



Environmental Change Threatens Freshwater Insect Communities in Northwest Africa: A Meta-Analysis

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OPEN ACCESS

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Specialty section:

This article was submitted to
Freshwater Science,
a section of the journal
Frontiers in Environmental Science

Received: 24 February 2021

Accepted: 15 July 2021

Published: 27 July 2021

Citation:

Kaczmarek N, Schäfer RB and
Berger E (2021) Environmental Change
Threatens Freshwater Insect
Communities in Northwest Africa:
A Meta-Analysis.
Front. Environ. Sci. 9:671715.
doi: 10.3389/fenvs.2021.671715

A climatic shift from temperate to arid conditions is predicted for Northwest Africa. Water temperature, salinity, and river intermittency are likely to increase, which may impact freshwater communities, ecosystem functioning, and related ecosystem services. Quantitative data and information on the impact of climate change on insect communities (e.g., richness, taxonomic and trait composition) are still scarce for Northwest Africa. In this study, we extracted information on freshwater insect occurrence and environmental variables in Northwest Africa from the results of a literature search to study potential consequences of changing climatic conditions for these communities. Our data set covered 96 families in 165 sites in Morocco and Algeria. We quantified the impact of several explanatory variables (climate, altitude, water temperature, conductivity, intermittency, flow, aridity, dams, and land cover) on richness, taxonomic and functional trait composition using negative binomial regression models and constrained ordination. Family richness in arid sites was on average 37 % lower than in temperate sites in association with flow, river regulation, cropland extent, conductivity, altitude, and water temperature. With 36 % of the studied temperate sites predicted to turn arid by the end of the century, a loss of insect families can be predicted for Northwest Africa, mainly affecting species adapted to temperate environments. Resistance and resilience traits such as small body size, aerial dispersal, and air breathing promote survival in arid climates. Future research should report insect occurrences on species level to allow for better predictions on climate change effects.

Keywords: macroinvertebrates, river intermittency, Northwest Africa, climate change, aridity, insect richness

INTRODUCTION

Northwest Africa is characterized by the temperate Mediterranean and arid Saharan climate and is subject to droughts (Schilling et al., 2012; Waha et al., 2017). In this region, rivers can be considered the arteries of life because all life is clustered around them. Arid climate is predicted to extend northwards covering increasing parts of the Maghreb until the mid- and late-21st century (Born et al., 2008; Beck et al., 2018). This will likely lead to increased salinity levels and flow intermittency in rivers (Williams, 1999) potentially affecting biodiversity and dependent human livelihoods (Arthington et al., 2010; Berger et al., 2018) through changes in the supply of ecosystem goods and services. Besides climate change, water abstraction (Dewson et al., 2007), flow modification (Martínez et al., 2013) and additional human-induced forms of secondary salinisation (Cañedo-Argüelles et al., 2013) related to human land use in the river catchment may exacerbate salinity levels and flow intermittency.

Benthic macroinvertebrates play an important role in the functioning of freshwater ecosystems (Wallace & Webster, 1996; Covich et al., 1999). By processing dead and living material and transferring the energy to freshwater and adjacent terrestrial food webs, macroinvertebrates contribute to ecosystem stability (Wallace and Webster, 1996; Giller et al., 2004). Macroinvertebrate abundance and richness has been shown to decrease with environmental stressors such as high water temperature (Durance and Ormerod, 2007), high salinity (Kefford, 1998; Arribas et al., 2019), and flow intermittency (Beauchard et al., 2003; Stubbington et al., 2009; Smeti et al., 2019). This, in turn, has been associated with a reduction in ecosystem functions such as nutrient cycling (Cao et al., 2018) and organic matter breakdown (Smeti et al., 2019). The anticipated increase in water temperature, salinity, and flow intermittency with future climate change suggests a reduction in macroinvertebrate abundance and richness, which may result in the local extinction of species in Northwest Africa. A loss of species can potentially be compensated by functionally similar species (Solan, 2004) as long as this species can maintain or increase its abundance. However, in the absence of compensation, the reduction of ecosystem functions through the loss of insect abundance and richness could adversely affect ecosystem services and human health (Strange et al., 1999).

Species that can thrive in arid climates show adaptations to drought and salinity or the ability to quickly recolonize after droughts. Resistance traits (e.g., desiccation resistance) can enable species to withstand long droughts (Stubbington et al., 2017). Ovoviviparity, multi-voltinism, and filter- and deposit-feeding, have been associated with increased salinity (Piscart et al., 2006; Szöcs et al., 2014). High female dispersal and short life cycles promote recolonization after droughts (Stubbington et al., 2017). Traits that increase resistance and resilience typically increase in communities that persist in harsh climatic conditions, because species that lack such traits go locally extinct. Notwithstanding, the occurrence of specific traits is not only driven by environmental conditions but complex abiotic and biotic interactions under phylogenetic constraints (Hamilton et al., 2020).

Studies on macroinvertebrates in Northwest Africa are still scarce and often focus on water quality and anthropogenic stressors on a local scale, and less on climate effects in the whole region. Trends in macroinvertebrate distribution and richness patterns in North Africa can be assessed by using a combination of climatic and hydrological variables (Beauchard et al., 2003). However, little is known about the impact that climate change can have on insect communities. While insect richness and abundance are decreasing as a response to anthropogenic land use intensification (Seibold et al., 2019), macroinvertebrate richness may increase in temperate regions of Europe by a northward shift of species from the highly diverse Mediterranean climate (Bonada et al., 2007). As a consequence of the increasing arid climate in Northwest Africa (Beck et al., 2018), a loss of richness, however, can be expected. Understanding the effects of arid and temperate climate on insect communities in Northwest Africa may help establish future scenarios for insect

communities and identify consequences for food webs, ecosystem functions, and related ecosystem services.

