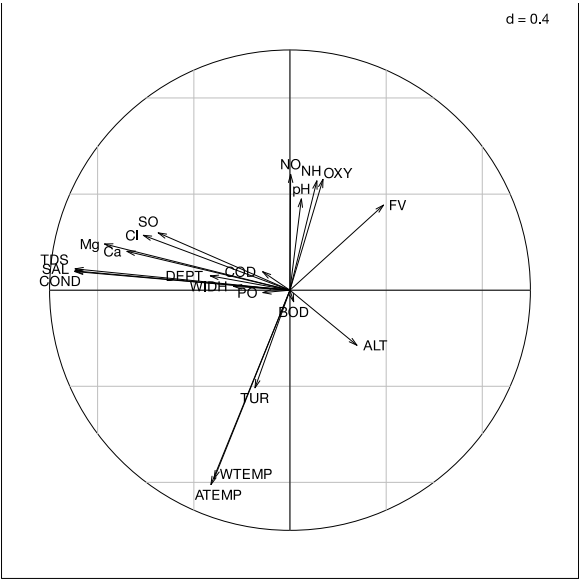


Figure 2.

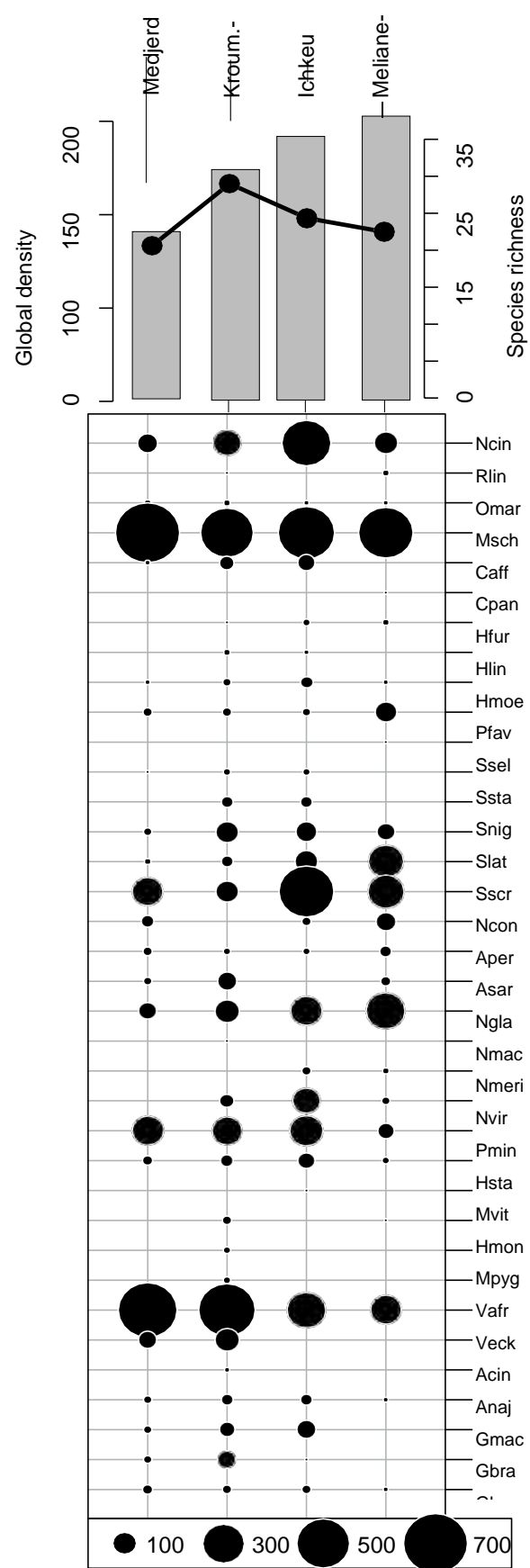


Figure 3.

