

Original Article

Ecological structure of aquatic macroinvertebrate communities in the Hauts Plateaux of Northeast Algeria

Estrutura ecológica das comunidades de macroinvertebrados aquáticos nos Hauts Plateaux do nordeste da Argélia

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Abstract

Aquatic macroinvertebrates are integral parts of functioning wetlands, inhabiting a diversity of aquatic ecosystems where communities are spatially structured. Macroinvertebrates of some Mediterranean regions such as North Africa are still not well studied. Here, we study the community structure of benthic macroinvertebrates in four different types of lotic and lentic wetlands in the semiarid Haut Plateaux of Northeast Algeria. Macroinvertebrates and 06 physicochemical parameters were sampled in 12 sites belonging to four types of habitats (lotic river, lentic river, dams, and sebkha [saline lentic water body]) during January–December 2021. Eventually, the character lentic-lotic was the most important variable affecting the affecting invertebrate communities in the Mediterranean region. The results revealed that sebkha and dams had a lower Shannon index than lentic and lotic rivers. Non-metric multidimensional scaling analysis showed a strong overlap between the community composition in lotic and lentic sites. However in the three types of aquatic groups lentic river, dam and lotic habitats showed a strong overlap between the community whereas sebkha was markedly separated. Redundancy analysis showed that water velocity and pH, were the main drivers of community structure of macroinvertebrates, revealed a strong effect with pH ($F_{1,8}=4.15$, $P=0.001$) and water velocity ($F_{1,8}=3.22$, $P=0.002$), separating lotic communities from those that inhabited dams, lentic rivers, and sebkhas. As conclusion, this study contributes to the better understanding of the community structure of macroinvertebrates in semiarid North Africa where wetlands have been experiencing high anthropogenic disturbance.

Keywords: abiotic factors, Algeria, freshwater, insects, monitoring, North Africa, Wetlands.

Resumo

Macroinvertebrados aquáticos são partes integrantes de zonas úmidas em funcionamento, habitando uma diversidade de ecossistemas aquáticos onde as comunidades são espacialmente estruturadas. Os macroinvertebrados de algumas regiões mediterrâneas, como o norte da África, ainda não foram especificamente analisados. Neste trabalho, almejou-se analisar a estrutura da comunidade de macroinvertebrados bentônicos em 4 tipos diferentes de pântanos lóticos e lênticos no semiárido Haut Plateaux do nordeste da Argélia. Os macroinvertebrados e 6 parâmetros físico-químicos foram amostrados mensalmente em 12 locais pertencentes a 4 categorias de habitats diferentes (rio lótico, rio lêntico, barragens e sebkha – corpo de água salina lêntica) de janeiro a dezembro de 2021. Os resultados revelaram que sebkha e barragens tiveram um pH mais baixo do que os rios lênticos e lóticos. A análise de escala multidimensional não-métrica mostrou uma forte sobreposição entre a composição da comunidade em sítios lóticos e lênticos, mas nos 3 tipos de sítios lênticos, barragem e rio lêntico mostraram uma forte sobreposição, enquanto sebkha foi marcadamente separado. A análise de redundância mostrou que a velocidade da água e o pH foram os principais impulsionadores da estrutura da comunidade de macroinvertebrados, separando as comunidades lóticas daquelas que habitavam barragens, rios lênticos e sebkhas. Assim, à guisa de conclusão, este estudo contribui para a melhor compreensão da estrutura da comunidade de macroinvertebrados no semiárido norte da África, onde as zonas úmidas têm sofrido alta perturbação antrópica.

Palavras-chave: água fresca, Argélia, fatores abióticos, insetos, monitoramento, norte da África, zonas úmidas.

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Received: March 15, 2023 – Accepted: April 4, 2023



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1. Introduction

Wetlands harbor a high biological diversity and provide many services to nature and people (Fu et al., 2018). Some of the ecological functions that wetlands provide include nutrient cycling (Bunn et al., 1999), carbon storage and gas regulation (Meng et al., 2017), flood control (Hey and Philippi, 1995), wildlife habitat provision (Jacobs et al., 2009), and maintenance of biodiversity and human needs (Hu et al., 2017). Wetlands are also one of the world's most biologically productive natural ecosystems (Li et al., 2020), even though they represent only a small portion of the planet's surface (Reid et al., 2019). The increase in anthropogenic disturbance due to climate change, pollution, and habitat fragmentation contributes independently or jointly to the degradation of the structural integrity of wetlands, as well as their physicochemical and biological characteristics (Fernandes et al., 2018).