We compiled data for Northwest Africa to quantify the associations between aquatic insect communities and environmental variables. The aim of our study was to study the response of aquatic insect richness to a change of climates based on an increase of arid conditions. Furthermore, we aimed to identify insect families that are likely vulnerable to climate change and traits that enable insects to thrive under arid conditions.

We hypothesized that (i) aquatic insect richness in Northwest Africa is lower in arid than in temperate climates; (ii) insect family composition differs between arid and temperate climates, in association with (iii) changes in specific traits, such as small body size, short life cycles, resistance against drought and salinity, and the ability for air breathing.

MATERIALS AND METHODS

Data Collection

Literature Search and Insect Occurrence Data

We used Web of Knowledge, Google Scholar, and the database MacroMED (Blanco-Garrido et al., 2013) to search for publications about macroinvertebrates in Northwest Africa using the keywords “macroinvertebrate*,” “invertebrate*,” and “insect*” together with “Algeria,” “Morocco,” and “Tunisia,” as well as their French translations. Given that most publications were limited to aquatic insects and Morocco and Algeria, we limited our study to this group in these two countries (**Figure 1**). Moreover, the references of the retrieved publications were screened for additional studies, called footnote chasing. The literature search was completed on June 15th, 2020. Publications that reported 1) presence/absence data for aquatic insects (not restricted to specific orders), 2) water temperature and conductivity, (iii) and were conducted in intermittent or permanent rivers, were used in the analysis (Supplementary Figure S1). This resulted in 18 publications (Supplementary Table S1). In all studies, aquatic insects were sampled by using either a Surber sampler or hand/kick net, except for Khebiza et al. (2006) that used a membrane pump. The sampling method was not reported in Giudicelli and Dakki (1984).

Insect and Environmental Variables

Insect and environmental variables were sampled one to 12 times per site. Therefore, we included “Number of samples per site” as a variable, to allow for checking the effect of the sampling frequency per site on family richness. Based on the given taxonomic resolution, we used the family level.

11 variables were gathered for analysis (**Table 1**), which describe the hydrological, geographic, and climatic conditions, as well as land cover. Water temperature and water electrical conductivity as a surrogate measure for salinity (hereafter conductivity) were extracted directly from tables or graphs in the selected papers using WebPlotDigitizer (Rohatgi, 2020). In the case of repeated measurements, a mean was calculated, because several publications already reported mean values.

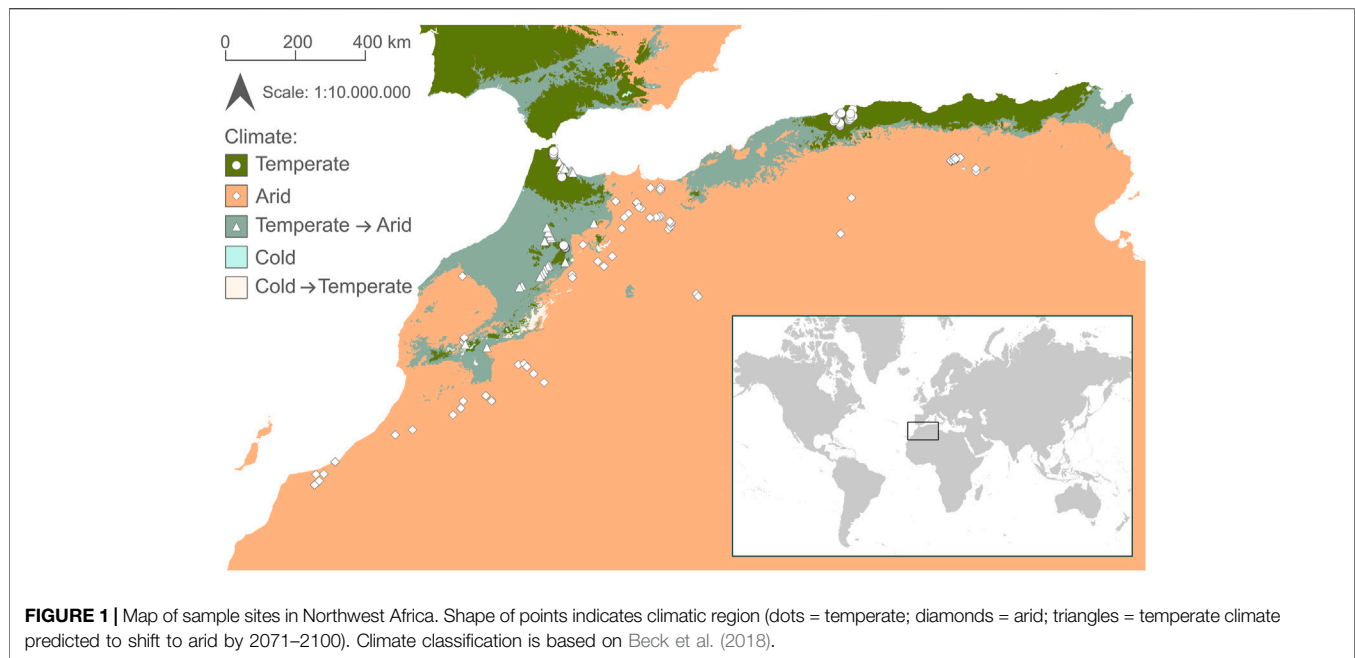


TABLE 1 | Environmental and anthropogenic variables used in the analyses with their unit, minimum (Min), maximum (Max) and average (Avg) values, standard deviation (SD), used transformation before data analysis and the source of the variables (“direct” indicates direct extraction from publications). Values for temperate and arid climate are reported in brackets, separated by a slash.