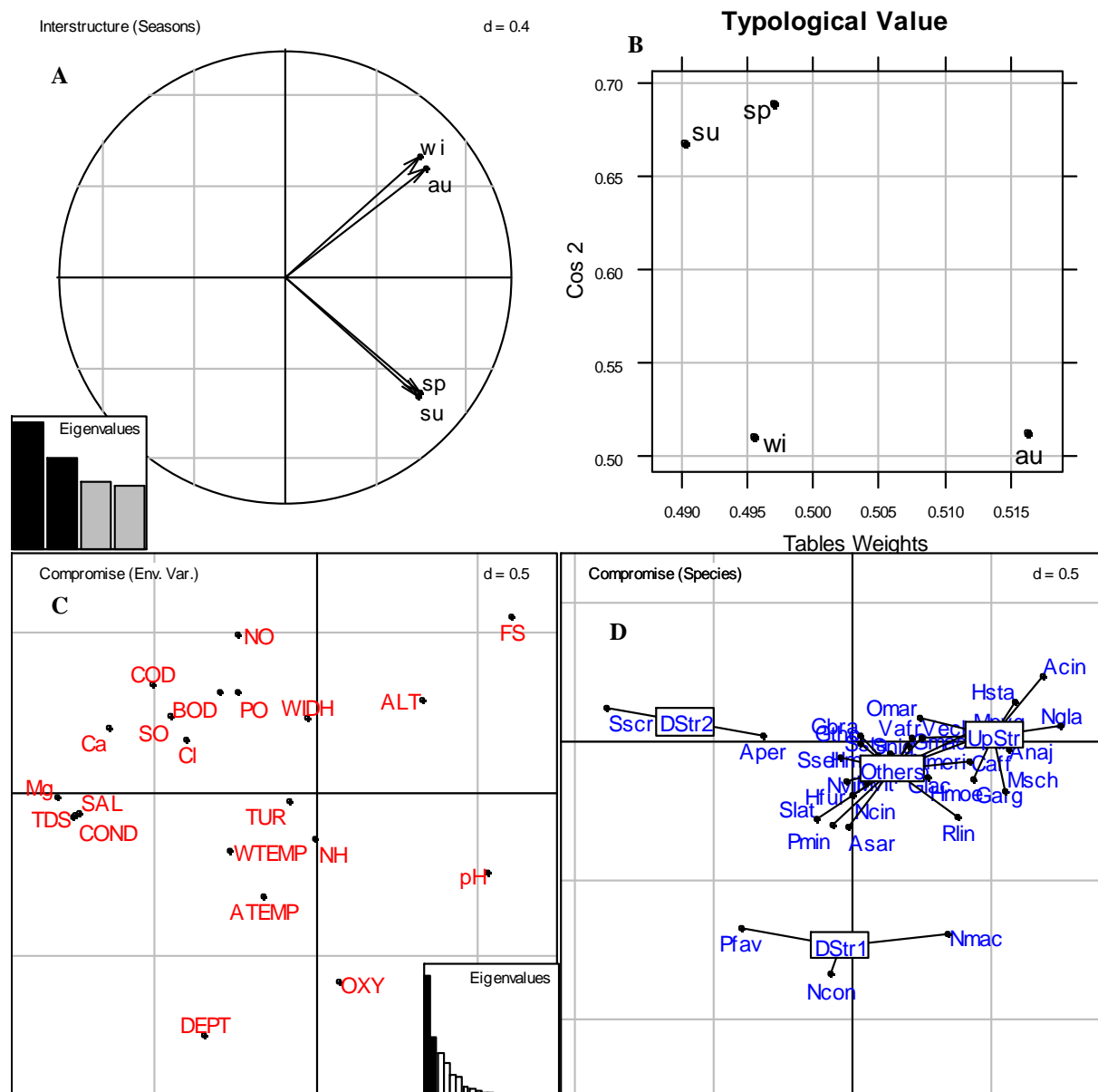


Figure 4.

