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Spatiotemporal patterns of macroinvertebrate functional habit groups in response to seasonal variations and anthropogenic pressures in the Martil Basin, Morocco

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Abstract. *Guellaf A, Kettani K. 2025. Spatiotemporal patterns of macroinvertebrate functional habit groups in response to seasonal variations and anthropogenic pressures in the Martil Basin, Morocco. Biodiversitas 26: 3227-3236.* Trait-based analysis of macroinvertebrates offers a comprehensive perspective for monitoring the integrity of aquatic ecosystems. This study examined the functional responses of macroinvertebrates to anthropogenic pressures and seasonal changes in the Martil Basin, Northwestern Morocco. Analyses were based on physicochemical and bacteriological variables (temperature, pH, electrical conductivity, dissolved oxygen, BOD_5, COD, TSS, Fecal coliforms, and Fecal streptococci), alongside hydro-morphological factors (current speed, water depth, and stream width). Macroinvertebrates and water were sampled over an annual cycle (spring, summer, autumn of 2017, and winter of 2018) at nineteen sites. The Functional Habit Group (FHG) composition varied significantly across sites and seasons. The abundance and taxa richness were highest in spring, with clingers being the most abundant group. Multivariate analyses revealed distinct upstream-downstream gradients, with sensitive taxa dominated by clingers correlated with high dissolved oxygen levels and low pollution levels in upstream areas. In contrast, tolerant taxa such as burrowers and swimmers dominated downstream sites impacted by agricultural runoff and urban pollution. A deeper understanding of the functional traits of macroinvertebrates and their responses to anthropogenic and environmental stressors can serve as a valuable tool for scientists and managers, providing complementary indicators for the development of biomonitoring frameworks and the preservation of aquatic biodiversity.

Keywords: Functional groups, macroinvertebrates, Martil Basin, Morocco

INTRODUCTION

Freshwater ecosystems are the basis of several functional biotic interactions across longitudinal (upstream-downstream), vertical (running water-groundwater), and lateral (riparian-riverbed) dimensions (García-Roger et al. 2013; Karaouzas et al. 2018). These processes are driven by different abiotic factors, including hydrological patterns, habitat heterogeneity, water chemistry, and nutrient availability, all of which vary depending on the location of the watercourses in the watershed (Hamid et al. 2020). In turn, macroinvertebrate communities, which constitute an important component of animal production in fluvial systems through their mosaics of microhabitats, are well suited for assessing and understanding ecological dynamics, hydrological characteristics, and water quality, and might consequently be used to detect spatiotemporal changes and anthropogenic pressures (Moniruzzaman et al. 2021).

Macroinvertebrate assemblages are vulnerable to alterations in hydrological connectivity and seasonal changes due to their dependence on microhabitats, nutrient loading, and refuges (Asmamaw et al. 2019). At the macrohabitat scale, the organization of benthic assemblages is based on habitat mosaics from lotic (riffles and runs) to lentic (pools) patches and the inorganic and organic matter available to faunal assemblages (Burgazzi et al. 2021). Consequently, riparian corridors and in-stream alterations, driven by changes in hydrologic patterns and human disturbances, can lead to shifts in the representation of functional traits and thus affect species distribution (Arenas-Sánchez et al. 2021).

Ecological functions are defined as a multitude of general biological traits that describe how organisms interact with environmental conditions (Benzina et al. 2021). Cummins (1974) initiated the classification of macroinvertebrates into specific Functional Habit Groups (FHGs) as an alternative approach, simplifying their distribution based on behavioral and morphological attributes related to locomotion, mobility, and interaction with the physical environment in aquatic ecosystems (Merritt et al. 2002). In addition to conventional bioindication approaches based on taxonomic composition and species abundance, functional trait analysis provides a more integrative framework for assessing how freshwater macroinvertebrates respond to environmental gradients. This perspective emphasizes the ecological relevance of trait-based assemblages, their spatial organization into FHGs and their functional contributions to ecosystem processes under varying degrees of environmental stress (Martini et al. 2021; Bendary et al. 2023). These trait-based indices capture key ecological dimensions such as niche differentiation, resource-use efficiency, resilience, and recovery. However, environmental disturbances and anthropogenic pressures can lead to shifts in trait composition, potentially resulting in functional homogenization (Belmar et al. 2019; Stamenković et al. 2024).

In Mediterranean streams, in addition to anthropogenic alterations and water pollution, hydrological variability represents a significant natural stressor that reflects temporal changes in macrohabitat patchiness, which in turn affects the structure and functioning of macroinvertebrate communities (García-Roger et al. 2013; Karaouzas et al. 2019; Pinna et al. 2024). Examining the relationships between habitats and biological traits is particularly critical in Mediterranean streams, where significant abiotic variability during the dry phase substantially affects hydrological patterns, disrupts the composition of functional feeding groups, and drives local extinctions (García-Roger et al. 2013). The importance of this research is evident in the numerous studies conducted in the Mediterranean region that have assessed and documented the relationships among functional groups, seasonal variations, and human-induced alterations, engaging our interest and furthering our understanding of these ecosystems (Canobbio et al. 2010; Sánchez-Carmona et al. 2012; Cabrini et al. 2013; Di Sabatino et al. 2014).

However, FHG studies in the southern Mediterranean basin have been largely overlooked, leaving a significant gap in our understanding of this critical region. In this context, this research aims to determine the spatiotemporal distribution of FHGs under the combined impacts of seasonal stressors and environmental variables in the Martil Basin, which occupies a strategic geographical position in Northwestern Morocco and faces substantial human-induced pressures (Guellaf et al. 2023). The primary goals of this study are: (i) to explore the relationships between FHGs and the seasonal fluctuations in the physicochemical, bacteriological, and hydrological characteristics within the Martil Basin; (ii) to understand the spatial distribution patterns of different FHGs across the basin, from upstream to downstream.