Variable	Description	Unit	Min	Max	Avg	SD	Transformation before data analysis	Source
Climate	Type of climate (temperate or arid)	-	-	-	-	-	-	Köppen-Geiger climate classification map, Beck et al. (2018)
Altitude	Height above sea level	Meters [m]	(7/0)	(1910/1710)	722.7 (530/839)	555.5 (612.1/477.5)	-	Direct/maps
Water temperature	-	Degrees Celsius [°C]	(8.9/7.8)	(28.7/33.1)	19 (17.7/20.1)	5 (3.7/5.7)	-	Direct
Flow regime	Type of flow (permanent or intermittent)	-	-	-	-	-	-	Direct
Global Aridity Index	Mean annual precipitation over mean annual evapotranspiration	Index value	(30/3)	(90/49)	39.5 (59.3/23.4)	22.1 (12.5/13.3)	-	RiverATLAS, Zomer et al. (2008)
Number of samples per site	Number of samples taken per site	-	(1/1)	(12/12)	5.4 (8.1/3.2)	4.7 (4.8/3.3)	-	Direct
Conductivity	Water conductivity	[μS/cm]	(167.6/202)	(4,059/93,667)	5,282.1 (1,124.4/8,663.1)	17,061.3 (772.3/22,453.7)	log	Direct
River area	Surface area of river reach in a 15 arc-second grid	Hectares [ha]	(0.47/0.15)	(20.43/70.94)	6.1 (6.4/5.9)	8 (5.3/9.6)	log	RiverATLAS, Lehner and Grill (2013)
Degree of regulation	Effect of upstream dams on natural flow regime. Ratio between total reservoir storage volume of upstream dams and total annual discharge volume available at reach	Percent [%]	(0/0)	(5,095/1968)	74.5 (116.5/40.3)	443.3 (616.9/216.2)	log (x+1)	RiverATLAS, Lehner et al. (2011)
Cropland extent	Percentage of cropland land cover at river reach	Percent [%]	(0/0)	(100/100)	25.5 (43.7/10.7)	34.5 (34.8/26.2)	log (x+0.1)	RiverATLAS, Ramankutty et al. (2008)
Urban extent	Percentage of urban land cover at river reach	Percent [%]	(0/0)	(100/71)	15.2 (23.9/8.1)	23.8 (29.6/14.3)	log (x+0.1)	RiverATLAS, Pesaresi and Freire (2016)

Coordinates (World Geodetic System 1984 Coordinate system (WGS-84)) and altitude were extracted directly from the publications. If information was missing, the location and altitude of the sites were estimated based on the presented maps. The general flow regime (permanent or intermittent) was extracted from the publications. River area, degree of regulation, Global Aridity Index, cropland extent, and urban extent (spatial extent of cropland/urban areas in reach catchment), were extracted from the RiverATLAS (version 1.0; Linke et al., 2019) using QGIS 3.8.2-Zanzibar (QGIS.org, 2021). Finally, the current and future climatic class of each site (arid, temperate) was assigned using the Köppen-Geiger climate classification map for present-day and future climate (Beck et al., 2018).

Trait Data

We used the trait database of Tachet et al. (2010) to obtain information for the insect families, including 11 biological traits with 60 modalities (Supplementary Table S2) associated with resilience and resistance to disturbances (Bonada et al., 2007). Among these are included traits such as size, life-cycle duration, reproduction, and feeding behavior. For each of these biological traits, different trait modalities are defined and the affinity of the taxa to each trait modality is represented by fuzzy coded scores (0 = no affinity, 1 = low affinity, 2 = moderate affinity, 3 = high affinity). These codes were transformed to relative frequencies for a given family. If traits were defined for a lower taxonomic level than family in the trait database, we assigned traits as follows: i) If only one species of a family occurred in the study region and traits were available for the species, these traits were assigned to the family. ii) In the case of multiple species from a family, we calculated a weighted mean based on its relative frequency of occurrence with respect to the total number of sites. For each site, we calculated an insect assemblage trait profile based on the relative frequencies of trait modalities for each family and the presence data of these families at a given site, by taking the sum for each trait modality from all present insect families and transforming these sums into relative frequencies for each trait (similar to Mondy et al., 2016). Trait information was missing for 15 out of 96 families and for four families few specific traits were missing. These families or traits were not considered for the calculation of the insect assemblage trait profiles.

Data Analysis

For all data analyses, we used RStudio (version 1.2.5019) and the packages “Vegan” (Oksanen et al., 2019), “car” (Fox and Weisberg, 2018), “DHARMA” (Hartig, 2020), “MASS” (Venables and Ripley, 2002), and “faraway” (Faraway, 2016), “reghelper” (Hughes and Team, 2017), “modEvA” (Márcia Barbosa et al., 2013), “indicpecies” (De Cáceres et al., 2016), “beanplot” (Kampstra, 2008), “MuMIn” (Barton and Barton, 2015).

