# scientific reports



## **OPEN**

# Spatial and seasonal patterns in fish assemblages of the Bakırçay river are associated with physicochemical and habitat parameters

Irmak Kurtul<sup>1</sup>, Phillip J. Haubrock<sup>1</sup>, Cüneyt Kaya<sup>1</sup>, Cüneyt Kaya<sup>1</sup>, Sadi Aksu<sup>1</sup>, Ali İlhan<sup>1</sup>, Hasan M. Sari<sup>1</sup>, Cem Aygen<sup>1</sup>, Ismael Soto<sup>1</sup>, Ben Parker<sup>1</sup>, Robert Britton<sup>1</sup>, Ali Serhan Tarkan<sup>1</sup>, Parkan<sup>1</sup>, Sanael Soto<sup>1</sup>, Ben Parker<sup>1</sup>, Robert Britton<sup>1</sup>, Ben Parker<sup>1</sup>, Robert Britton<sup>1</sup>, Sanael Soto<sup>1</sup>, Ben Parker<sup>1</sup>, Robert Britton<sup>1</sup>, Sanael Soto<sup>1</sup>, Ben Parker<sup>1</sup>, Robert Britton<sup>1</sup>, Ben Parker<sup>1</sup>, Ben Parker<sup>1</sup>, Robert Britton<sup>1</sup>, Ben Parker<sup>1</sup>, B

The significance of long-term biodiversity monitoring studies for the protection of natural biodiversity and human well-being is well recognised by the Turkish scientific community. Despite understanding the ecological importance of freshwater ecosystems, spatially or temporally congruent studies using high resolution biodiversity monitoring data from Turkish freshwater resources remain scarce. To determine a biodiversity baseline for future studies, biological and environmental sampling was carried out in 15 different locations from the highly anthropogenically impacted Bakırçay River and its catchment in Western Anatolia between 2017 and 2018. A total of 17 fish species from 10 families were recorded, belonging mainly to the Cyprinidae and Leuciscidae families. These included six non-native, six regionally endemic, and five native species. The endangered endemic Alburnus attalus was the most widespread species, whereas several non-native species were restricted to single sites. Patterns in community composition were primarily associated with pH and stream order. However, community metrics such as species richness, Pielou's evenness, and the Shannon-Wiener diversity index were not significant. Intensifying anthropogenic activity within the Bakırçay basin suggests that sources of pollution and other detrimental stressors like non-native species should be managed to protect riverine biodiversity and maintain the provision of ecosystem services. Our findings therefore not only present a baseline for future studies on fish biodiversity and community composition, but also the possible onset of future monitoring studies in the region. Our findings underline the importance of long-term biomonitoring studies for the conservation of Türkiye's freshwater ecosystems to monitor changes occurring over time.

Keywords West anatolia, Bakırçay river, Freshwater fish, Fish ecology, Ecological modeling

<sup>1</sup>Marine and Inland Waters Sciences and Technology Department, Faculty of Fisheries, Ege University, Bornova, Izmir, Türkiye. <sup>2</sup>Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Poole, Dorset, UK. <sup>3</sup>Faculty of Fisheries and Protection of Waters, University of South Bohemia in České Budějovice, South Bohemian Research Centre of Aquaculture and Biodiversity of Hydrocenoses, Zátiší 728/II, Vodňany 389 25, Czech Republic. <sup>4</sup>Center for Applied Mathematics and Bioinformatics, Department of Mathematics and Natural Sciences, Gulf University for Science and Technology, Hawally, Kuwait. <sup>5</sup>Faculty of Fisheries, Recep Tayyip Erdogan University, Rize 53100, Türkiye. <sup>6</sup>Department of Ecology, Faculty of Science, Charles University, Prague 2, Czech Republic. <sup>7</sup>Vocational School of Health Services, Eskişehir Osmangazi University, Eskisehir, Türkiye. <sup>8</sup>Department of Biosciences, Faculty of Health and Life Sciences, University of Exeter, Exeter, Devon, UK. <sup>9</sup>Department of Ecology and Vertebrate Zoology, Faculty of Biology and Environmental Protection, University of Lodz, Lodz, Poland. <sup>10</sup>Department of Basic Sciences, Faculty of Fisheries, Muğla Sıtkı Koçman University, Muğla, Türkiye. <sup>11</sup>Irmak Kurtul and Phillip J. Haubrock contributed equally to this work. <sup>12</sup>Robert Britton and Ali Serhan Tarkan equally contributed senior authorship to this work. <sup>12</sup>email: irmak.kurtul@gmail.com; cuneyt.kaya@erdogan.edu.tr