MATERIALS AND METHODS

Study area

The present study was conducted in the Martil watershed, situated in the northwestern portion of the Rif Mountain range in Northern Morocco. This basin, part of the Tangier-Tetouan-Al Hoceima region, drains a relatively modest area of approximately 1,259 km².

The climate of the Martil Basin is typically Mediterranean, with a distinct rainy and cold season from October to April and a dry and hot season extending from May to September. The hydrological regime exhibits distinct seasonal variations, with heavy rainfall occurring during winter and spring and minimal flows in summer and autumn. The main hydrological features are intermittency and irregularity. The mean annual precipitation ranges between 500-750 mm, while the average temperature varies from 15°C to 19°C (Karrouchi et al. 2016).

The upper section of the basin is predominantly characterized by forested patches and natural areas, featuring steeply sloping streams and rugged, complex topography. The midlands are primarily characterized by hilly or semi-flat landscapes, which are typically semi-natural and predominantly used for agriculture and rural activities. In the lower part of the basin, the Oued Martil, from which the watershed derives its name, originates in Tamouda at the confluence of its primary tributaries (Oued Mhajrat, Oued Khemis, and Oued Chekkoûr). It flows through the cities of Tetouan and Martil before emptying into the Mediterranean Sea (Guellaf and Kettani 2021; Bekkali et al. 2024). The watershed is heavily influenced by human activities, with agricultural, industrial, and urban areas contributing substantial amounts of mineral, organic, and nutrient-rich discharges from untreated wastewater. These discharges have resulted in a rapid decline in water quality throughout the basin (Figure 1).

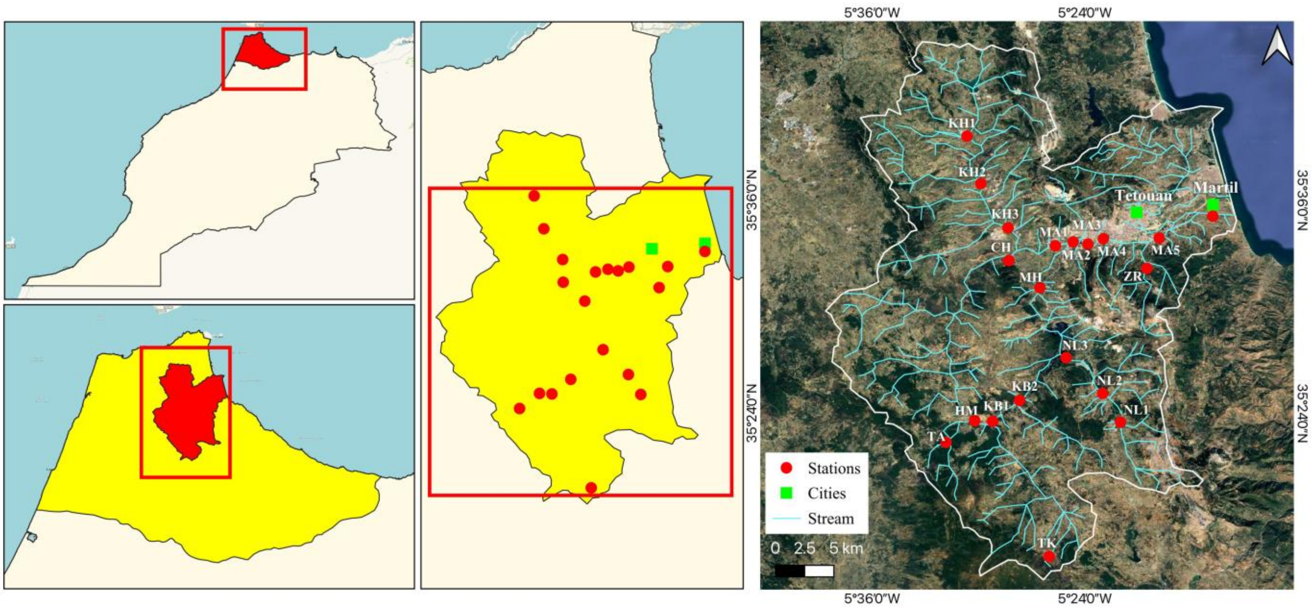

Figure 1. Location of the study area and distribution of the sampling sites (S1 to S19) from the Oued Martil River Basin, Morocco

Procedures

Water and benthic macroinvertebrate samples were collected over an annual cycle (spring, summer, autumn of 2017, and winter of 2018) from 19 sampling sites across stream orders. These sites were selected along an upstream-downstream gradient, covering the major hydrogeological zones of the Martil Basin.

Sampling and identification of macroinvertebrates

Benthic macroinvertebrates were sampled once per season (winter, spring, summer, and autumn) using the kick-net sampling method with a standard hand net (25×25 cm) to ensure representative coverage of all available habitats. The collected samples were transferred to plastic containers and preserved in 95% ethanol for further analysis. In the laboratory, macroinvertebrates were sorted, counted, and identified primarily to the family level using a binocular microscope, following the identification key of Tachet et al. (2002). Species-level identification was further assisted by taxonomic specialists from our research team at the Laboratory of Ecology, Systematics, and Conservation of Biodiversity.

Each species was categorized into FHGs according to the classifications of Merritt et al. (2002) and Canobbio et al. (2010), which included the following categories: clingers (Cg), climbers (Cb), sprawlers (Sp), burrowers (Bu), swimmers (Sw), and skaters (Sk) (Table 1).