Association Between Family Richness and Environmental Variables

To analyze for differences in the richness of insect families between arid and temperate climate (hypothesis 1), we used Welch’s *t*-test given heterogeneous variances (Figure 2). To

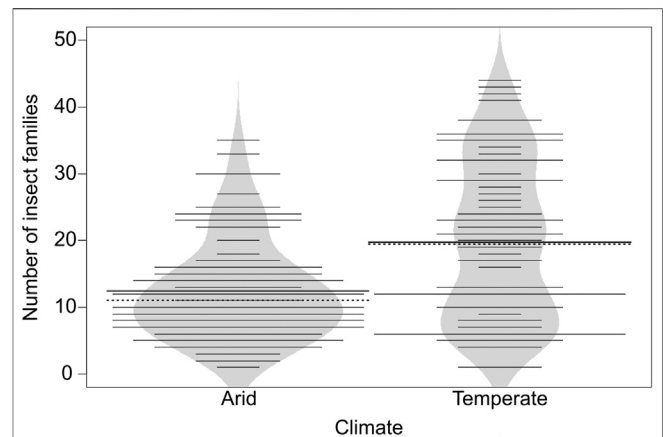


FIGURE 2 | Beanplot for number of insect families for arid ($n = 91$) and temperate climate ($n = 74$) in Northwest Africa. Bold line indicates mean of each group (arid = 12.44; temperate = 19.76), dashed lines indicates median of each group (arid = 11; temperate = 19.5), thin lines individual observations, polygon and length of lines density of observations. Means differ significantly between the two climates (Welch’s *t*-test, $n = 165$, $t(116.47) = -4.6$, $p < 0.001$). For details on beanplots see Kampstra (2008).

identify environmental variables that can explain family richness, we used negative binomial regression models. The variable “Climate” was removed from analyses due to collinearity (VIF >5) with the Global Aridity Index, which captures climatic conditions in terms of evaporation and precipitation. Five variables were log-transformed prior analysis because they were left-skewed (Table 1). We used a backward stepwise model selection by AIC to select the best fitting model. The resulting best-fit model was checked for model assumptions.

Association Between Family Composition and Environmental Variables

Before analysis, we excluded rare families that occurred in less than five percent of sites (<8 sites) from the analysis (Legendre and Gallagher, 2001). Canonical Correspondence Analysis (CCA) was used to analyze the relationship between insect families and environmental variables (hypothesis 2). We selected CCA because a detrended correspondence analysis (DCA) showed a unimodal gradient (gradient length of 3.29) (Legendre and Legendre, 2012). The best fit model was selected using a stepwise model selection with the adjusted R^2 as the goodness of fit metric.

To identify families that are characteristic for arid and temperate climate, we used an Indicator species analysis. For each family, an indicator value was calculated, which is highest when taxa are either present in one of the climates but not the other or present in all sites of one climate (Borcard et al., 2018). We checked for a significant association of families with the climate types by using a permutational test.

Association Between Traits and Environmental Variables

To analyze the association of traits with climate change-related environmental variables (hypothesis 3), we used Redundancy

TABLE 2 | AIC model selection with regression estimates for the included environmental variables (altitude (Alt), Global Aridity Index (GAI), intermittent flow regime (Flow), conductivity (log-transformed; logCond), cropland extent (log-transformed; logCrop), degree of regulation (log-transformed; logReg), river size (log-transformed; logSize), number of samples per site (Samp), water temperature (Temp)), degrees of freedom (Df), Log-likelihood (LL), information score of the model (AIC), delta and AIC weight for all models within a delta of 2 (* = final model). Regression estimates with standardized variables are indicated in brackets for the final model.

Model	574*	576	830	638	62
Intercept	3.48 (2.83)	3.02	3.32	3.76	3.76
Alt	-0.0002 (-0.13)	-0.0002	-0.0002	-0.0002	-0.0003
GAI	-	0.004	-	-	-
Flow	-0.42 (-0.42)	-0.4	-0.4	-0.4	-0.4
logCond	-0.12 (-0.16)	-0.1	-0.12	-0.13	-0.1
logCrop	0.06 (0.19)	0.05	0.05	0.06	0.06
logReg	-0.11 (-0.2)	-0.11	-0.11	-0.11	-0.1
logSize	-	-	-	0.03	-
Samp	-	-	0.01	-	-
Temp	0.02 (0.11)	0.03	0.02	0.02	-
Df	8	9	9	9	7
LL	-567.01	-566.11	-566.4	-566.82	-569.05
AIC	1,150.9	1,151.4	1,152	1,152.8	1,152.8
Delta	0	0.43	1.01	1.85	1.86

Analysis (RDA) given a gradient length of 1.37 in DCA (Legendre & Legendre, 2012), by using the insect assemblage trait profiles. As in CCA, stepwise model selection was used to identify the best-fit model.

RESULTS

The literature search resulted in 766 publications, of which 724 were excluded after screening titles and abstracts (Supplementary Figure S1). Of the remaining 42 publications, we included 18 in our analysis that met the inclusion criteria (Supplementary Table S1). Most publications were excluded based on missing taxa lists or environmental parameters. The number of sites in the publications ranged from 1 to 28 (mean = 9.2). In total there were 165 sites covering a wide range of environmental conditions (Table 1). 91 sites were located in arid climate and 74 in temperate climate, of which 27 (36%) are predicted to shift towards arid climate by 2071–2,100 (Figure 1).

Association Between Family Richness and Environmental Variables

The number of families per site ranged from 1 to 44 (mean = 15.72, SD = 10.33), with 96 families in total. Family richness was 37% lower in arid ($n = 91$, mean = 12.44, SD = 7.39, median = 11) compared with temperate ($n = 74$, mean = 19.76, SD = 11.94, median = 19.5) climate (Welch's t -test, $n = 165$, $t(116.47) = -4.6$, $p < 0.001$) (Figure 2).