Numerous populations of native, and particularly endemic, fish species are affected simultaneously by anthropogenic pressures including overexploitation, climate change, droughts, environmental pollution, habitat destruction, and biological invasions<sup>1</sup>. The exacerbating and cumulative effects of these stressors can lead to the extirpation of entire populations, resulting in the loss of pivotal services and functions provided by natural freshwater ecosystems<sup>2</sup>, affecting even the most resilient species and the most resistant ecosystems<sup>3</sup>.

The deterioration of freshwater ecosystems has led to a decline in global fish biodiversity<sup>4</sup>. This global biodiversity crisis, however, manifests unevenly across regions, reflecting the complex interplay of ecological, geographical, and anthropogenic factors<sup>5</sup>. The direction and magnitude of these stressors on fish species ultimately depend on the individual traits of the affected species (e.g. pollution tolerance) and their interaction with the environment. However, native fish species are known for being less tolerant to anthropogenic stress when compared to non-native species<sup>6,7</sup>. Türkiye, with its rich historical legacy and varying economic conditions<sup>8</sup>, emerges as a critical hotspot for environmental challenges, including the conservation of native fish species due to the number of endemic species and those of conservation concern<sup>9</sup>. The country's unique biodiversity is under siege—not only from the direct impacts of pollution, overexploitation and biological invasions, but also from a broader failure to recognise and protect the value of its vital freshwater ecosystems<sup>10-12</sup>. This neglect is further fueled by economic disparities that prioritise short-term gains over long-term environmental sustainability, thus putting Türkiye's delicate freshwater ecosystems at increased risk of irreversible harm<sup>12</sup>. Türkiye has about 200 endemic species nationally<sup>13</sup>, many of which have economic and conservation value such as with various localised endemic species including the Khabur spirlin Alburnoides emineae Turan, Kaya, Ekmekçi & Doğan, 2014, the Filyos spirlin Alburnoides turani Kaya, 2020, the Kaklık killifish Anatolichthys irregularis (Yoğurtçuoğlu & Freyhof, 2018), the Hassa loach Oxynoemacheilus amanos Kaya, Yoğurtçuoğlu & Freyhof, 2021, the Khabur two-spot loach Oxynoemacheilus chaboras Kaya, Kurtul, Aksu, Oral & Freyhof, 2024, the Aras trout Salmo araxensis Turan, Kottelat & Kaya, 2022, and the Murat trout Salmo baliki Turan, Aksu, Oral, Kaya & Bayçelebi,

On the other hand, the rapid spread of invasive fish species in Türkiye poses a significant threat to native aquatic ecosystems<sup>12</sup>. Notably, species such as the Gibel Carp *Carassius gibelio* (Bloch, 1782), Topmouth gudgeon *Pseudorasbora parva* (Temminck & Schlegel, 1846), and the Mosquitofish *Gambusia holbrooki* Girard, 1859 have emerged as major ecological disruptors. *Carassius gibelio* quickly proliferates in still waters, outcompeting native species for resources<sup>21</sup>, while *P. parva* competes with local fish and is particularly harmful due to its vectoring of various pathogens, further threatening biodiversity<sup>22</sup>. *Gambusia holbrooki*, initially introduced for mosquito control, has spread rapidly and now consumes food resources crucial to native species<sup>23</sup>. These invasive species, with their high reproductive rates and adaptability, dominate freshwater ecosystems in Türkiye, reducing indigenous species habitats/niches and disrupting ecosystem services. Management steps and interventions are thus critical to conserve native and endemic species facing extinction.

Biodiversity is steadily declining globally<sup>24</sup>, often overshadowed by a combination of willing neglect and a pervasive lack of awareness<sup>25</sup>. This deterioration can remain unnoticed because recognising a decline requires prior knowledge of the ecosystem's original state<sup>26</sup>. This is also true for the Bakırçay River, an important and biodiverse watercourse in Western Türkiye that is heavily impacted by anthropogenic activity. While the number of species is not especially diverse at a regional level, the documented ichthyofaunal changes and the highly mixed nature of the assemblage of endemic, non-native and native species makes the location a particularly interesting site in which to examine spatiotemporal trends in assemblages in relation to physicochemical and habitat parameters.