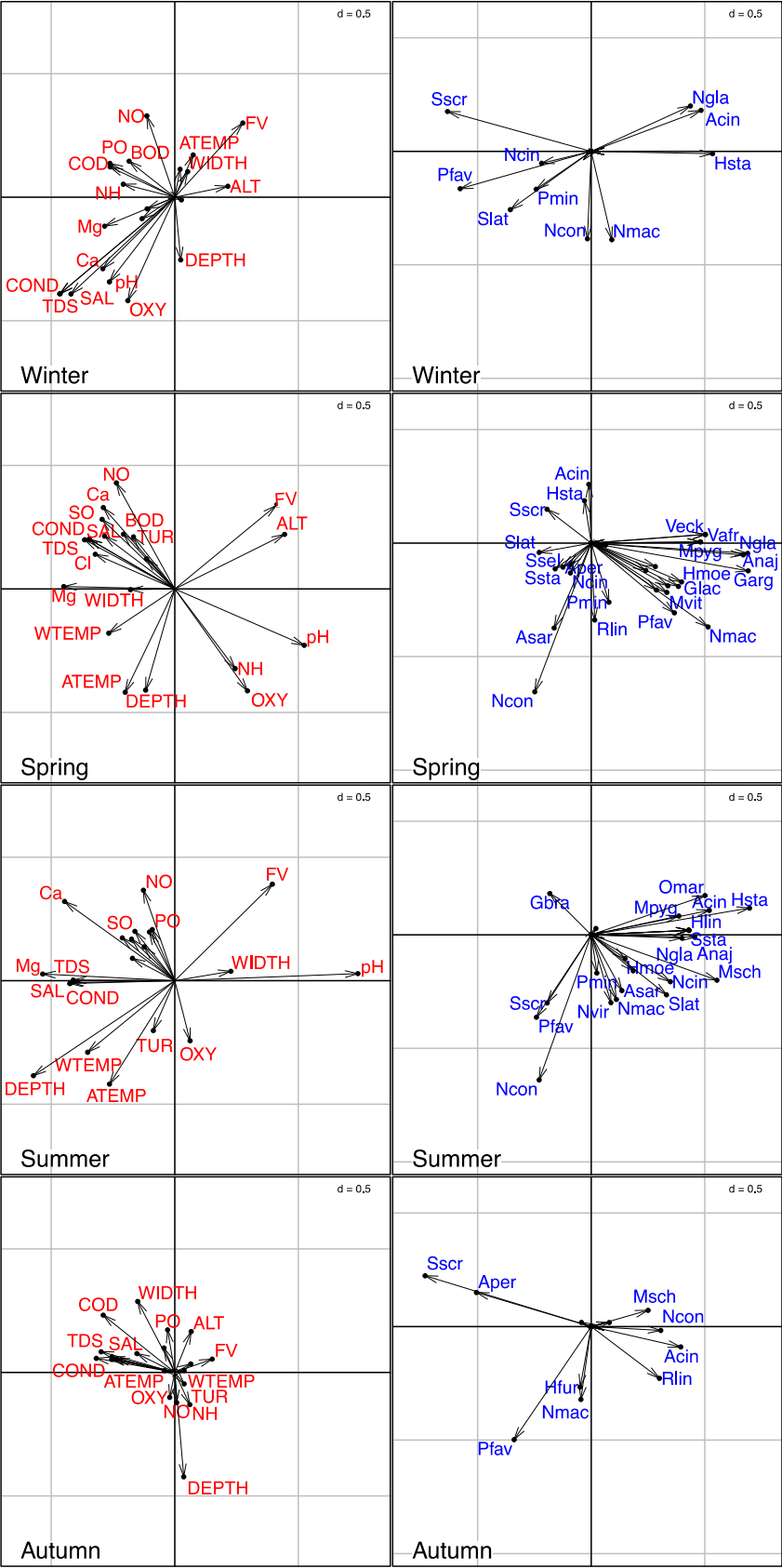


Figure 5.