Variation in family richness was associated with altitude, flow regime, conductivity, cropland extent, degree of regulation, and water temperature. Family richness was lower in sites with higher altitude, higher regulation, higher conductivity, and intermittent

flow, but increased with higher water temperature and larger extent of cropland areas (Table 2). The variables “Number of samples per site,” “Global Aridity Index,” “River area,” and “Urban extent” were not included in the best-fit model.

Association Between Family Composition and Environmental Variables

The best-fitting CCA model for community composition included water temperature, number of samples per site, altitude, flow regime, conductivity, cropland extent, urban extent, Global Aridity Index, river area and degree of regulation. These variables explained 18% of the variation, where 7.1% of the total variation (39% of constrained variation) was explained by the first two axes. Axis 1 shows a gradient of water temperature, conductivity, and aridity (Figure 3). Axis 2 shows a gradient of number of samples per site and urban extent. Most insect families occurred in less arid sites with low or medium water temperature and conductivity (Figure 3) such as Ephemeroptera and Plecoptera. The family Micronectidae was associated with aridity and high water temperature and conductivity. Most families of Diptera occurred more frequently in sites characterized by a higher extent of croplands and urbanization.

In the Indicator Species Analysis, one family (Micronectidae) was associated with arid climate and 33 (48%) families were associated with temperate climate (Table 3).

Association Between Traits and Environmental Variables

In the best-fitting RDA model, the assemblage trait profile was explained by conductivity, degree of regulation, water temperature, urban extent, aridity, and flow regime. These variables explained 19% of the variation, of which 16% of the total variation (82% of the constrained variation) was explained by the first two axes. Axis 1 represents a gradient of conductivity urban area extent and degree of regulation (Figure 4), whereas axis 2 shows a gradient of water temperature, conductivity, degree of regulation, and flow regime. The traits “Life cycle duration,” “Reproduction,” and “Respiration” were mainly associated with axis 1, whereas “Potential number of cycles/year,” “Dispersal,” and “Food” were mainly associated with axis 2 (Figure 4).

DISCUSSION

Association Between Family Richness and Environmental Variables

In Northwest Africa, large parts of temperate climate are predicted to turn to arid climate by the end of the century (Beck et al., 2018), and this will likely affect 36% of the temperate sites in our study. On average family richness was 37% lower in arid than in temperate climates, supporting our first hypothesis. Hence, the family richness of sites that will shift towards an arid climate will likely decrease over time. Although the loss of some families could be partly compensated by the