To halt biodiversity loss in freshwater habitats like the Bakırçay River drainage and to protect endemic and native species facing extinction, management interventions based on informed concern are urgently needed<sup>27</sup>. Effective management, however, requires an established baseline that enables the investigation of trends in freshwater communities to infer changes in their actual status<sup>28</sup>. For this purpose, we collected seasonal data on fish community compositions from 15 sites across the Bakırçay River drainage and used environmental and ecological niche models to investigate how fish communities varied with spatial and physicochemical trends. We hypothesise that (i) there will be substantial spatial variation in the fish diversity of the Bakırçay drainage and that these variations are predictable across (ii) longitudinal and latitudinal gradients, (iii) seasons, and (iv) are associated with physicochemical differences.

### Materials and methods Study area

The Bakırçay River originates in the Boz Mountains in western Türkiye and flows in a generally westward direction through the Aegean region (provinces such as İzmir and Manisa), eventually reaching the Aegean Sea. The river has a total length of 129 km, the basin covers an area of 3,356 km<sup>229</sup> and is both economically and ecologically valuable, supporting a diversity of flora and fauna.

Over the past century, the Bakırçay River has been heavily altered by diverting water for irrigation to sustain the region's agriculture. Increasingly intense drought periods impact the Bakırçay River drainage during summer periods which have resulted in the construction of several reservoirs. Consequently, modifications to the drainage area have further intensified the cycle of drought, triggering severe and far-reaching physicochemical and ecological changes such as the alteration of natural flow regimes, loss of riparian habitats, a decline in native fish populations, and the proliferation of invasive species<sup>30</sup>.

Despite the Bakırçay River drainage conservation value for endemic and native fishes, available information on its native biodiversity and natural history remains limited. The first detailed study on the river identified eight species from three families<sup>31</sup>, later expanding to 12 species<sup>32,33</sup>. The discovery of the non-native fish species *P. parva* was reported from within the Yortanlı reservoir in 2006<sup>34</sup> and an endemic species, *Alburnus attalus* Özuluğ & Freyhof, 2007, was additionally described a year later<sup>35</sup>. A more recent estimate reported 17 species (3

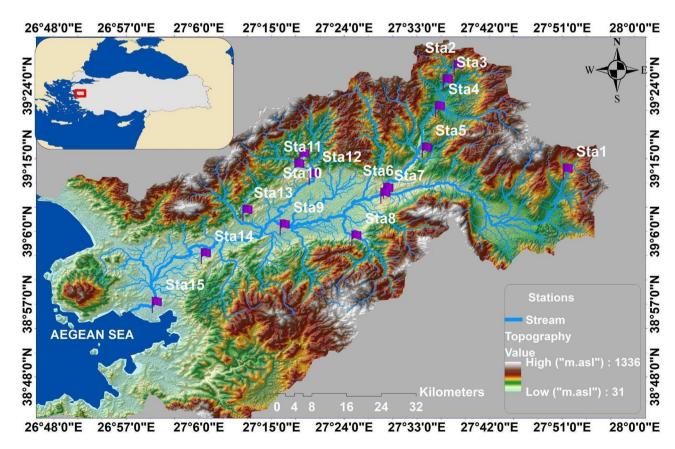
non-native, 3 endemic and 11 native) belonging to 7 families<sup>36</sup> and includes *Luciobarbus lydianus* (Steindachner, 1896) which has recently been treated as a synonym of Greek barbel *Luciobarbus graecus* (Steindachner, 1895)<sup>37</sup>. Among the species listed above, European eel *Anguilla anguilla* (Linnaeus, 1758) (Critically Endangered)<sup>38</sup>, *Alburnus attalus* (Endangered)<sup>39</sup>, and *Chondrostoma holmwoodii* (Boulenger, 1896) (Vulnerable)<sup>40</sup> are classified as threatened species as listed in the IUCN red list, while on the other hand, *P. parva, Carassius gibelio*, the Big-Scale Sand-Smelt *Atherina boyeri* Risso, 1810 and *Gambusia holbrooki* as least concern, non-native species in the river catchment. Past taxonomic ambiguity in the grouping of species (e.g. the listing of Black Sea chub *Petroleuciscus borysthenicus* (Boulenger, 1896) and European bitterling *Rhodeus amarus* (Bloch, 1782) under the family Cyprinidae<sup>36</sup> and some species having had recent name-changes (e.g. the synonymy of *Luciobarbus lydianus* with *L. graecus* as suggested<sup>37</sup>, further necessitate an updated taxonomic assessment of the system.