Table 1. List of functional habitat groups of macroinvertebrate taxa in the Martil Basin, Morocco, during the study period

FHG	Macroinvertebrate taxa
Burrowers (Bu)	**Ephemeroptera:** *Ephoron virgo* **Odonata:** *Onychogomphus uncatus, Onychogomphus forcipatus, Cordulegaster boltonii algirica, Cordulegaster* sp. **Diptera:** *Ibisia* sp., *Probezzia* sp., *Chironomus dorsalis, Chironomus Pe 3, Chironomus plumosus, Chironomus riparius, Demicryptochironomus vulneratus, Dicrotendipes septemmaculatus, Glyptotendipes gripekoveni, Limnophora* sp., *Tipula* sp.
Skaters (Sk)	**Hemiptera:** *Aquarius cinereus, Aquarius najas, Gerris brasili, Gerris gibbifer, Gerris thoracicus, Hebrus pusillus, Hydrometra stagnorum, Velia ioannis, Velia noualhieri*
Swimmers (Sw)	**Amphipoda:** *Gammarus* sp. **Ephemeroptera:** *Cloeon dipterum, Procloean concinnum* **Hemiptera:** *Corixa affinis, Micronecta scholtzi, Parasigara rivularis, Parasigara transversa, Sigara lateralis, Trichocorixa verticalis verticalis, Anisops sardeus, Notonecta maculata, Notonecta meridionalis, Notonecta obliqua, Plea minutissima* **Coleoptera:** *Aulonogyrus striatus, Gyrinus dejeani, Gyrinus urinator, Haliplus lineatocollis, Peltodytes caesus, Peltodytes rotundatus, Noterus laevis, Agabus bipustulatus, Agabus brunneus, Agabus conspersus, Agabus didymus, Agabus nebulosus, Ilybius chalconatus, Deronectes faimairei, Deronectes hispanicus, Nebrioporus clarkii, Hydroporus discretus, Hydroporus lucasi, Hydroporus memnonius, Hydroporus obsoletus, Graptodytes ignotus, Graptodytes varius, Stictonectes optatus, Laccophilus minutus, Helophorus atlantis, Helophorus algiricus, Hydrochus grandicollis, Anacaena bipustulata, Anacaena globulus, Anacaena lutescens, Berosus hispanicus, Hemisphaera guignoti, Enochrus bicolor, Laccobius atrocephalus atrocephalus, Laccobius neapolitanus* **Diptera:** *Culicidae, Dixa puberula, Dixa* sp.
Clingers (Cg)	**Gastropoda:** *Physella acuta, Melanopsis* sp., *Ancylus fluviatilis* **Ephemeroptera:** *Acentrella almohades, Baetis fuscatus, Baetis maurus, Baetis pavidus, Baetis punicus, Baetis rhodani, Ecdyonurus rothschildi, Epeorus sylvicola, Rhithrogena* sp., *Choroterpes atlas, Choroterpes volubilis, Habrophlebia* sp., *Serratella ignita* **Plecoptera:** *Hemimelaena flaviventris, Isoperla kir, Eoperla ochracea, Siphonoperla lepineyi, Capnioneura* sp., *Capnopsis schilleri, Leuctra* sp. **Odonata:** *Chalcolestes viridis* **Coleoptera:** *Hydraena allomorpha, Hydraena bisulcata, Hydraena cordata, Hydraena rigua, Ochthebius difficilis, Elmis maugetii velutina, Limnius intermedius, Limnius opacus opacus, Oulimnius fuscipes, Oulimnius troglodytes, Riolus villosocostatus, Stenelmis consobrina consobrina, Dryops algiricus, Dryops gracilis, Dryops lutulentus, Dryops sulcipennis, Pomatinus substriatus* **Trichoptera:** *Rhyacophila fonticola, Rhyacophila munda, Agapetus* sp., *Hydroptila vectis, Wormaldia* sp., *Chimarra marginata, Cheumatopsyche atlantis, Hydropsyche fezana, Hydropsyche iberomaroccana, Hydropsyche lobata, Hydropsyche maroccana, Hydropsyche pellucidula, Ecnomus deceptor, Psychomyia pusilla, Polycentropus kingi, Mesophylax aspersus* **Diptera:** *Prosimulium rachiliense, Metacnephia blanci, Simulium pseudequinum, Oxycera* sp., *Chrysops relictus, Heptatoma pellucens, Tabanus maculicornis, Hybomitra bimaculata, Tabanus quatuornotatus*
Sprawlers (Sp)	**Isopoda:** *Proasellus* sp. **Ephemeroptera:** *Caenis luctuosa, Caenis pusilla* **Plecoptera:** *Nemoura* sp., *Protonemura* sp., *Brachyptera algirica, Brachyptera auberti, Brachyptera* sp. **Odonata:** *Libellula quadrimaculata, Sympetrum striolatum, Trithemis kirbyi ardens, Zygonyx torridus* **Diptera:** *Hemerodromia* sp., *Eleophila* sp.
Climbers (Cb)	**Odonata:** *Calopteryx haemorrhoidalis, Calopteryx* sp., *Ischnura graellsii, Pyrrhosoma nymphula, Anax* sp., *Aeshna mixta, Boyeria irene* **Hemiptera:** *Nepa cinerea*

Physicochemical and habitat analyses

Water samples were collected and analyzed seasonally in conjunction with the sampling of aquatic macroinvertebrates. The physicochemical and bacteriological analyses were based on the measurement of 12 parameters. The temperature (°C), pH, conductivity (µS/cm), and dissolved oxygen (mg/L) were measured in situ using a portable multiparameter probe (EUTECH CyberScan PCD 650). The Biochemical Oxygen Demand (BOD5), Chemical Oxygen Demand (COD), and Total Suspended Solids (TSS) were measured using a Pastel multiparameter UV analyzer. Other physicochemical parameters, including nitrites (NO_2^-), nitrates (NO_3^-), and sulfates (SO_4^{2-}), were analyzed using UV absorption spectroscopy. Bacteriological parameters, including fecal coliforms (CFU/100 mL) and fecal streptococci (CFU/100 mL), were measured using a filtration unit (Pall Gelman). All analyses followed the protocols outlined by Rodier et al. (2009). Additionally, hydrological variables, including current velocity (m/s), streambed width (m), and channel depth (cm), were estimated from three measurements for each sampling site.