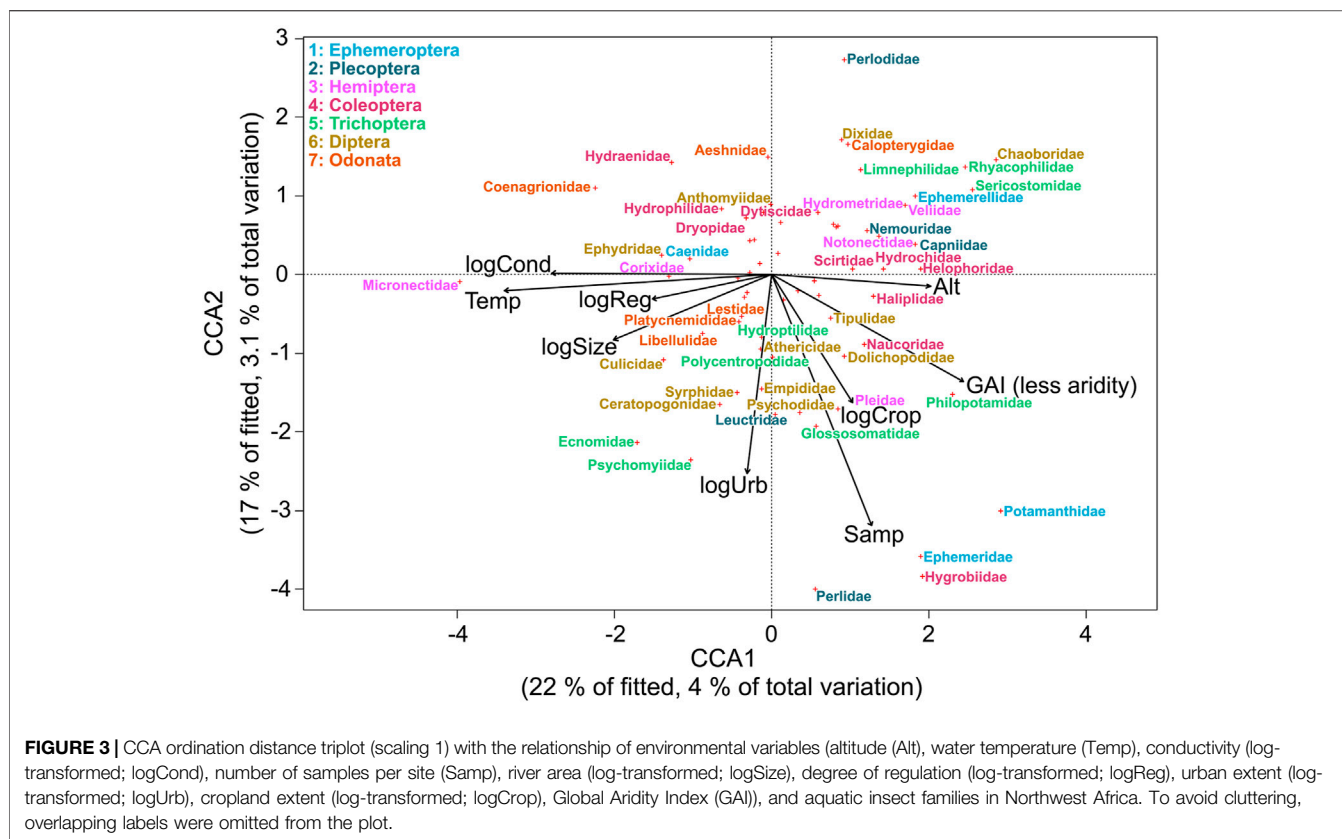


FIGURE 3 | CCA ordination distance triplot (scaling 1) with the relationship of environmental variables (altitude (Alt), water temperature (Temp), conductivity (log-transformed; logCond), number of samples per site (Samp), river area (log-transformed; logSize), degree of regulation (log-transformed; logReg), urban extent (log-transformed; logUrb), cropland extent (log-transformed; logCrop), Global Aridity Index (GAI)), and aquatic insect families in Northwest Africa. To avoid cluttering, overlapping labels were omitted from the plot.

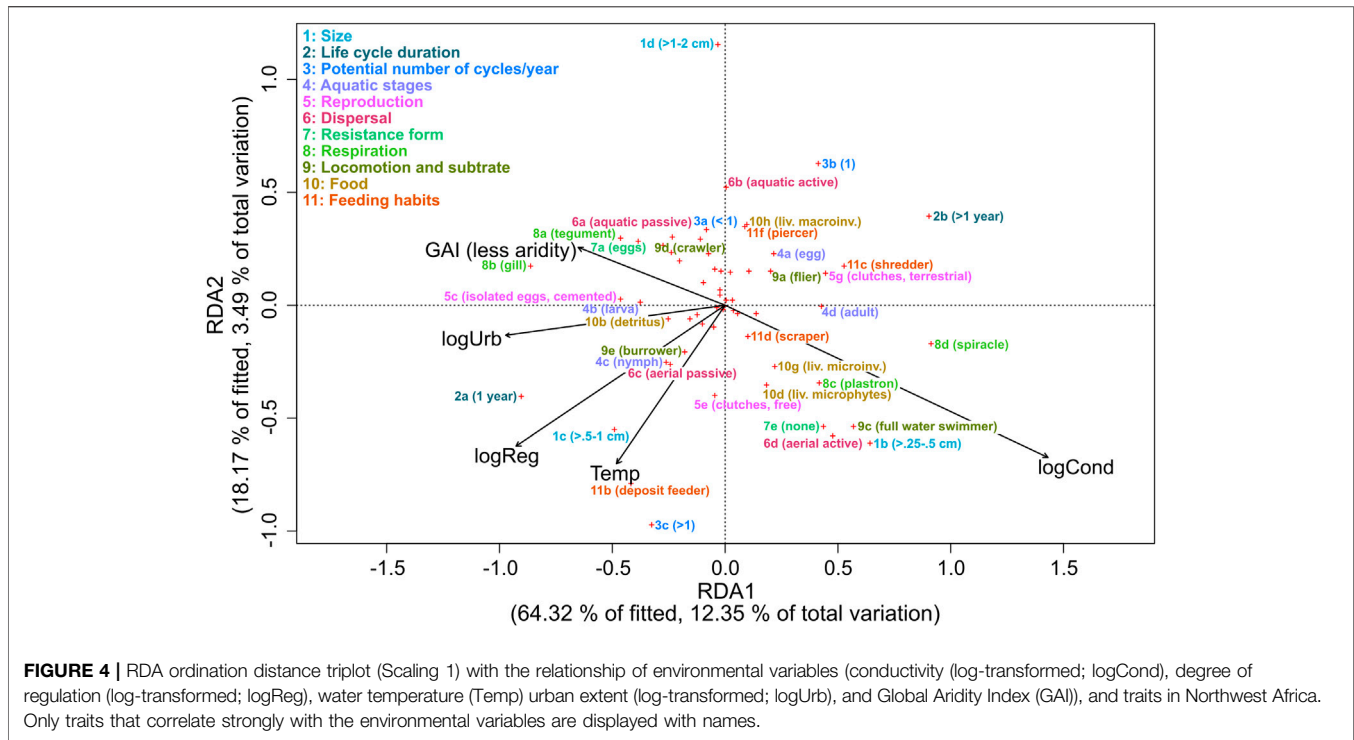
TABLE 3 | Results of Indicator Species Analysis showing families associated with arid and temperate climate, test statistics and indicator value (IndVal).

Arid climate			Temperate climate					
Family	IndVal	p-value	Family	IndVal	p-value	Family	IndVal	p-value
Micronectidae	0.25	0.003	Psychodidae	0.42	<0.001	Gyrinidae	0.23	0.05
-	-	-	Hygrobiidae	0.36	<0.001	Limoniidae	0.22	0.006
			Gomphidae	0.36	<0.001	Ephemeridae	0.21	0.01
			Leuctridae	0.34	<0.001	Chironomidae	0.21	0.01
			Tipulidae	0.32	<0.001	Glossosomatidae	0.21	0.01
			Perlidae	0.31	<0.001	Rhyacophilidae	0.21	0.01
			Nemouridae	0.31	<0.001	Elmidae	0.2	0.01
			Calopterygidae	0.3	<0.001	Simuliidae	0.2	0.02
			Potamanthidae	0.3	<0.001	Mesoveliidae	0.2	0.02
			Empididae	0.3	<0.001	Notonectidae	0.2	0.01
			Vellidae	0.28	<0.001	Tabanidae	0.19	0.02
			Ceratopogonidae	0.28	<0.001	Dryopidae	0.19	0.02
			Philopotamidae	0.27	<0.001	Perlodidae	0.19	0.02
			Syrphidae	0.27	0.005	Heptageniidae	0.19	0.02
			Anthomyiidae	0.26	<0.001	Ephemerellidae	0.18	0.03
			Halplidae	0.25	0.001	Athericidae	0.17	0.05
			Polycentropodidae	0.24	0.003	-	-	-

invasion of other families adapted to arid environments, this may be insufficient to maintain the current level of richness (Dornelas et al., 2019; Morghad et al., 2019).