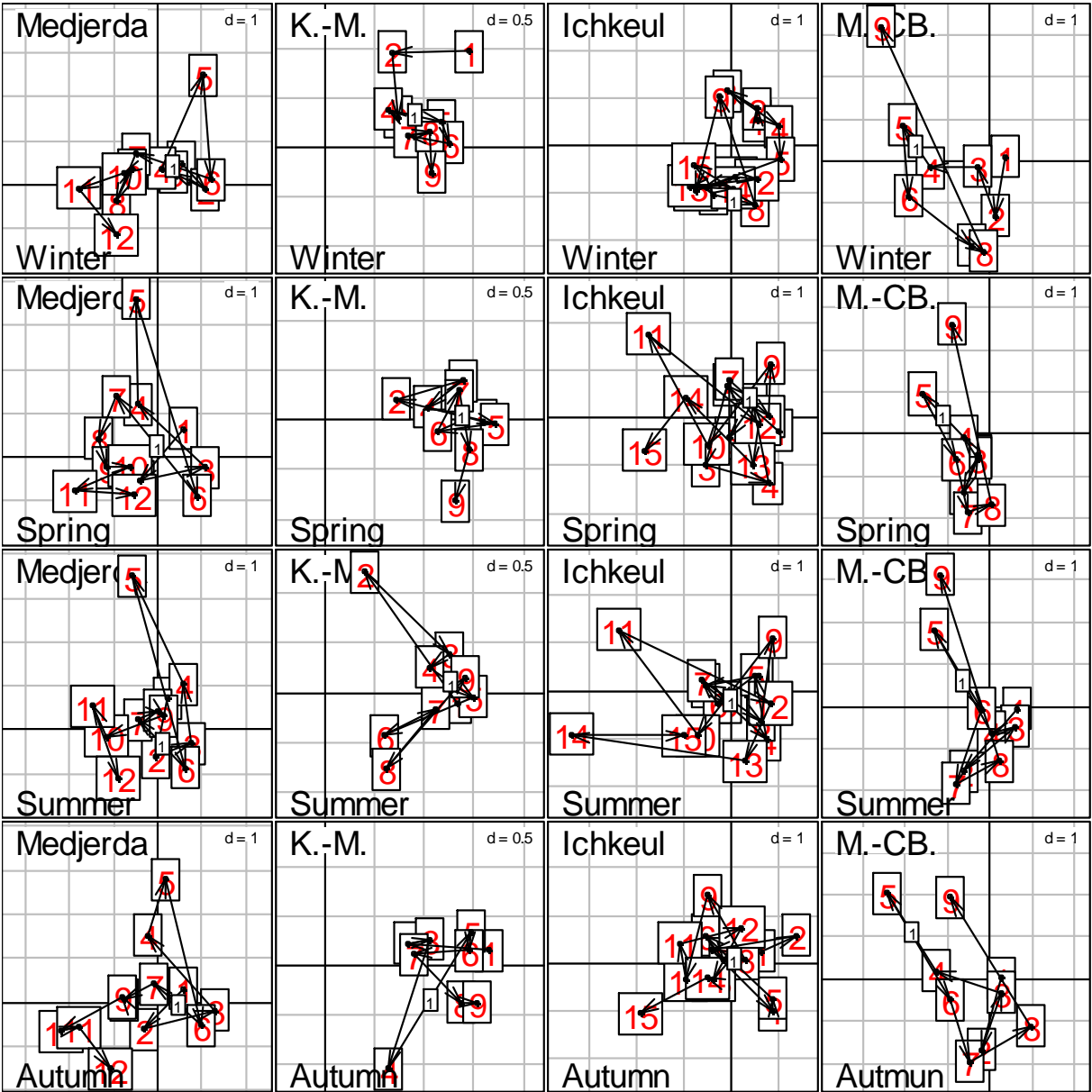


Figure 6A.