Physicochemical factors spatially structure communities in aquatic environments (Allan et al., 2021), and contribute to the local and regional diversity of aquatic fauna and flora. For instance, at the regional scale, communities are influenced by factors such as dissolved oxygen, temperature, and salinity which usually vary from one aquatic habitat to another (Figueroa and De los Rios-Escalante, 2021). Environmental factors also change in time, particularly in temperate regions (e.g., from one season to another), influencing the life cycle of aquatic organisms and determining their abundance and community composition across time (Smeti et al., 2019). In addition, anthropogenic factors tend to change the physicochemical characteristics of water, influencing the structure and diversity of aquatic organisms (Ferguani and Arab, 2013). Understanding the seasonal changes in physicochemical factors is crucial to determine the factors that drive the abundance and composition of aquatic communities.

In the Mediterranean hotspot of biodiversity (Myers et al., 2000), aquatic macroinvertebrates are adapted to fluctuating climatic conditions characterized by hot and dry summers and cool and wet winters. According to research, inland Mediterranean macroinvertebrates were shown to be more varied than temperate macroinvertebrates (Bonada et al., 2007). Aquatic macroinvertebrates have not been well studied in North Africa where wetlands vary in persistence, salinity, and variability in water velocity. Determining the community structure of aquatic macroinvertebrates in these regions is a priority to establish local programs of biomonitoring. In the last two decades, studies in different groups of macroinvertebrates in North Africa have described their ecology, life cycle, and adaptation (Jelassi et al., 2013, 2018; Mahdjoub et al., 2015; Khelifa et al., 2019) demonstrating notable taxonomic richness and endemism, and revealing several human challenges to the long-term survival of aquatic biodiversity (Khelifa et al., 2021a, b, c).

In this study, we aim to understand the structure of benthic macroinvertebrate communities in different types of wetlands in the semiarid high plateaux of Northeast Algeria (Khenchela and Oum El Bouaghi province). We sampled monthly macroinvertebrates and 06 physicochemical parameters in 12 sites belonging to four types of habitats

(slow-flowing river, fast-flowing river, sebkha [saline lentic water body], and dams) during January–December 2021. We specifically assessed potential differences between different habitat types in (1) macroinvertebrate richness, abundance, and diversity; (2) physicochemical parameters of the water of all sites; and (3) the congruence between the spatial pattern of community composition and abiotic parameters of the water. We hypothesize that (1) habitat type determines the community structure and taxonomic diversity (Jelassi et al., 2018), (2) the magnitude of congruence in macroinvertebrate communities in freshwater and saline water will be low compared to lentic and lotic freshwater systems (Khemaissia et al., 2018), and (3) salinity and lotic-lentic character of the water will be the most important drivers of community composition (Piscart et al., 2005; Buffagni et al., 2009).

2. Material and Methods

Study area: The study was conducted in the high plateaux of Northeast Algeria, specifically in the province of Khenchela and the Wilaya of Oum El Bouaghi. This region is characterized by a semiarid climate with cool and cold winters and, hot and dry summers. The region is known for its very heterogeneous physical and natural environments with three distinct natural regions: the high plains of the North, the mountainous area in the West and, the steppe and Saharan landscapes in the South. Agriculture is one of the main economic activities for the rural population in the region, which is currently undergoing rapid expansion of anthropogenic activities.

We selected 12 wetlands, including six lotic (river) and six lentic sites (lentic part of river, dam, and sebkha) (Figure 1; Table 1). The selection of study sites was based on geographic localization. Due to climate and basin-scale regulatory factors, river types in distinct geographic areas are predicted to have diverse hydrological regimes

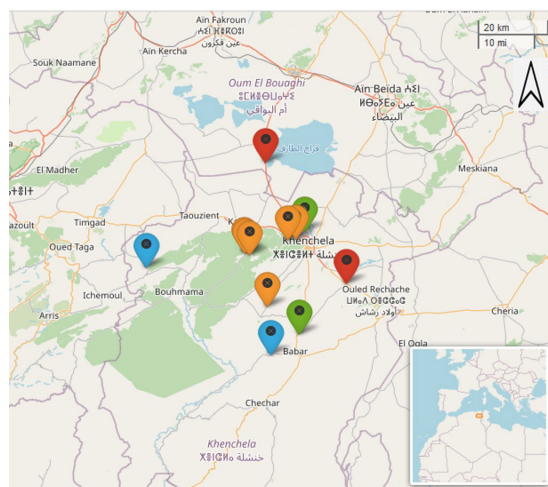


Figure 1. Geographic distribution of the study sites in Northeast Algeria. The map was generated from the leaflet R package. Blue marker refers to dam, orange marker refers to lotic river, red marker refers to sebkha, and green marker refers to lentic river.