Data analysis

Principal Component Analysis (PCA) was performed to explore the spatial distribution patterns of the sampling sites. Additionally, a chord diagram was used to visualize the temporal variability and assess the relationships between seasonal dynamics. The analyses were performed using OriginPro 2024. Furthermore, to examine the distribution patterns of FHGs across the sampling sites in relation to environmental factors, a Canonical Correspondence Analysis (CCA) was conducted using XLSTAT 2024.

RESULTS AND DISCUSSION

Results

Macroinvertebrate assemblages

During the four seasons, 10,695 aquatic macroinvertebrate individuals were collected across 19 sampling sites in the Martil Basin. The collected specimens represented three phyla (Annelida, Mollusca, and Arthropoda), encompassing 12 orders, 68 families, 112 genera, and 139 distinct species. The insect class was the most dominant, with Coleoptera (53 taxa) being the most diverse, followed by Diptera (27 taxa) and Hemiptera (21 taxa).

Across all sampling seasons, the families Simuliidae (1,864 individuals), Baetidae (1,404 individuals), and Chironomidae (1,398 individuals) exhibited the highest abundance and frequency of occurrence, collectively accounting for 44% of the total abundance. Notably, Dytiscidae (Coleoptera) comprised the most diverse family, with 16 distinct taxa.

In the Martil River basin, the highest overall taxonomic diversity was recorded at the upstream station of Oued Tkaraa (TK), where 72 taxa were identified. The peak diversity at this station occurred during spring, when 42 taxa were recorded. Oued Zarka (ZR) exhibited the highest macroinvertebrate abundance, peaking at 746 individuals during autumn. Conversely, the Roumana station (MA4), located in the lower Oued Martil section and subject to significant anthropogenic pressure, exhibited the lowest species richness and abundance (Figure 2).

The FHGs exhibited a heterogeneous distribution, with significant spatial and seasonal variations across different localities in the Martil Basin during the study period. Clingers were the most dominant group, accounting for 60% of the total abundance, followed by swimmers (16%), burrowers (14%), skaters (5%), sprawlers (4%), and climbers (1%) (Appendix 1, Figure 3).

Seasonal variation in macroinvertebrate FHGs

PCA was conducted to explore the spatial distribution patterns of the sampling sites based on the abundance of FHGs. The first two principal components collectively accounted for 70.07% of the total variance, with Axis 1 explaining 52.94% and Axis 2 explaining 17.13%.

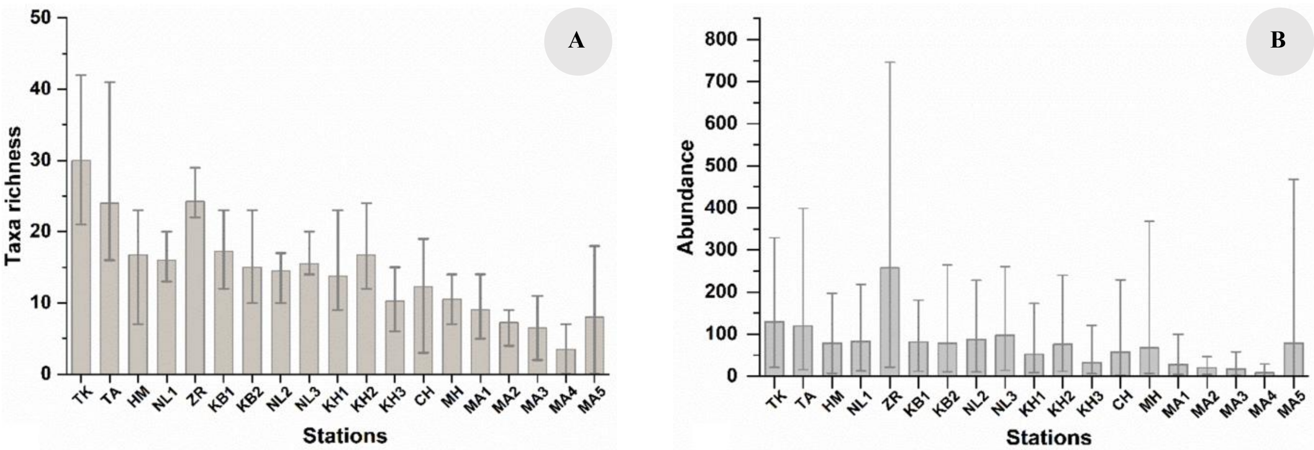

Figure 2. A. Seasonal variation in taxa richness, B. Abundance of macroinvertebrates in the Martil Basin, Morocco, throughout the study period