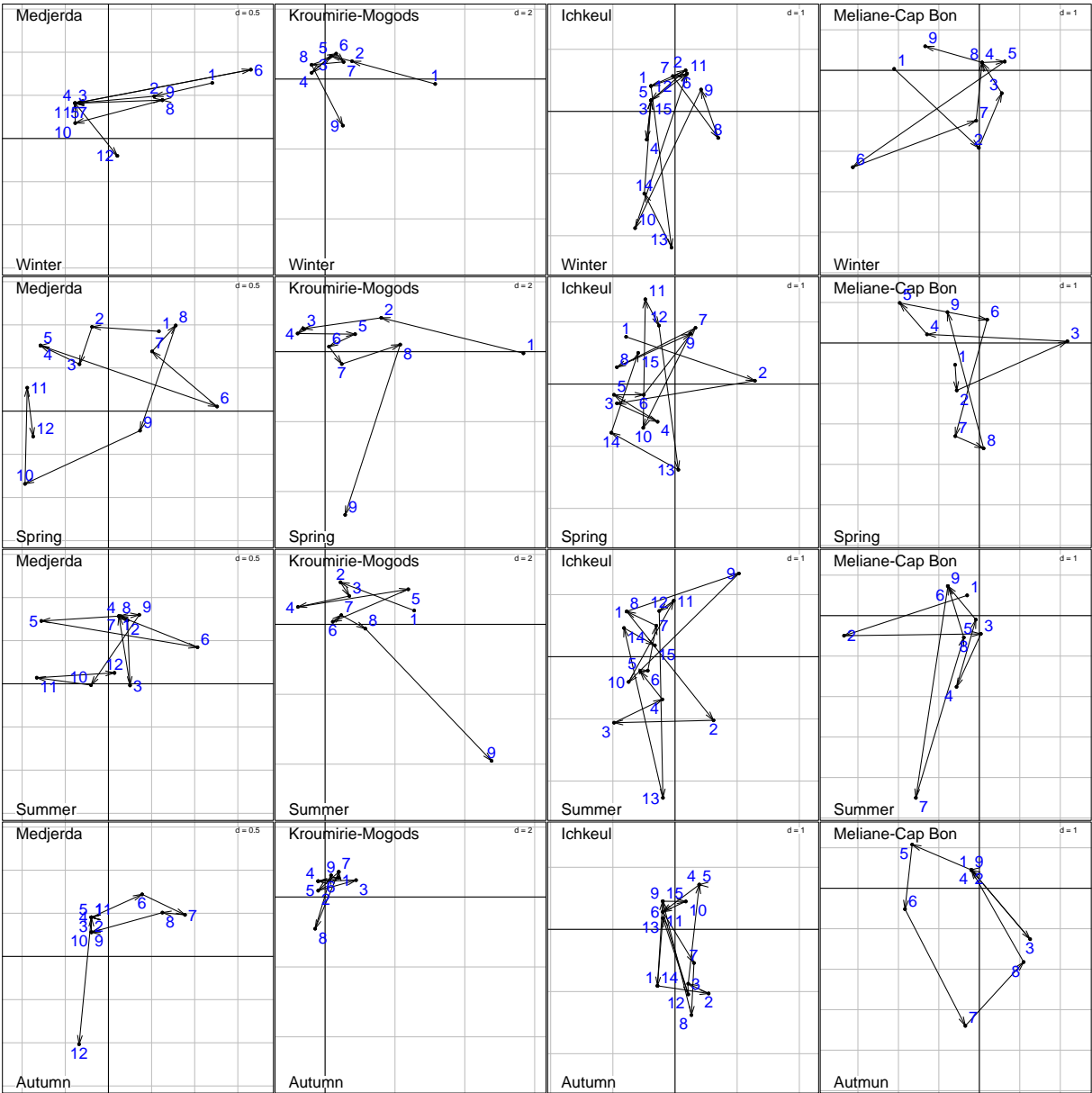


Figure 6B.

Figure 1. Map indicating the location of the study sites within the four catchments (Medjerda, Kroumirie-Mogods, Ichkeul and Meliane-Cap Bon) in northern Tunisia (Site codes and names are presented in Supplementary Table S1) .

Figure 2. PCA biplot of indicating the physicochemical variables with the greatest loading on the first two axes –see Table 1 for definition of environmental codes.

Figure 3. (a) Plot of the spatial changes in aquatic Heteroptera Global density (ind/m²) and Species richness during the study period (b) Plot of the spatial changes in mean density for each of the 36 species in the four catchments (Medjerda, Kroumirie-Mogods, Ichkeul and Meliane-Cap Bon) in northern Tunisia (codes for species names are defined on Table 2).

Figure 4. General plot of the STATICO method: Interstructure factor map (A) and the table weight and Cos² are shown in (B). Compromise factor map for environmental variables (C) and for taxa (D) using STATICO analysis on the 45 sites data in the four catchments of northern Tunisia from January to December 2013. See Tables 1 and 2 for definitions of environmental and taxonomic codes respectively.

Figure 5. Intrastructure plot of the STATICO analysis for environmental parameters (red, left) and water bugs (blue, right) at each season. See Tables 1 and 2 for definitions of environmental and taxonomic codes respectively

Figure 6A. Intrastructure plot of the STATICO analysis detailing the environmental parameters for the sampling sites by catchment and season. See Tables S1 for site names and further details.

Figure 6B. Intrastructure plot of the STATICO analysis of the water bugs for the sampling sites by catchment and season. See Tables S1 for site names and further details.