Table 1. Geographical coordinates, habitat types, and depth of the study sites in Algerian High Plains.

Code	Site	Lotic/Lentic	Ecosystem	Habitat type	Latitude (N)	Longitude (E)	Altitude (m)	Average Depth (cm)
Site1	Barbar River	Lotic	River	Lotic river	35°24.818'	6°57.691'	1061	10
Site2	Hammam Essalihine River	Lotic	River	Lotic river	35°27.103'	7°04.898'	1032	11.9
Site3	Ibkan River	Lotic	River	Lotic river	35°25.295'	6°56.731'	1031	10
Site4	Issoual River	Lotic	River	Lotic river	35°25.031'	6°56.944'	1039	15.3
Site5	Tamagra River	Lotic	River	Lotic river	35°17.027'	7°00.987'	1099	9.6
Site6	Tanout River	Lotic	River	Lotic river	35°27.200'	7°06.376'	1036	4.9
Site7	Lake of Garaet El Taref	Lentic	Sebkha	Sebkha	35°38.801'	7°00.729'	835	14
Site8	Lake of Ouled Msallem	Lentic	Sebkha	Sebkha	35°20.498'	7°15.728'	1073	18
Site9	Baghaï River	Lentic	River	Lentic river	35°28.458'	7°08.028'	981	39
Site10	El H'tiba River	Lentic	River	Lentic river	35°12.802'	7°06.991'	980	9.2
Site11	Babar Dam	Lentic	Dam	Dam	35°09.761'	7°01.742'	941	15
Site12	Tagharist Dam	Lentic	Dam	Dam	35°22.985'	6°38.631'	1222	16

(Monk et al., 2006). Some sites (El H'tiba River, Ibkan River and the lake of Garaet El Taref) have a temporary hydroperiod and tended to dry out in the summer. One of the sites (Garaet El Taref) which is the largest water body in the region, has been a Ramsar site since 2004.

Sampling protocol: To assess and monitor changes in the physicochemical and biological quality of freshwater, we sampled the macroinvertebrates and six physicochemical parameters (water speed, conductivity, O₂, pH, salinity, and water temperature) in each site monthly from January 2021 to December 2021. We used multi-parameter Multi 3620 IDS WTW to estimate the physicochemical parameters. The measurements were taken near the bank in lentic sites and in the middle of the watercourse in lotic sites. The probe was submerged in the water at a depth of about 10 cm. All measurements were taken during 08:00 and 16:00. We made sure to take physicochemical measurements before sampling the macroinvertebrates to avoid biased data due to habitat perturbation. Macroinvertebrates were sampled using a dipnet (50 cm diameter, 500 µm mesh size) with the kick sampling method in lotic sites based on the AQEM project (Hering et al., 2003), and the S3i sampling method for lentic sites. During our sampling, one collector spent a total of 2 h per site per visit throughout the study. The collected samples were preserved in 80-96% ethanol in bottles labelled with the site name and date of collection. In the laboratory, the samples were sorted, and identified under a stereoscope. Since some taxonomic groups of macroinvertebrates were difficult to identify at the species or genus level, taxa were identified at the family level using identification keys (Tachet et al., 2010; Oscoz et al., 2011). While most macroinvertebrates were at the larval stage, some taxa were at the adult stage (Tachet et al., 2010).

Statistical analysis: All statistical analyses were carried out using the R program (R Development Core Team, 2023). We used the Wilcoxon test to determine whether taxonomic richness (log-transformed log[x+1]), abundance (log-transformed log[x+1]), and Shannon index were significantly different between lotic and lentic sites.

We used ANOVA to assess whether the latter variables differed significantly across sites and the four habitat types. We also tested whether the six physicochemical parameters differed significantly among sites and habitat types using ANOVA, and between lotic and lentic sites using Wilcoxon test. Significant ANOVA tests were followed with a posthoc Tukey test to test for differences among pairs of habitat types.

To understand the structure of community composition of benthic macroinvertebrates in lentic and lotic habitats, we performed nonmetric-multidimensional scaling (NMDS) ordinations based on Bray-Curtis distances and Wisconsin square root transformation using the *adonis2* function from the *vegan* package (Oksanen et al., 2013). Using the *metaMDS* function, we determined that the final solution of the global multidimensional scaling was reached after 20 interactions, showing a stress value of 0.15. Using the *adonis* permutation tests based on Bray-Curtis dissimilarities, we tested for potential differences in taxonomic composition of benthic macroinvertebrates between habitat types and seasons (winter [December to February], spring [March to May], summer [June to August], and autumn [September to November]) with multivariate ANOVA (PERMANOVA). We also performed pairwise comparisons between habitat types using the pairwise *Adonis* package (Martinez Arbizu, P. 2020).