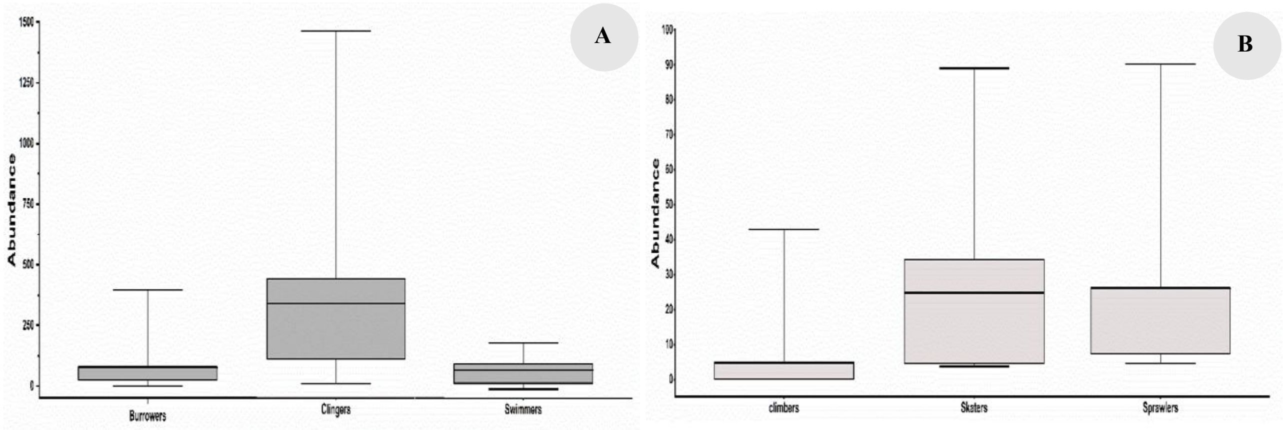

Figure 3. Box plots (mean, min-max) showing the variation in the abundance of functional habit groups in the Martil Basin, Morocco, over the study period. A. Abundant group, B. Rare groups

The analysis revealed a clear distinction between upstream/midstream and downstream sites. The sampling sites in the upper and middle sections of the basin were predominantly positioned on the positive side of Axis 1. In comparison, the downstream sites were projected on the negative side. The positive direction of Axis 1 was strongly correlated with the majority of habitat traits. Axis 1 (PC1) showed moderate positive correlations with clingers (r: 0.460), skaters (r: 0.511), swimmers (r: 0.492), and sprawlers (r: 0.436). In contrast, Axis 2 (PC2) was more associated with climbers (r: 0.674) and burrowers (r: 0.582) (Table 2).

In the upper right quadrant of the PCA plot, the TK site is closely associated with climbers. In addition, TK, NL2, NL1, and KH2 were characterized by a high proportion of sprawlers and swimmers. In contrast, sites such as TA, ZA, KB1, KB2, HM, and NL3 clustered in the lower right quadrant, showing a positive correlation with clingers and skaters. Burrowers were primarily associated with downstream sites, particularly MA5 and MH, as indicated by their position in the upper-left quadrant of the plot (Figure 4).

The chord diagram was used to analyze the temporal variability and relationships between seasonal factors and the distribution of macroinvertebrates according to functional habit traits. The diagram illustrates representative divisions for seasons and habit groups, with the thickness of the connecting lines proportional to the abundance of organisms (Figure 5). Seasonal trends reveal pronounced contrasts in the abundance of FHGs. Spring had the highest total abundance, with 3,186 individuals recorded, followed by winter (2,674 individuals), summer (2,406 individuals), and autumn (2,429 individuals).

Clingers clearly dominated the study period, with a total of 6,451 individuals recorded. Although their distribution was relatively equitable across seasons, higher abundances were noted in the winter and spring. Burrowers, typically associated with lentic systems, were represented by a total of 1,478 individuals. Their abundance was particularly high during seasons with stable hydrological conditions, especially in spring. The swimmers, represented by 1,739 specimens, showed a strong preference for pools and slow-flowing stream sections. This group was mainly associated with stable and dry periods, particularly during spring and summer. Similarly, skaters (surface-dwelling species) and climbers (typically found in ponds, puddles, and swamps) were represented by 489 and 88 specimens, respectively. Both seasons were more abundant than in autumn and winter. In contrast, sprawlers, which are commonly found in lotic rocky habitats, were represented by 450 specimens and were more abundant during autumn and winter.

Table 2. Correlation coefficients between habitat functional groups and the first two principal components (PC1 and PC2) from the PCA

FHG	Coefficients of PC1	Coefficients of PC2
Burrowers	-0.055	0.582
Climbers	0.303	0.674
Clingers	0.460	-0.344
Skaters	0.511	-0.241
Sprawlers	0.436	0.157
Swimmers	0.492	0.083

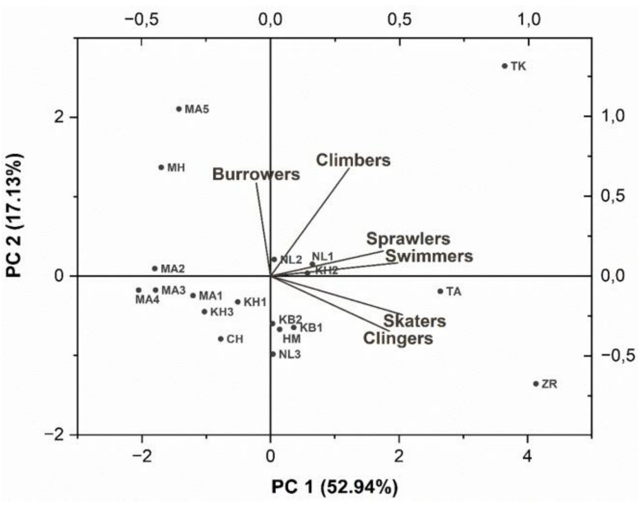

Figure 4. Principal Component Analysis (PCA) biplot (axes F1 and F2: 70.07%) based on the abundance of FHGs at sampling stations in the Martil Basin, Morocco