### Data collection.

In total, 15 sampling sites (4 lentic and 11 lotic) were selected (Fig. 1; Supplementary Table S1). Each site was sampled four times (once per season), conducted between October 2017 and July 2018. During the biological sampling process, the physicochemical properties (temperature, pH, dissolved oxygen, conductivity, salinity) of the water were determined in situ using a WTW Multi 3430 measuring probe (Supplementary Table S2). Environmental parameters (e.g. pH, dissolved oxygen, temperature) were measured in situ at each station. Although exact measurement times varied slightly due to field logistics, sampling followed a fixed station order resulting in each site being sampled at approximately the same time of day across seasons, typically between late morning and early afternoon, to minimise diel variation. In fish sampling, a 'Samus 725 G' model electro shocker was utilised in lotic habitats, while multi-mesh gill-nets (10-20-30-40-50 mm) conforming to the 'TS EN 14757 Water Quality' standard were employed in lentic habitats. To calculate abundance, catch per unit effort (CPUE) was determined as the number of fish captured per unit of cumulative fishing time. Following the sampling process, the fish were euthanised using an overdose of phenoxyethanol (1 ml/L) and then fixed in 4% formaldehyde. Upon arrival at the laboratory, samples were identified the species level<sup>36,41</sup>. The identified specimens were then labelled and catalogued in the Inland Fish Section of the Ege University Fisheries Faculty Collection (ESFM).

### **Environmental modeling**

Kernel density estimations (KDE) were applied to describe the characteristics of physicochemical parameters in the study region. Kernel density estimation constructs a smooth density surface by placing a kernel function at



**Fig. 1**. Basin topography and geographic location of the sampling sites (numbered purple flags) in the Bakırçay River within Western Anatolia (Türkiye). The river flows from west to east and enters into the Aegean Sea near station 15. The map was created with ArcGIS Pro 3.4.

each data point and summing their contributions, with the bandwidth controlling the degree of smoothing and the spatial variation in the estimated density. For this, each point was fitted with a continuous, smoothly curved surface with the highest value at its location. When the distance from the point increases, this value gradually decreases, eventually tapering off to zero when the search radius is equal to that specified<sup>42,43</sup>. We performed KDE based on the seasonal average of each physicochemical parameter. ArcGIS Pro version 3.4 was used for all these analyses (https://www.esri.com/en-us/home).

### Ecological niche model

In order to calculate the individual contributions of physicochemical variables to the distribution of species, we used the BIOMOD2 package<sup>44</sup>, implementing model simulations including 'GLM', 'GBM', 'GAM', 'CTA', 'ANN', 'SRE', 'FDA', 'MARS', 'RF', 'MAXENT', and 'MAXNET'<sup>44,45</sup>. In order to evaluate the models, we used the area under the curve (AUC) and the true skill statistic (TSS). AUC values range between 0 and 1, with 1 indicating 100% accuracy, and 0.5 indicating only partial predictive discrimination<sup>46</sup>. Similarly, the TSS values range from 0 to 1, with higher values indicating higher predictive ability, and values below 0.2 showing no predictive ability (TSS -0.2)<sup>45,47</sup>. Single models with AUC and TSS values below 0.7 were excluded from the final model<sup>45</sup>.

### Statistical analyses.

An abundance-based distance matrix of the sampled communities was built from each sampled site using the *vegdist* function of the R package vegan<sup>48</sup>. Then, we used a two-directional model selection to identify relevant predictors of community compositions using the *step* function. This approach identified pH and stream (i.e. strahler) order to shape community compositions (Supplementary Table S3). Then, a Canonical Analysis of Principal Coordinates (CAP) for factors whose levels were found to be significantly different was applied, thus identifying the variables contributing more consistently in differentiating the levels. Spearman correlations for each variable with the first CAP axis, the only one found informative in differentiating community compositions, are reported. PERMANOVA and CAP were performed using the *adonis2* and *capscale* function of the vegan R package, respectively<sup>49</sup>. For all tests, the level of significance under which the null hypothesis was rejected was  $\alpha = 0.05$ . Additionally, we used a Permutational Analysis of Variance (PERMANOVA; 2 orthogonal fixed factors: "pH", and "Stream Order" [1, 2, 3, 4]; sums of squares: type III, partial; permutation of residuals under a reduced model) to test if the community compositions differ according to the pH gradient or Stream Order.