To determine the relationship between the abiotic factors and the composition of benthic communities (based on abundance), we used redundancy analysis (RDA) model (Legendre and Legendre, 1998). Prior to this analysis, we removed collinearities among explanatory variables (six abiotic factors) using the *vif.cca* function and applying a threshold of < 2 to retain variables. We retained only five explanatory variables after removing dissolved oxygen because of high correlation with salinity (spearman's correlation: $r = 0.85$, $P = 0.0004$). We also standardized all environmental variables and Hellinger-transformed the community data. We determined whether the full RDA model was significant using the ANOVA function

of the vegan package. We then used a forward selection procedure to reveal the most influential abiotic factors on the benthic community composition using the ordiR2step function. We reported both R2 and adjusted R2 (corrected for the number of explanatory variables) estimated using the RSquareAdj function. Values are mean±SD.

3. Results

Diversity of macroinvertebrate community: We collected a total of 8031 individuals of macroinvertebrates including 45 families, belonging to 14 orders and five classes (Table S1). Insecta was the class with the largest number of families (N=38, 84.4% of families; nine orders). With 8 families, Diptera was the order with the largest number of families, followed by Gastropoda (N=2, 4.4%; 1 order), Malacostraca (N=2, 4.4%; two orders), Clitellata (N=2, 4.4%; two orders), then Enoplea (N=1, 2.2%; 1 order).

There was a large variation among sites in the overall taxonomic (familial) richness (ANOVA: $F_{11,107} = 6.30$, $P < 0.0001$) with an average of 17.0 ± 6.61 families, a minimum of two families recorded at Lake Ouled Msallem, and a maximum of 26 families recorded at Tanout River. Taxonomic richness per visit was significantly higher in lotic than lentic sites (Wilcoxon test: $W = 1218.5$, $P = 0.006$). However, overall, we recorded a similar taxonomic richness with 12 orders and 38 families in lentic sites (N=6, Table 1) and 13 orders and 38 families in lotic sites (N=6). In all six lotic rivers, we recorded 38 families, whereas, in each pair of sites of sebkha, dam, and lentic river, we recorded 20, 22, and 25 families, respectively.

Total abundance of all macroinvertebrates across the entire study period had an average \pm sd of 661.1 ± 360.7 with a minimum of 19 recorded individuals in Lake Ouled Msallem, and a maximum of 1432 individuals recorded in Babar Dam. The collected samples were dominated

by Ephemeroptera (41%) and Diptera (31%), which both accounted for 72% of individuals of all taxa. The top dominant families among Ephemeroptera were Baetidae (13.8%) and Caenidae (22.3%), whereas the top dominant families among Diptera were Chironomidae (18.1%) and Simuliidae (10.5%). The number of individuals of families collected per visit in lotic sites (N=4170) and lentic sites (N=3763) was not significantly different (Wilcoxon test: $W = 1739.5$, $P = 0.89$). There was only a marginal difference in abundance among the four habitat types (ANOVA: $F_{11,107} = 2.63$, $P = 0.07$). Among lentic habitats, we collected a higher abundance of macroinvertebrates in lentic rivers with 1638 individuals, followed by dams with 1487 and sebkha with 638.

Shannon index across the entire study period was variation among sites (ANOVA: $F_{11,107} = 6.03$, $P < 0.0001$). The overall average \pm sd was 1.94 ± 0.79 , with a minimum of 0.32 at Lake Ouled Msallem, and a maximum of 2.94 at Tanout River. Shannon index was on average higher in lotic sites (2.32 ± 0.55) than in lentic sites (1.57 ± 0.88) (Wilcoxon test: $W = 1197$, $P = 0.005$). Shannon index was also significantly different across the four habitat types (ANOVA: $F_{11,107} = 5.56$, $P = 0.004$). When comparing the three lentic habitat types, the average \pm sd Shannon index was higher in dams (1.93 ± 0.49), than in lentic rivers (1.46 ± 1.10), and sebkha (1.33 ± 1.42).

Physicochemical parameters: Figure 2 presents the distribution of six physicochemical parameters in four habitat types. All six parameters showed a significant difference among sites (ANOVA: $P < 0.0001$), revealing spatial variation in physicochemical parameters (Figure 2). All six parameters (water depth, dissolved oxygen, pH, salinity, water temperature, and water velocity) were significantly different ($P < 0.008$). Lentic sites had higher values in water depth (23.4 ± 23.5 vs 10.6 ± 8.6 cm), dissolved oxygen (8.3 ± 0.7 vs 7.9 ± 0.6 mg·l⁻¹), and salinity (1.6 ± 1.1 vs 0.6 ± 0.5 g·l⁻¹). Lotic sites had higher values in pH (7.4 ± 0.3 vs 7.2 ± 0.5), and water temperature (19.9 ± 1.1 vs 19.3 ± 1.0 °C).