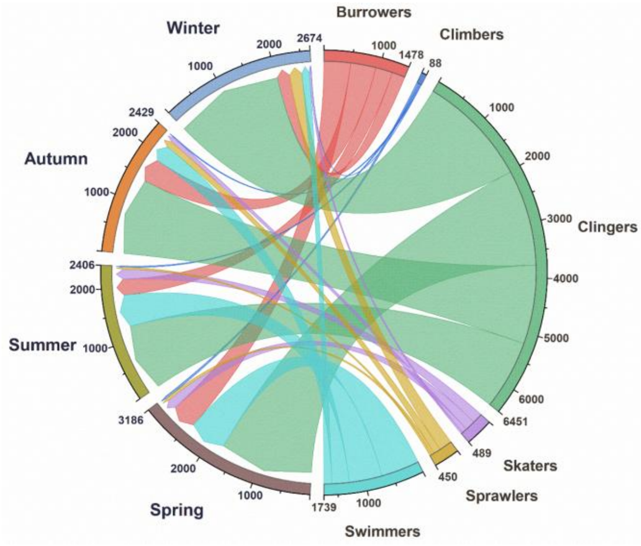

Figure 5. Chord diagram illustrating the distribution of FHGs based on their abundance across the four seasons during the study period in the Martil Basin, Morocco

Correlations between environmental variables and macroinvertebrate FHGs

The surface water temperature exhibited seasonal variation, with the lowest value recorded in spring at station TA (17.3°C) and the highest value in summer at station MA3 (32.5°C). pH remained slightly alkaline, ranging from 6.5 to 8.41, with no significant variations. The electrical conductivity showed notable variation, ranging from 26.5 µs/cm at TK to 2,900 µs/cm at M5 in spring. The dissolved oxygen levels varied significantly, ranging from 0.9 mg/L in summer at M5 to 19.5 mg/L at TK in autumn.

BOD5, COD, and TSS exhibited similar trends. Station NL3 recorded the lowest values for these parameters in autumn, with concentrations of 3.8, 10.5, and 10.6 mg/L for the three parameters in autumn. The highest values were recorded at station MA4 in summer, reaching 120, 340, and 420 mg/L, respectively. Spatioseasonal nitrite, nitrate, and sulfate loads followed similar patterns, with notably elevated concentrations at agricultural stations. Station NL2 recorded the highest concentrations of these parameters during autumn, with values of 0.22, 42.25, and 166.80 mg/L, respectively. The highest concentrations of Fecal Coliforms (FC) and Fecal Streptococci (FS) were recorded at site MA3, reaching 750 FC/100 mL and 12,000 FS/100 mL, respectively (Table 3).

CCA was conducted to examine the distribution patterns of FHGs across sampling sites in relation to environmental factors. Each species was identified by a unique code consisting of the abbreviation of its functional group followed by the first letter of its family. Distinct colors were assigned to each group: clingers (navy blue), climbers (sky blue), sprawlers (gray), burrowers (green), swimmers (red), and skaters (yellow).

The first two CCA axes collectively explained 61.7% of the variation in the Ephemeroptera, Plecoptera, Trichoptera (EPT) species-environment relationships, with Axis 1 accounting for 19.79% and Axis 2 for 14.97% (Figure 6).

Along the negative direction of Axis 1, Dissolved Oxygen (DO) showed a strong association with sensitive EPT clinger species, primarily from the genera *Rhithrogena* and *Habrophlebia* (Ephemeroptera), *Capnioneura* and *Capnopsis* (Plecoptera), and *Wormaldia* and *Rhyacophila* (Trichoptera). Additionally, lotic Coleoptera species from genera such as *Hydraena*, *Dryops*, and *Anacaena* were closely associated with this axis. Lotic Plecoptera species, including genera such as *Brachyptera* and *Nemoura*, classified as sprawlers, were also prominently distributed in this region of the ordination space.

Moreover, lentic swimmer species were primarily represented by sensitive Hemiptera genera (e.g., *Corixa* and *Notonecta*), as well as Coleoptera species such as *Stictonectes* and *Graptodytes*. Skater Hemiptera, including genera like *Aquarius* and *Gerris*, were also identified in this section of the ordination. Climber taxa, encompassing Odonata, Coleoptera, and Hemiptera species, featured representatives such as *Anax*, *Nepa,* and *Agabus*, whereas the other environmental parameters were negatively correlated with Axis-1. These taxa seemed to be associated with highland locations (TK, TA, KB1, HM, and NL3).

Table 3. Mean±SD showing the spatiotemporal variations in the environmental parameters recorded at the different surveyed sites of the Martil Basin throughout the study period

Parameter	Spring	Summer	Autumn	Winter
Temperature (°C)	21.5±3.07	27.8±3.365	13.7±3.27	12.6±2.10
pH	7.58±0.226	7.60±0.528	7.71±0.524	7.59±0.300
Electrical conductivity (µS/cm)	843±1229	1009±1662	773±738	683±739
Dissolved oxygen (mg/L)	7.08±1.81	4.29±3.77	4.17±5.50	3.67±2.40
Biological oxygen demand (mg/L)	20.2±8.79	20.0±26.6	15.6±8.73	10.2±6.24
Chemical oxygen demand (mg/L)	37.4±17.5	47.3±73.4	39.5±18.0	26.1±12.3
Suspended matter (mg/L)	73.8±44.3	77.3±94.0	70.6±42.0	33.8±25.3
Nitrite (mg/L)	0.033±0.051	0.027±0.038	0.039±0.064	0.053±0.047
Nitrate (mg/L)	4.39±5.54	8.91±10.1	16.1±14.2	11.8±8.87
Sulfate (mg/L)	63.9±23.5	52.7±221	73.6±40.1	64.1±37.7
Fecal coliforms (CF/100 mL)	180±221	22.5±38.7	111±141	20.6±16.0
Fecal streptococci (SF/100 mL)	1232±1504	1376±3072	648±709	123±187
Current Speed (m/s)	3.95±2.93	5.55±3.18	4.81±3.20	3.48±2.92
Water depth (m)	0.375±0.296	0.292±0.251	0.303±0.256	0.395±0.320
Stream width (m)	18.2±31.1	16.1±31.7	17.6±32.4	20.7±33.2