The loss of insect family richness was associated with a shift towards intermittent flow and higher conductivity. These findings are in accordance with several studies on macroinvertebrate richness in intermittent (Beauchard et al., 2003; Soria et al.,

2017) and highly saline rivers (Velasco et al., 2006; Arribas et al., 2019; Berger et al., 2021). With the decrease of precipitation and the increase of evapotranspiration predicted in future climate scenarios for Northwest Africa (Terink et al., 2013), intermittency is likely to increase (Döll & Schmied, 2012). An increase in water and soil salinity can also be expected in association with droughts, as well as a reduction in flow due to



human alterations of rivers, and water abstraction for irrigation of agricultural lands (Williams, 1999; Pitman and Lauchli, 2002; Herbert et al., 2015). This suggests future species loss. With family richness being on average 37% lower in arid than in temperate sites, our model suggests that intermittent flow and increasing conductivity will play major roles in the loss of richness.

Water temperature increased insect family richness in our model, whereas altitude had a negative effect. We have hypothesized a decrease of insect families with rising water temperatures based on the assumption of impaired oxygen uptake in species lacking respiratory adaptations to cope with reduced oxygen, such as plastron and spiracle (Datry et al., 2017). The increase of family richness with increasing water temperature may be explained by the low family richness of high altitude streams with colder water temperature (Jacobsen, 2004) in our study. By contrast, other studies found an increase in family richness with altitude in Northwest Africa (Beauchard et al., 2003; Benzina et al., 2019), while abundance decreased (Benzina et al., 2019). In our dataset, we further saw a decrease of family richness in water temperatures exceeding around 20°C. If rising water temperatures exceed the temperature tolerances of specific insect families, these could be threatened by local extinction (Dallas and Ketley, 2011).

Variables related to human activities, such as a higher degree of regulation, were negatively associated with insect family richness, while the extent of cropland showed a positive association. This is in line with previous findings that hydromorphological alterations of rivers can reduce macroinvertebrate richness (Martınez et al., 2013), due to reduced water quality, disconnection of river sections, and changes in flow regime (McAllister et al., 2001; Navarro-Llacer et al., 2010). Increasing water demand under climate change in

Northwest Africa reinforces the importance of water reservoirs for agricultural and potable water use likely resulting in more water regulation (Ayt Ougougdal et al., 2020). This reflects a global trend of increasing river regulation putting freshwater biodiversity at risk (Zarfl et al., 2015). We were surprised to find a positive association between the extent of cropland and insect family richness because most studies suggest a negative impact of agricultural activities on family richness (Genito et al., 2002; Hepp et al., 2010). In our study, cropland areas were more frequently located in temperate areas with lower aridity, which may have masked the negative impact of agriculture.

We used family level data to study associations with environmental variables. Taxonomic richness at the species level and the use of abundance data could show stronger associations with environmental conditions and help to detect variability on a smaller scale (Leung and Dudgeon, 2011).

Association Between Family Composition and Environmental Variables

The Indicator Species analysis showed that nearly half of the insect families in our study were associated with temperate climate and only rarely or never occurred in arid climate, which is in line with the finding of reduced family richness in the latter. These families will likely be foremost affected by changing environmental conditions, whereas only a few families, like Micronectidae, seem to better tolerate arid conditions and could potentially profit from an extension of arid climate (Domisch et al., 2013). The occurrence of insect families is mostly associated with lower aridity, and lower to medium water temperatures and conductivity, explaining their

absence in arid environments. Thus, local extinction of species by loss of suitable habitats in Northwest Africa could be minimized by limiting global warming to 1.5°C (Warren et al., 2018).

However, the variance explained by the CCA was relatively low, probably due to the variability of single species inside a family with species showing different associations with environmental variables. Missing stressors (such as local pollution and pesticides) which we did not cover in our model and biogeographic limitations in species distribution could further explain the low variance. As “number of samples per site” was also explaining the distribution of families, consistent sampling methods (e.g., AQEM Consortium (2002)) and the use of metabarcoding for species identification (Elbrecht et al., 2017) could help to overcome these problems.

While the orders of Ephemeroptera, Plecoptera, and Trichoptera (EPT taxa) were mainly associated with low aridity, low water temperature, and low conductivity, we saw a higher variability in the other insect orders. This matches the results of Díaz et al. (2007), where the EPT taxa were more associated with pristine mountain environments than with saline sites. Also, 12 out of 23 EPT families included in the analysis were associated with temperate climate in the Indicator Species Analysis, which suggests these taxa to be good indicators for measuring effects of present and future environmental changes (Wallace and Webster, 1996) in North Africa.

Climate conditions shifting along altitudinal gradients may increase the importance of high altitude habitats with low water temperatures as potential refuge habitats for lowland species (Walther et al., 2009). Insect families, such as Capniidae, were associated with high altitudes and low water temperatures. While species from lowland sites could escape increasing water temperatures by moving upwards to colder mountain streams, suitable habitats for families associated with high altitudes and low water temperatures in our analysis could get lost by changes in environmental conditions (Domisch et al., 2011; Domisch et al., 2013).