To describe the fish communities of the Bakırçay River, we computed the total number of observed species (i.e. species richness), Pielou's evenness, and the Shannon-Wiener diversity index for each site using the vegan R package<sup>49</sup>. We then performed a series of linear mixed models (LMMs) using a space-for time approach<sup>50</sup> to investigate spatial patterns (i.e. as a function of longitude and latitude) in the observed species richness and community composition (using Pielou's evenness and the Shannon-Wiener diversity index). For this, we used the *lmer* function of the R package lme4<sup>51</sup>. Then, to investigate seasonal differences in the identified species richness across space (longitude and latitude) and the previously identified factors "pH" and "Stream Order" for samples collected in every season independently, we used a series of generalised linear models using the *glm* function of the R package lme4<sup>51</sup>.

### **Legal permissions**

All necessary permits for field sampling were obtained from the General Directorate of Fisheries and Aquaculture, Ministry of Food, Agriculture and Livestock of the Republic of Türkiye (dated 07/04/2017, reference number 67852565-140.03.03-E828075), and the General Directorate of Nature Conservation and National Parks, Ministry of Forestry and Water Affairs (dated 27/04/2017, reference number 72784983-488.04-95616).

### Results

### Fish composition of Bakırçay river drainage

Overall, the study identified 17 species belonging to ten families (Acheilognathidae, Anguillidae, Atherinidae, Cobitidae, Cyprinidae, Leuciscidae, Nemacheilidae, Gobiidae, Gobionidae and Poeciliidae; Table 1). Of these 17 species, six were categorised as regionally endemic and five as native with most fish belonging to the Cyprinidae (five species) and Leuciscidae (four species) families (Table 1). Among these species, we identified six non-native species (*Atherina boyeri, Carassius gibelio*, Common carp *Cyprinus carpio* Linnaeus, 1758, *Gambusia holbrooki*, Caucasian dwarf goby *Knipowitschia caucasica* (Berg, 1916) and *Pseudorasbora parva*). Total fish abundance varied among sampling stations, with Büyükdere-Yağcılı Creek junction (Sta. 4), Yağcılı Creek (Sta. 6), and İlyasdere (Sta. 12) exhibiting the highest abundances, while Çaltıkoru reservoir (Sta. 11), the river mainstay (Sta. 7), and Sevişler reservoir (Sta. 5) had the lowest individual abundances. The six non-native species made up 14.53% of individual fishes (species range 0.03–12.12%), the six regionally endemic fishes 43.39% (range of 0.67–14.08%) and native species contributed the remaining 42.08% of fishes (Supplementary Table S4).

By number of sites, the most common species was the endangered and regionally endemic *Alburnus attalus*, whereas the non-native *C. carpio*, *G. holbrooki*, *A. boyeri*, and *K. caucasica* were found in only one location each (Supplementary Table S4). Considering both the number of sites present and the local abundance within each, regionally endemic species were more numerous than non-native species (Table 1; Supplementary Table S4).

### Data analyses

Investigating the drivers of community composition, the CAP1 was found to be significant (p = 0.002; squared canonical correlation of  $\delta 1 = 0.736$ ), separating communities by the combination of factor "pH" and "Stream Order" (Fig. 2a). Additionally, the CAP identified a high degree of overlap with no significant differences in community composition across seasons (p > 0.1; Fig. 2b). Linear mixed models found no significant patterns for species richness, Pielou's evenness and the Shannon-Wiener diversity index (p > 0.05), but there was a consistent