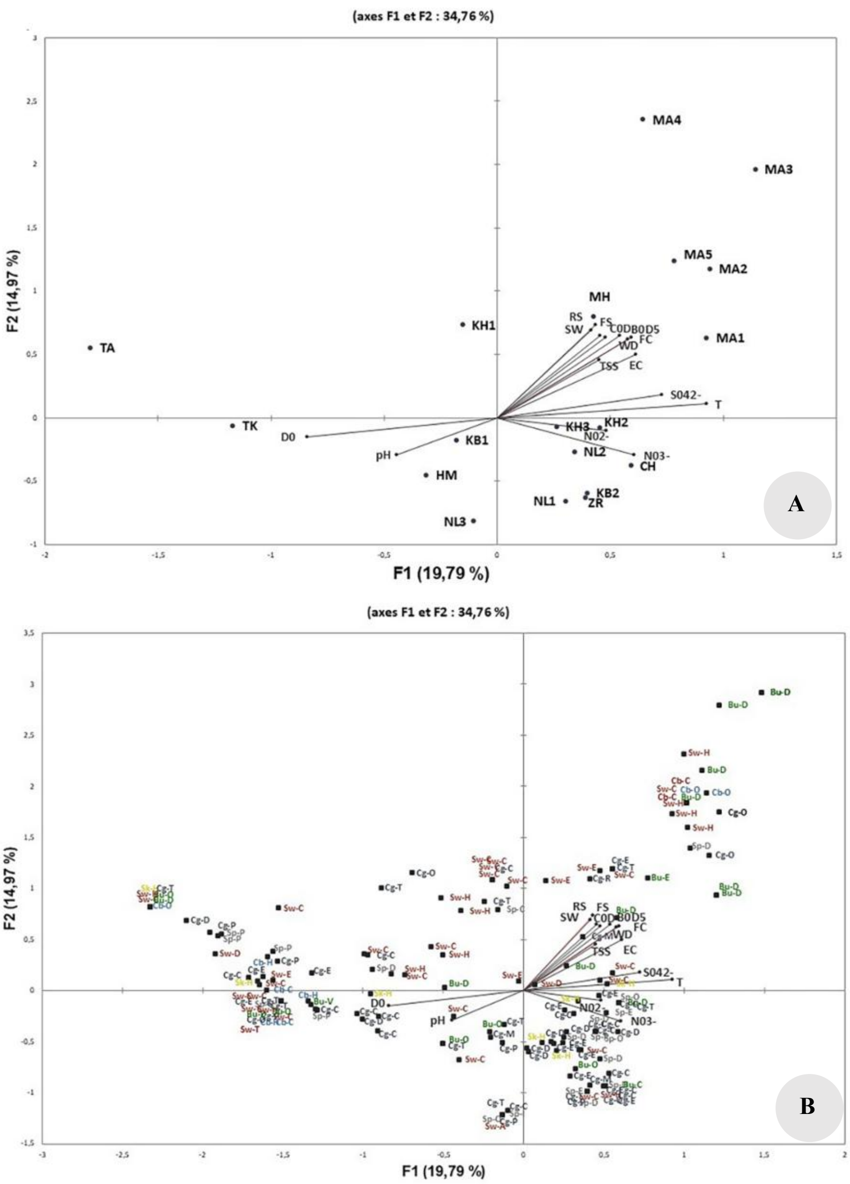

Figure 6. Canonical Correspondence Analysis (CCA) biplots showing: A. Sampling sites in relation to environmental features and B. Taxa in relation to environmental features

The lower right quadrant of the plot encompasses species associated with midstream localities (KB2, NL1, NL2, ZR) and foothill reaches (CH, KH2, and KH3), which are influenced by agricultural land use and elevated nutrient pollution. These species are predominantly represented by members of the clinger functional group, particularly Simuliidae species from the genus *Simulium*, as well as pollutant tolerant EPT taxa such as *Baetis* and *Choroterpes*. Trichoptera species from the genera *Hydropsyche* and *Cheumatopsyche* were also well-represented in this quadrant. A significant number of sprawlers were observed, including Tabanidae species (e.g., *Hybomitra* and *Tabanus*), Ephemeroptera (e.g., *Caenis*), and Plecoptera (e.g., *Protonemura*), alongside Odonata species from the Libellulidae family. Additionally, tolerant skater species from Hemiptera genera (e.g., *Velia* and *Gerris*) and swimming beetles such as Aulonogyrus, as well as Hemiptera species like Trichocorixa, were noted in this section of the ordination space. The high species diversity observed in this area can be attributed to the predominance of limestone substratum, which characterizes the majority of the sampling sites (ZR, NL1, and NL2).

The upper section of the same quadrant is characterized by tolerant species positively associated with relatively broad and deep lowland areas, influenced by elevated temperatures as well as high levels of bacteriological, mineral, and organic pollutants. These species are predominantly burrowers belonging to the Diptera (e.g., *Chironomus*, *Glyptotendipes*) and Ephemeroptera (e.g., *Ephoron*) orders. In addition, tolerant swimmer species, including Odonata (e.g., *Aeshna*), Coleoptera (e.g., *Gyrinus*, *Nebrioporus*), Ephemeroptera (e.g., *Cloeon*), and

Hemiptera (e.g., *Sigara*, *Anisops*, *Micronecta*), dominate this region. Furthermore, some tolerant species from the EPT clinger group, such as *Ecnomus* and *Choroterpes*, are also present in this quadrant.