Table 1. Summary of environmental parameters for the 45 sites from the four catchments (Medjerda; Kroumirie-Mogods; Ichkeul; and Meliane-Cap Bon) in northern Tunisia during the study period. Definition of environmental parameter codes: channel width (WIDT) and water depth (DEPT), altitude (ALT), salinity (SAL), electrical conductivity (COND), total dissolved salt (TDS) dissolved oxygen (OXY), water temperature (WTEMP), air temperature (ATEMP), flow velocity (FV), calcium (Ca²⁺), magnesium (Mg²⁺), sulphates (SO₄²⁻), chloride (Cl⁻), nitrates (NO₃⁻), nitrite (NO₂⁻), ammoniac (NH₄⁺), orthophosphate (PO₄³⁻), chemical oxygen demand (COD), biological oxygen demand (BOD₅).

Environmental parameters	Global			Winter			Spring			Summer			Autumn			F values (df)
	Min	Max	Mean ±SD	Min	Max	Mean ±SD	Min	Max	Mean ±SD	Min	Max	Mean ±SD	Min	Max	Mean ±SD	
ALT (m)	1	398	105.4±117	1	398	105.4±117	1	398	105.4±117	1	398	105.4±117	1	398	105.4±117	0
Width (m)	2	40	12.01±10.3	2	40	11.8± 10	2	40	11.8±10	2	40	11.8± 10	2	40	11.8± 10	0.03
Depth (cm)	5	50	19.66±14.15	5	50	19.6±14.2	5	50	19.6±14.2	5	50	19.6±14.2	5	50	19.6±14.2	0
pH	6.8	8.69	7.8±0.33	7.2	8.45	7.82±0.34	7.4	8.7	8±0.24	6.8	8.06	7.5±0.26	7.3	8.42	7.84±0.28	25.94* **
SAL (psu)	0.1	7.6	1.2±1.15	0.1	3.8	1.06±0.97	0.1	3.8	1.4±1.1	0.1	7.6	1.5±1.4	0.1	3.5	1.16±1	1.52
COND (µS cm ⁻¹)	212	13100	2515±2071	212	7400	2058± 1736	382	7520	2806±2036	388	13100	2883±2495	245	6510	2314±1895	1.65
TDS (mg L ⁻¹)	154	10558	1864±1570	154	5508	1523± 1302	259	5597	2080±1542	263	10558	2141±1930	179	4845	1710±1420	1.61
OXY (mg L ⁻¹)	1	11.8	6.38±2.11	1	11.8	6.59±2.8	1.4	9.25	5.83±1.83	1.2	6.68	5.36±1	1.1	9.77	7.74±1.53	13.13* **
Turbidity (NTU)	0	71	4.44±13.22	0.1	16	3±3.9	0.0	60	7.45±12.84	0.3	64	16.5±16.6	0.1	71	6.77±12.41	9.69* **
Water Temp (°C)	2	30	16.66±6.42	2	20	10.5±3.6	16	24	19.92±2.42	18	30	24.4±2.9	8	18.5	11.7±1.95	258.3* **
Air Temp (°C)	5	42	19.08±8.93	5	17	13.2±3.25	12	35	22.64±6.43	23	42	30±5	7	14	10.5±1.63	180.96* **
FV (cm s ⁻¹)	2.5	159	36.4± 31.95	3.3	159	42.07±30	2.6	63	21 ±17.7	2.6	58.82	21.8±15.9	4.5	153	54.85±39	16.24* **
Ca ²⁺ (L ⁻¹)	14	540.8	156.1± 90.9	14	341.3	136.9± 78.6	30	540.8	167.8±103	33	540.8	166±96	30	389	153±82.2	1.12
Mg ²⁺ (L ⁻¹)	3.5	277.9	59.77± 52.9	3.5	201.7	51.94±47.64	5.9	277.9	67.57±45.7	5.9	277.9	61±54.6	7.7	207	58.2±49.8	0.68