Species	IUCN Status	<b>Ecological Status</b>
Acheilognathidae	•	
Rhodeus amarus (Bloch, 1782)	LC	Native
Anguillidae		
Anguilla anguilla (Linnaeus, 1758)	CR	Native
Cobitidae		
Cobitis fahireae Erk'akan, Atalay-Ekmekçi & Nalbant, 1998	LC	Native
Cyprinidae		
Barbus pergamonensis Karaman, 1971	LC	Regionally Endemic
Capoeta bergamae Karaman, 1969	NT	Regionally Endemic
Carassius gibelio (Bloch, 1782)	LC	Non-native
Cyprinus carpio Linnaeus, 1758	LC	Non-native
Luciobarbus graecus (Steindachner, 1895)	LC	Native
Leuciscidae		
Alburnus attalus Özuluğ & Freyhof, 2007	EN	Regionally Endemic
Chondrostoma holmwoodii (Boulenger, 1896)	VU	Regionally Endemic
Petroleuciscus smyrnaeus (Boulenger, 1896)	LC	Regionally Endemic
Squalius fellowesii (Gunther, 1868)	LC	Native
Nemacheilidae		
Oxynoemacheilus theophilii Stoumboudi, Kottelat & Barbieri, 2006	LC	Regionally Endemic
Atherinidae		
Atherina boyeri Risso, 1810	LC	Non-native
Gobiidae		
Knipowitschia caucasica (Berg 1916)	LC	Non-native
Gobionidae		•
Pseudorasbora parva (Temminck & Schlegel, 1846)	LC	Non-native
Poeciliidae		
Gambusia holbrooki (Baird & Girard, 1853)	LC	Non-native

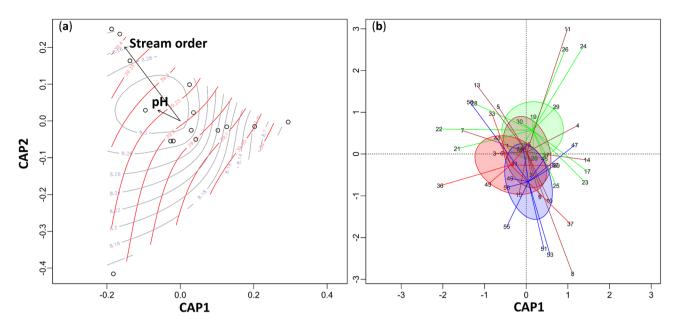
**Table 1**. The species collected in this study. Species are grouped by family and details are also provided of the current IUCN status category (LC: least concern, CR: critically endangered, NT: near threatened, EN: endangered, VU: vulnerable)<sup>52</sup> and ecological status category for each.

decrease in richness with longitude and an increase with latitude (Fig. 3). The initial model selection process found pH, longitude and stream order best defined species communities with additional analyses confirming pH and stream order as the most significant drivers of community composition (PERMANOVA pH: p = 0.009; stream Order: p = 0.038).

Generalised linear models additionally identified a consistent – albeit non-significant – decrease in species richness with increasing longitude and a contrasting increase with latitude across all seasons (Fig. 4a, b). Richness also declined in all seasons (except winter) with an increase in pH (Fig. 4c), whereas in spring and summer richness increased yet declined in autumn and winter with increasing stream order (Fig. 4d). Finally, investigating the spatial and seasonal variations in physicochemical predictors of fish communities (e.g. temperature, pH), the KDA analysis revealed that each parameter varies seasonally (Supplementary Fig. 1). A number of spatial seasonal trends were also identified, namely: (1) Temperature was low in the summer months within the lower basin, while it was high in the winter within the lower basin; (2) dissolved oxygen was low in the lower basin in winter and in the spring in the middle basin; and (3) pH was at its lowest level in winter within the lower basin (Fig. 5).

### Discussion

This study aimed to assess the fish fauna of the Bakırçay River drainage, examining seasonal distribution differences and ecological changes, thereby providing a biodiversity baseline for future studies in the region. The present study identified 17 species belonging to ten families (Table 1), with additional families identified within the Bakırçay River than identified by İlhan et al. 36 (17 species from seven families) and also contrasting with other assessments. Notably, species belonging to the Mugilidae family and *Salaria pavo*, previously reported 32,53, were absent in our study, possibly due to their marine origins, migratory natureand potential hindrance by anthropogenically created obstacles. Seasonal and spatial differences in fish distributions demonstrate the importance of temporal sampling and we recognise that variations in study data likely reflect differences in species abundance, catchability and taxonomy. Nevertheless, the study data identify the presence of Anatolian endemic species including *A. attalus* (endangered) and *C. holmwoodii* (vulnerable), demonstrating the conservation importance of the region and the need for management.