Discussion

This study highlights the interdisciplinary nature of our research. We demonstrate the critical role of seasonal variations in hydrological and physicochemical factors across longitudinal, lateral, and vertical dimensions, along with land use patterns, in shaping hydrological connectivity. This has significant implications for habitat suitability, water quality, and the distribution of FHG in the Martil Basin (Di Sabatino et al. 2014; Bernal et al. 2025). This study revealed that the seasonal distribution of FHGs, particularly during low-flow periods, significantly alters the structure and function of invertebrate communities. This is due to reductions in habitat extent, water quality, resource exchange and availability, and longitudinal and lateral habitat connectivity (Fornaroli et al. 2019; Herbst et al. 2019).

Swimmers, skaters, and climbers (e.g., Coleoptera, Hemiptera, Odonata, and some Ephemeroptera species), typically found in lentic freshwater habitats (Merritt and Wallace 2003), became more abundant during the dry period, likely due to behavioral adaptations to stagnant or low-current conditions. In contrast, riffle taxa, particularly sprawlers (e.g., Plecoptera and Ephemeroptera), were significantly reduced during the dry period as riffle habitats dried up (Fenoglio and Bo 2024). Generalist taxa inhabiting fine sediments with low sensitivity to reduced flow, high temperatures, and organic matter accumulation, such as burrowers (e.g., some Odonata and Diptera, particularly Chironomidae) (Merritt et al. 2002; Merritt and Wallace 2003) and some tolerant clingers (e.g., Trichoptera, Baetidae, Hydraenidae, Elmidae, and Dryopidae), were restricted to slow-flowing habitats and hyporheic zones but maintained stable abundance (Herbst et al. 2019). This reflects their ability to adapt to varying hydrological phases and habitat conditions. Conversely, rewetting periods characterized by high flows, increased oxygen levels, turbidity, and nutrient loading were associated with burrowers and some sensitive clinger taxa.

The study results are consistent with previous studies on the effects of hydrological and climatic changes on functional groups (Canobbio et al. 2010; Kim et al. 2014; Herbst et al. 2019; Sripanya et al. 2023).

The multivariate analysis visually illustrated the spatial differentiation of sampling sites, highlighting the dynamic patterns of macroinvertebrate distribution driven by functional traits. The results indicate that the most sensitive taxa, such as sprawlers and clingers, were positively correlated with Dissolved Oxygen (DO) and negatively correlated with other physicochemical variables. These taxa showed a strong preference for oligotrophic water bodies, primarily in the upper and middle reaches, which are characterized by natural land use and minimal anthropogenic stressors, particularly during autumn and winter.

Conversely, elevated water temperatures during spring and summer indicated shifts in environmental conditions within highland streams. These conditions favored habit modes associated with drying phases, including climbers, skaters, and swimmers, such as taxa from Corixidae, Gyrinidae, and Baetidae (e.g., Cloeon). These groups are typically adapted to slow-flowing or stagnant habitats, demonstrating ecological resilience under seasonal flow regime changes. Overall, our results are consistent with those of previous studies on macroinvertebrate functional traits (Herbst et al. 2019; Sripanya et al. 2023).

Sites along the middle river courses were characterized by positive nitrate (NO_3^-) loadings and moderately elevated mineral pollutant levels, reflecting nutrient concentrations from agricultural runoff, including fertilizers and pesticides (Liu et al. 2019; Salem 2021). In these natural/agricultural sites, the dominant functional traits were swimmers, which thrive in low-flow conditions during dry phases, and clingers, which are associated with lotic habitats. These findings are consistent with those of previous studies (Liu et al. 2023; Sripanya et al. 2023).

Lowland areas dominated by agricultural and urban land use showed a significant association between mineral, organic, and bacterial pollutants, and hydrological dynamics, particularly during dry seasons, favoring eurybiontic species such as burrowers and tolerant swimmers. Our results align with multiple studies indicating that swimmers and burrowers tend to proliferate in polluted aquatic ecosystems (Akamagwuna et al. 2021; Liu et al. 2023; Sripanya et al. 2023; Marino et al. 2024). This pattern can be attributed to various factors, including rising temperatures, reduced flow rates from river rehabilitation, and the construction of a second dam (Barrage Martil). In addition, untreated domestic wastewater discharges have significantly increased organic matter concentrations, further degrading water quality. These cumulative pressures have made the downstream section of Oued Martil a significant pollution hotspot (Arenas-Sánchez et al. 2021; Guellaf et al. 2021).

Seasonal hydrological fluctuations and anthropogenic pollution are expected to significantly alter the ecological balance of the Martil Basin, with increased drought frequency and more irregular flow regimes potentially having profound effects on the composition and functioning of macroinvertebrate communities (Dorić et al. 2023). Sensitive groups, such as sprawlers, depend on fast-flowing, oxygen-rich riffles and are particularly vulnerable during prolonged dry periods. In contrast, more tolerant groups, such as swimmers and burrowers like Chironomidae, may become more dominant in these altered conditions. This shift is not just a change in species composition. Still, it could also disrupt vital ecosystem functions such as nutrient cycling and organic matter processing, which could be compromised with the decline of specialized taxa like Plecoptera. The proliferation of generalist species may lead to functional homogenization, which has been observed in other Mediterranean basins under both climatic and anthropogenic pressures (Bruno et al. 2019; Arenas-Sánchez et al. 2021; Theodoropoulos and Karaouzas 2021). If these trends are seen in the Martil

Basin, the river system could evolve from a biologically diverse and dynamic system into a simplified one, with diminished ecological integrity.

This study's findings highlight the need for further research in other regions of Morocco and North Africa to better understand the relationships between environmental factors and the structural and functional diversity of macroinvertebrates. Such studies are essential for developing bio-typological classifications and improving the ecological health of various watercourse types in the southern Mediterranean. These serve as a complementary approach to enhancing the ecological integrity of freshwater ecosystems, especially in developing countries. This integrated perspective can help develop targeted conservation strategies and enhance the resilience of aquatic ecosystems under rising anthropogenic pressures.

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