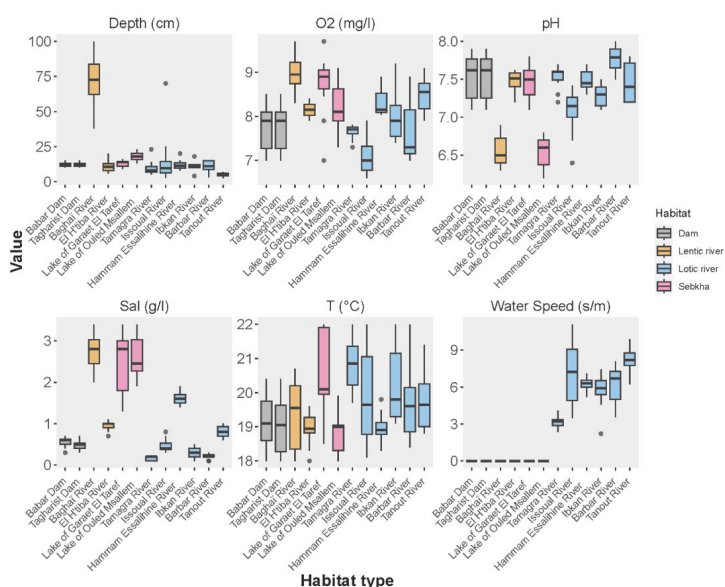


Figure 2. Boxplot showing the distribution in physicochemical parameters in all study sites grouped in four habitat types (Northeast Algeria).

When comparing sites based on habitat type, all six parameters showed a significant difference (ANOVA: $P < 0.002$), indicating that different habitat types had different physicochemical characteristics. Tukey tests showed that almost all combinations of habitat types were significantly different with lentic rivers and sebkha presenting the highest values for water salinity whereas lotic rivers and dams showed lower values. pH had lower values in lentic rivers and sebkha, but higher values in lotic rivers and dams. Water depth was on average higher in lentic rivers than in other habitat types. Water temperature was higher in lotic rivers than in lentic rivers and dams, but all other combinations of habitat types were not significantly different (Table S2).

Characterization of macroinvertebrate communities: The NMDS ordination revealed that taxonomic communities in lotic and lentic sites showed some overlap, indicating that macroinvertebrate communities had some similarities (Figure 3a). The PERMANOVA showed a significant

difference between lotic and lentic sites ($F_{1, 117} = 8.92$, $P = 0.001$), and among the four habitat types ($F_{1, 117} = 6.33$, $P = 0.001$). The pairwise comparison between the four habitat types showed significant difference among all pairs ($P < 0.005$, Table S3). When splitting the data into four aquatic groups (Dam, lentic river, sebkha, and lotic habitats), we found that sebkha was separated from the two other lentic habitats, but still overlapped with lotic river whereas dam and lentic river showed a larger overlap (Figure 3b). We also found a significant difference between seasons for lotic and lentic sites ($F_{7, 118} = 2.24$, $P = 0.001$). Pairwise comparisons showed that seasonal differences occurred only among habitat types, for instance, autumn communities of lentic sites were significantly different than autumn, spring, and winter communities of lotic sites (Figure 4; Table S4). Due to the lack of statistical power, we did not perform seasonal pairwise comparison between the four habitat types.

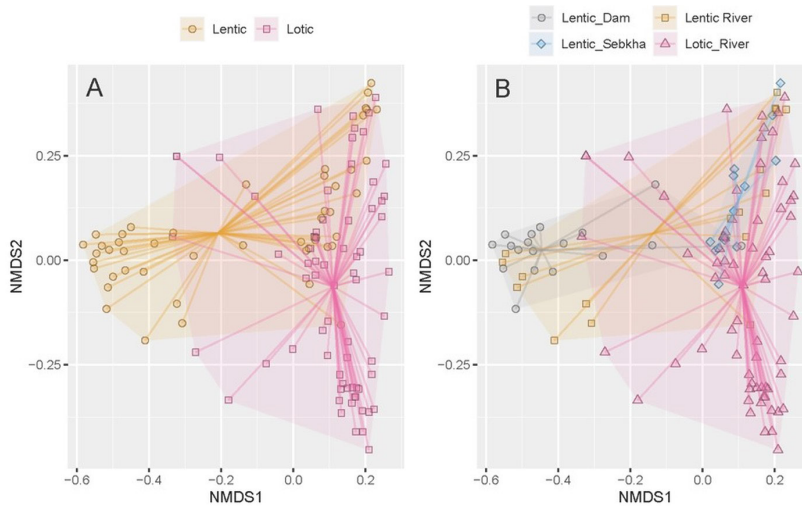


Figure 3. NMDS ordination diagram of the taxonomic distribution of macroinvertebrate communities. Hulls represent two habitat types (A): lotic and lentic, and four habitat types: lotic, sebkha, dam, and lentic river (B).