SO ₄ ²⁻ (L ⁻¹)	13.5	3100	239.3±568.1	13	872.3	176.72±185	21	3100	273.6±488	33	3100	304±492	13	872	202±197	1.16
Cl ⁻ (L ⁻¹)	0.1	2600	268.9± 457	0.1	1491	194.96±268	37	2600	324±589.7	37	2600	347±584	0.1	1491	209±267	1.3
NO ₃ ⁻ (L ⁻¹)	0.26	581.9	44.47±90.57	0.5	114	27.5±31	0.5	103.7	26.4±29.7	0.5	92	22.24±24.7	0.2	581	101±162	9.09* **
NH ₄ ⁺ (L ⁻¹)	0.02	81.2	2.3±14.47	0.06	12.3	1.7±2	0.02	2.34	0.64±0.54	0.1	2.42	0.7±0.49	0.03	81.2	6.3±16.7	4.57* **
PO ₄ ³⁻ (L ⁻¹)	0.1	8.73	0.31±0.77	0.1	8.73	0.38±1.28	0.15	2.6	0.28±0.43	0.15	4	0.31±0.68	0.1	2.47	0.28±0.4	0.15
COD (mg L ⁻¹)	15	1025	39.89±84.77	16	1025	57.87±155.2	16	181	31.1±26.8	16	33	33±34	15	323	37.5±52	0.94
BOD5 (mg L ⁻¹)	0.3	102	2.98±10.5	0.5	31	2.39±2.39	0.3	56	3.1±10.43	0.3	8.72	2.88±8.7	0.5	102	3.5±15	0.08

F values: between groups mean square/within-groups mean square.

Significant difference between sampled seasons: (***)p < 0.001).

Table2. List of species and their codes used in STATICO analysis.
Average (range) species density (ind/m²) and abundance (%) of aquatic Heteroptera during the study period.
Species in bold represent the most abundant species.

	Family	Species	Codes	Global density (ind/m ²)	Abundane (%)
Nepomorpha	Nepidae	<i>Nepa cinerea</i> L.	Ncin	508.33	7.82
	Ranatridae	<i>Ranatra linearis</i> L.	Rlin	25	0.38
	Ochteridae	<i>Ochterus marginatus</i> L.	Omar	16.66	0.26
	Micronectidae	<i>Micronecta scholtzi</i> F.	Msch	1458.33	22.43
	Corixidae	<i>Corixa affinis</i> L.	Caff	58.33	0.89
		<i>Corixa panzeri</i> F.	Cpan	8.33	0.13
		<i>Hesperocorixa furtiva</i> H.	Hfur	25	0.26
		<i>Hesperocorixa linnaei</i> F.	Hlin	16.66	0.26
		<i>Hesperocorixa moesta</i> F.	Hmoe	58.33	0.89
		<i>Parasigara favieri</i> P.	Pfav	100	1.54
		<i>Sigara selecta</i> F.	Ssel	8.33	0.13
		<i>Sigara stagnalis stagnalis</i> F.	Sstag	50	0.77
		<i>Sigara nigrolineata nigrolineata</i> F.	Snig	83.33	1.28
		<i>Sigara lateralis</i> L.	Slat	175	2.69
		<i>Sigara scripta</i> R.	Sscr	250	3.84
	Naucoridae	<i>Naucoris maculatus conspersus</i> S.	Ncon	658.33	10.13
	Notonectidae	<i>Anisops debilis perplexus</i> P.	Aper	91.66	1.41
		<i>Anisops sardeus sardeus</i> H.	Asar	50	0.77
		<i>Notonecta glauca</i> L.	Ngla	66.66	1.02
		<i>Notonecta maculata</i> F.	Nmac	433.33	6.66
		<i>Notonecta meridionalis</i> P.	Nmer	41.66	0.13
		<i>Notonecta viridis</i> D.	Nvir	16.66	0.26
	Pleidae	<i>Plea minutissima</i> L.	Pmin	166.66	2.56
Gerromorpha	Hydrometridae	<i>Hydrometra stagnorum</i> L.	Hsta	450	6.92
	Mesoveliidae	<i>Mesovelia vittigera</i> H.	Mvit	125	1.92
	Hebridae	<i>Hebrus montanus</i> K.	Hmon	8.33	0.13
	Veliidae	<i>Microvelia pygmaea</i> D.	Mpyg	33.33	0.51
		<i>Velia eckerleini</i> T.	Veck	33.33	0.51
		<i>Velia africana</i> T.	Vafr	33.33	0.5
	Gerridae	<i>Aquarius cinereus</i> P.	Acin	1116.66	17.18
		<i>Aquarius najas</i> De G.	Anaj	41.66	0.64

		<i>Gerris maculatus</i> T.	Gmac	50	0.26
		<i>Gerris brasili</i> P.	Gbra	58.33	0.89
		<i>Gerris lacusrtis</i> L.	Glac	116.66	1.79
		<i>Gerris argentatus</i> S.	Garg	91.66	1.41
		<i>Gerris thoracicus</i> S.	Gtho	50	0.77