Our results suggest that many insect families benefit from agricultural and urban areas in the catchment. This could be due to rich food sources entering the river from the surrounding cropland (MacFarlane, 1983) and suitable conditions in areas of human settlements. Kietzka et al. (2018) found that the loss of most dragonfly species mainly affected endemics, while generalists can cope with the increase of anthropogenic land use. Similarly, other generalist insect species were found to better cope with the change in environmental conditions than endemic species (Domisch et al., 2013). However, we do not know if endemic species were less able to cope with environmental stressors in our case since we only looked at the family level.

Some aquatic insects such as the vector mosquito *Culex pipiens* transmit diseases like malaria, West Nile virus, and Zika virus (Farajollahi et al., 2011). In our analysis, the family Culicidae (mosquitoes) was positively correlated with higher water temperature and conductivity and thus may profit from climate change as was previously reported (Ramasamy and Surendran 2012). However, not all species within the family of Culicidae are vectors of diseases. Species level identification is required in future studies to better understand potential human health effects through an increase of disease-transmitting mosquitoes (Marselle et al., 2021).

Association Between Traits and Environmental Variables

Environmental conditions shape trait profiles of insect communities by acting as a filter (Statzner et al., 2001). In our study, conductivity, degree of regulation, water temperature, urban extent, aridity, and flow regime explained the differences in insect trait profiles. Similarly, conductivity and water temperature were among the most influential variables of trait profiles in a study from a Mediterranean semi-arid climate (Díaz et al., 2007).

Resilience traits can promote recolonization after natural events such as droughts (Leigh et al., 2016; Stubbington et al., 2017). The environmental variables related to arid climate, aridity, high water temperatures, and conductivity were associated with active aerial dispersal in Redundancy Analysis (RDA). Also, the degree of regulation was positively correlated to aerial dispersal. Aerial dispersal can promote recolonization and help to maintain local populations (Bogan et al., 2017). If large parts of rivers dry out, aquatic insects with the ability to fly, such as coleopterans and hemipterans, are the main colonizers (Díaz et al., 2007; Stubbington et al., 2017).

Resistance traits can help to cope with stressors such as drying rivers and high salinity (Leigh et al., 2016; Stubbington et al., 2017). In the RDA, full water swimmers, respiratory adaptations, and small body size were associated with aridity and high conductivity. The ability to swim (full water swimmers) becomes more important when flow recedes and river sections are separated (Datry et al., 2017) because it allows to reach food sources that are no longer transported by the water current. Due to a fast ion-uptake in saline water and lower oxygen levels in standing or slow running water of intermittent streams, special strategies of respiration are required (Kefford et al., 2016; Datry et al., 2017). In the RDA, adaptations that allow air breathing such as plastron and spiracle show to be associated with high conductivity and aridity (Chessman, 2015; Datry et al., 2017), whereas tegument and gill show the opposite affinity in the model. Resistance against droughts like housing against desiccation and terrestrial clutches also support survival in dry conditions (Díaz et al., 2007; Vidal-Abarca et al., 2013; Datry et al., 2017). However, these traits were non-responsive in our analysis to the environmental variables related to arid climate. Matching the concept of r-strategists (MacArthur & Wilson, 1967), smaller body size and a higher number of reproductive cycles per year were associated with an increase arid environmental stressors, suggesting that these traits provide resistance in arid environments (Díaz et al., 2007; Stubbington et al., 2017).

With a change of environmental conditions towards arid environments with higher water temperature and conductivity, aquatic insect communities need to adapt to changing food sources by a change of feeding habits (Díaz et al., 2007). Similar to Díaz et al. (2007), we found a change of food sources from macroinvertebrates to microphytes, along a gradient of rising water temperatures and conductivity. Further, deposit feeders were associated with high water

temperatures, which is in accordance with the river continuum concept (Vannote et al., 1980).

CONCLUSION

Our results show that a change towards hot and arid climate will likely reduce aquatic insect family richness in temperate regions of Northwest Africa. Climate change induced aridity, high water temperatures, high conductivity and intermittent flow could be intensified by a higher water demand and hydromorphological alterations. Droughts and reduced water quantity and quality could put various insect families, mainly endemics from temperate regions, at risk of local extinction. Traits that increase the ability to survive in arid environments (such as small size, aerial dispersal, ability for air breathing) increase the potential to cope with high water temperatures and conductivity, whereas species lacking such adaptations could be highly affected by a changing environment. A loss of family richness could lead to negative impacts on nature's contribution to human well-being. Protecting and restoring river ecosystems and promoting sustainable water use could limit species loss driven by climate change. Future studies should analyze abundances and use species level identification for a more refined assessment of climate change impact on local insect communities, which could be achieved using metabarcoding.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

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AUTHOR CONTRIBUTION

All authors contributed to conception and design of the study, contributed to article and statistical analysis revision, read, and approved the submitted version. NK performed literature search, data collection and statistical analysis and wrote the article.

FUNDING

The study was funded by the SALIDRAAjuj-01UU project through the Program on Social-Ecological Research by the German Ministry of Education and Research (Grant # 01UU1906). The publication was funded by the Open Access Fund of the University of Koblenz-Landau.

ACKNOWLEDGMENTS

We kindly thank the authors of the 18 publications for the original data we used in the analysis and for providing additional data. Further, we thank our colleagues for critical and helpful discussions and Stefan Kunz for helping with assigning the traits to taxa. We thank the Germany Ministry of Education and Research (BMBF) for financial support (SALIDRAAjuj-01UU 1906). Finally, we are very thankful for the constructive critique by the two reviewers and would like to thank the organizers of this special issue.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fenvs.2021.671715/full#supplementary-material>

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