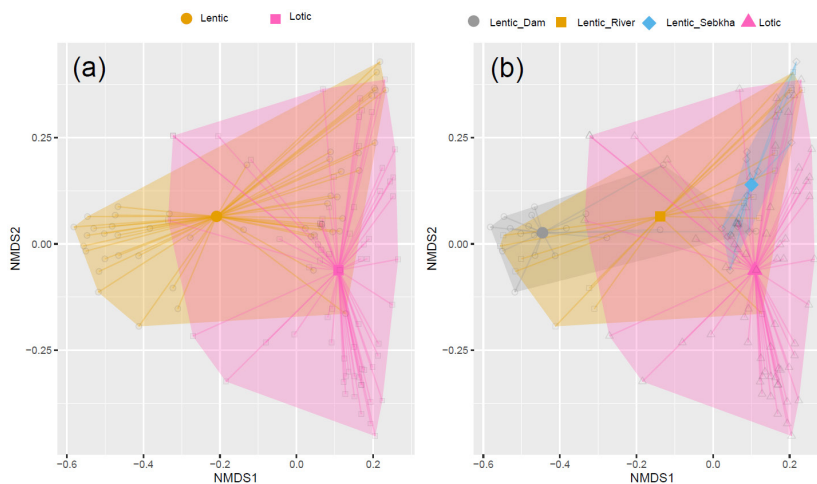


Figure 4. NMDS ordination diagram of the taxonomic distribution of macroinvertebrate communities of aquatic systems in Algerian High Plains across seasons. Hulls represent four seasons.

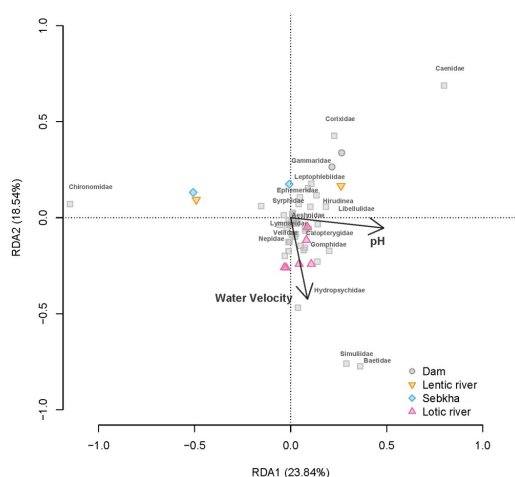


Figure 5. Redundancy analysis (RDA) of the macroinvertebrate communities of aquatic systems in Algerian High Plateaux in four habitat types: lotic river, lentic river, sebkha, and dam. A forward modeling procedure selected pH, salinity, and water velocity as predictors. Family names that overlapped a lot at the center of the plot were removed.

The first two RDA explained 72.5% of the variance, with 40.2% for RDA1 and 32.3% for RDA2. RDA based on the abundance of families showed that the surveyed lentic sites were grouped together and separated from the lotic sites. Our general RDA model was significant ($F_{5,6} = 2.36$, $P = 0.002$). Our model had an adjusted R^2 of 0.38. The forward selection of the RDA model revealed a strong effect of pH ($F_{1,5} = 3.71$, $P = 0.003$) and water velocity ($F_{1,5} = 2.90$, $P = 0.002$) on the abundance of macroinvertebrate taxa (Figure 5). These two explanatory variables explained 29.5% of the variables (Adjusted $R^2 = 0.29$). RDA showed that water velocity separated two benthic macroinvertebrate groups with more taxa correlated with lotic sites than with lentic sites. RDA showed that the three lentic types of sites exhibited some taxonomic differences.

4. Discussion

Our study determined the structure of macroinvertebrate communities in different aquatic habitats in the Haut Plateaux of North Algeria; a region that has not attracted much ecological research attention in the community ecology of aquatic systems. Based on repeated surveys of the abundance of benthic taxa (families) in different aquatic habitat types (lotic river, lentic river, dam, and sebkha), we found that macroinvertebrate communities were more diverse in lotic than lentic sites, and they exhibited some overlap in their community composition. In lentic habitats, taxonomic composition was more similar between freshwater sites (dams and lentic river) than in the brackish sites (sebkha). Finally, our RDA analysis revealed the physicochemical parameters that contributed most to the structure of macroinvertebrate communities.

Diversity in different lotic and lentic sites: The dominance of Ephemeroptera and Diptera in our macroinvertebrate survey is congruent with other studies carried out in Mediterranean

wetlands (Fierro et al., 2019) as well as other regions. The dominant families of Ephemeroptera (Baetidae and Caenidae) and Diptera (Chironomidae and Simuliidae) are known to perform long-distance dispersal actively or passively (Barber-James et al., 2008), allowing them to establish populations in various wetlands, including isolated ones. Similar to other studies (Piscart et al., 2005; Buffagni et al., 2009), we found that the lentic-lotic character of water body was an influential factor in determining the structure of macroinvertebrates at the family level. The hypothesis that the diversity of benthic macroinvertebrates would be higher in lentic sites than in lotic sites, which is typical in temperate environments (Piscart et al., 2005), was not supported by our data. Benthic taxa that usually dominate lentic sites are usually Odonata, Coleoptera, Hemiptera and Mollusca (Piscart et al., 2005). For instance, in some taxonomic groups such as Odonata, taxonomic richness at the level of family, genus or species is higher in lentic than lotic habitats in North Africa (Khelifa et al., 2021a, b, c), although the proportion of endemic species is higher in lotic sites (Khelifa et al., 2016). In our study, we found that the richness and diversity of benthic macroinvertebrates were higher in lotic than in lentic sites. These differences were not due to a comparative bias between temporary and permanent wetlands since the same number of sites (two lotic [Barbar river and Ibkan river] and two lentic [El Htiba river, Lake Garaet El Taref] sites) experienced drought in summer. The observed discrepancy in diversity among lentic and lotic habitats is likely due to the types of lentic sites we surveyed in this study. Our study did not include notoriously biodiverse aquatic habitats such as ponds and marshes (Florencio et al., 2014). Instead, our study included lentic parts of rivers, dams, and sebkhas. Lentic parts of rivers, especially those downstream, usually maintain a lower faunistic diversity than more lotic upstream sites (Buffagni et al., 2009). This has been observed in different taxonomic groups of macroinvertebrates such as insects (e.g., Ephemeroptera and Trichoptera (Buffagni et al., 2009); Odonata (Khelifa, 2019)). In fact, lower water velocity increases particle sedimentation and the accumulation of organic matter, which serves as food for invertebrates, increasing respiration rate, decreasing the levels of dissolved oxygen, and welcoming taxa that tolerate anoxic conditions (Graeber et al., 2013). A taxon that frequently inhabits lentic parts of rivers is Chironomidae (Armitage et al., 2012), which often dominates the benthic communities of this habitat (De Haas et al., 2006). The lower abundance and diversity of macroinvertebrates recorded in dams are most likely due to the low habitat complexity, nutrient availability, and vegetation density, which are essential to harbor a highly diverse benthic fauna (Jelassi et al., 2013). We recorded the lowest faunistic diversity in the brackish sebkhas. Concordant with our study, (Khemaisia et al., 2018) found that the lowest richness of crustaceans (Amphipoda and Isopoda) was found in sebkhas, compared to lagoons, dams and hill reservoirs. Brackish and saline wetlands are typically inhabited by a low number of taxa that can tolerate high levels of salinity. In fact, Piscart et al., (2005) found that taxonomic richness of macroinvertebrates declined substantially in high salinity in a stream in northeastern France with a salinity gradient that varied between 0.21–2.60 g l⁻¹.

Physicochemical characteristics of the water: Our study revealed that the different lotic and lentic sites had distinct physicochemical characteristics. pH, salinity, and water resistance were clearly higher in lentic sites. The lentic Baghai river and Lake Ouled Msallem were the only slightly acidic sites among all surveyed localities. These lower pH could be the result of acidic inputs from urban and agricultural runoff, weathering of rocks, and acidifying gas (Stets et al., 2014). The overall higher salinity in lentic sites was not only due to the brackish water of sebkhas (Garaet El Taref and Lake Ouled Msallem), but also the high salinity of Baghai river. In lentic sites, the physicochemical parameters of dams were relatively different than those in sebkhas and lentic parts of the river. The variability of physicochemical parameters across the different aquatic sites shows the diversity of abiotic factors that occurs in Northeast Algeria, reflecting a capacity to host a diversity of ecological communities and ecosystem functioning.

It is important to note that our sampling protocol has limitations and weaknesses in measuring some physicochemical parameters. For example, temperature data were recorded at different times of the day, which may have caused some of the observed temperature variations to be due to diel patterns rather than spatial differences. Nonetheless, we employed a random sampling order across multiple visits, which could have reduced the sampling bias of water temperature. However, future studies should consider using temperature loggers to capture spatiotemporal variations in temperature regimes and enable robust comparisons across different sites.

Environmental influences on macroinvertebrate community structure: Our NMDS analysis showed that lentic and lotic sites overlapped substantially in community composition, whereas RDA showed that pH and water velocity were the main contributors to the structure of macroinvertebrate communities. These factors have been highlighted by previous studies as key determinants of community composition and diversity in aquatic systems (Johansson and Brodin, 2003). Macroinvertebrates of sebkhas were separated from dams, whereas lentic rivers overlapped with both sebkhas and dams. The marked separation of communities in sebkhas and dams was most likely due to the large difference in abiotic conditions between the two habitat types, including water salinity and dissolved oxygen which were both higher in sebkhas. Both of the latter abiotic factors play a key role in structuring macroinvertebrate communities (Piscart et al., 2005). Dams were characterized by the occurrence of Corixidae, which represent omnivorous pioneer colonizers of aquatic habitats (Haedicke et al., 2017). We observed a noticeable difference in community composition between lotic rivers and dams, which highlights that dams are rarely used by lotic taxa, thus representing barriers to the connectivity of populations of lotic macroinvertebrates. Dams also tend to alter physicochemical, biological, and ecological processes in lotic ecosystems (Barbarossa et al., 2020). In extreme drought periods, North African rivers experience a decline in water flow, which is exacerbated by the water abstraction of dams, leading to the disappearance of lotic habitats and the extirpation of macroinvertebrates, including sensitive species (Khelifa et al., 2021a, b, c).

We found that predatory insects such as Dytiscidae, Coenagrionidae, and Nepidae were more dominant in lotic habitats although the latter usually inhabit both lentic and lotic habitats (DeWalt et al., 2010). Both sebkhas, on the other hand, were dominated by Gammaridae, which is typically the case for amphipods in saline aquatic habitats (Piscart et al., 2005). In a study on the Amphipoda of Tunisian wetlands, (Khemaisia et al., 2018) found that eight and three species were recorded in lagoons and sebkhas, respectively, but no species was recorded in dams and hill reservoirs. Furthermore, we found that there were significant seasonal changes in macroinvertebrate community composition. This could be due to various factors, including hydrology, emergence of taxa (transition from the aquatic larval stage to the terrestrial adult stage), seasonal emigration, and variability in the phenology of taxa (Leunda et al., 2009; Giam et al., 2017).

Overall, our findings reveal the abiotic determinants of the community structure of macroinvertebrates in a diversity of wetlands with distinct abiotic conditions in a semiarid environment. We highlight that some habitats might not serve as a refuge to communities experiencing anthropogenic disturbance or extreme climate events (Khelifa et al., 2022). Thus, we argue that habitat protection and biodiversity conservation that considers the diversity of habitats and landscapes is crucial to maintain wildlife and ecosystem services.

Acknowledgements

We thank Ministère de l'Enseignement Supérieur et de la Recherche Scientifique (MESRS) for funding the project and project MECESUP UCT 0804. We thank Dr. Dambri Besma for helpful advice in macroinvertebrate sampling, and Dr. Hadjab Ramzi, Dr. Khammar Hichem, and Dr. Saheb Menouar for providing equipment. Also, the authors express their gratitude to M.I. and S.M.A. for their valuable comments for improve the manuscript. Conflicts of Interest: The authors declare no conflict of interest.

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Supplementary Material

Supplementary material accompanies this paper.

Table S1. Checklist and average abundance of taxa collected in each site during our study in the Haut Plateaux of Northeast Algeria. S1-S12 refer to Site1-Site12 (see Table 1).

Table S2. Posthoc Tukey tests assessing differences in the physicochemical parameters among habitat types. diff: difference; lwd: lower 95% confidence interval; upr: upper 95% confidence interval; p adj: adjusted P-value.

Table S3. Pairwise differences in community composition of macroinvertebrates of four aquatic habitat types. The analysis was carried out following a significant PERMANOVA.

Table S4. Pairwise differences in community composition of macroinvertebrates across seasons in lotic and lentic sites. The analysis was carried out following a significant PERMANOVA.

This material is available as part of the online article from <https://doi.org/10.1590/1519-6984.273010>