**Fig. 2.** Ordination of species richness across sites with environmental fitting. (a) CAP plot showing the direction and influence of environmental variables (pH and stream order) on species composition across sampling sites. (b) CAP plot illustrating seasonal overlap in community structure, indicating no significant differences among seasons. CAP: Canonical Analysis of Principal Coordinates. Arrows represent the strength and direction of environmental correlations.

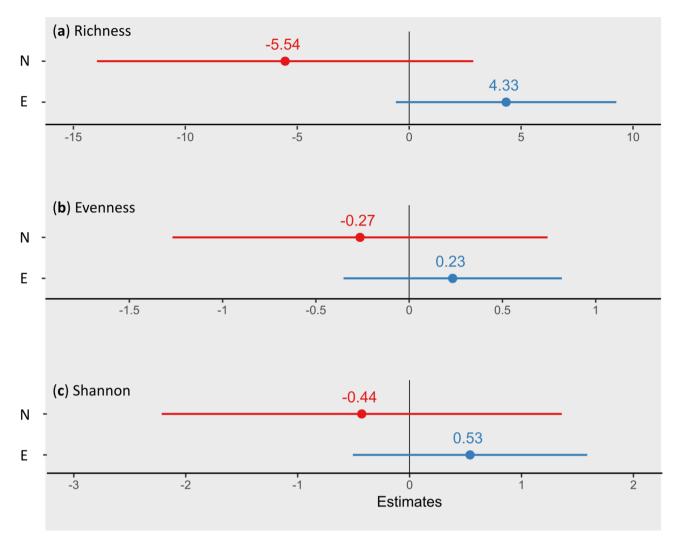
### Management implications

Our findings, while showing no significant trends in species richness across the lower and upper regions, do indicate some clear patterns following differences in e.g. pH that can (re-)structure fish communities. Such changes can occur likely by altering habitat suitability or physiological tolerances for certain species. For instance, increasingly alkaline conditions can favor tolerant non-native species, while a slight acidification could limit the distribution of sensitive native/endemic species<sup>54,55</sup>. Similarly, the significant effect of stream order indicates that habitat complexity and flow dynamics, which change with stream size, play a central role in determining community composition 56,57. Lower-order streams may support smaller-bodied, habitat-specialist species, while higher-order sections may favor generalist or migratory species due to broader habitat availability<sup>58,59</sup>. Although seasonal differences in species richness were observed across sampling stations, these were not statistically significant in terms of community composition (CAP, p > 0.1), suggesting that richness may vary without corresponding shifts in overall assemblage structure. Given the absence of migratory species in the system, it is likely that some species were not detected in all seasons due to temporal changes in environmental conditions (e.g. high flow in winter, drying in summer<sup>33,36</sup> affecting detectability or local presence. Therefore, seasonal differences are better interpreted as variability in species presence or richness rather than turnover in overall community structure. Although some predictors such as latitude and seasonal variation did not show significant effects on species richness, the observed directional trends (e.g. richness increasing with latitude) suggest that broader-scale environmental gradients and unmeasured variables (e.g. habitat structure, local hydrology) could still be influencing fish communities. This highlights the need for long-term, more spatially comprehensive monitoring and multi-seasonal monitoring to distinguish true ecological shifts from sampling-related variability and detect subtler ecological changes.

However, it is important to acknowledge that our inferences regarding fish assemblages are based on seasonal catch data, which, while informative, may not capture the full complexity of actual community structure. Factors such as gear selectivity, species-specific detectability, habitat accessibility, and temporal variability—including fluctuations in environmental conditions across and within seasons—can all influence catch rates and species representation in our samples. As such, our results provide valuable insights into spatial and seasonal patterns in fish occurrences, but may underestimate the presence of less detectable, cryptic, or migratory species, and should be interpreted with these methodological limitations in mind.

### Additional recommendations for conservation

Regarding anthropogenic impacts, it is crucial to understand how the river is utilised and the specific species targeted by local communities, whether for consumption, recreation, or other uses<sup>60</sup>. Almost the entire Bakırçay River drainage is strongly anthropogenically modified. The five dams on the river drainage are important factors directly affecting the riverine fishes and limiting their habitat<sup>61</sup>. The Bakırçay River has been straightened and the likelihood of flooding the valley floor is decreased by the dams that run parallel to its path. On the valley floor, smaller natural watercourses have been replaced by drainage and irrigation channels<sup>62</sup>. One of the most important threats to the water quality of Bakırçay River drainage is the presence of the Soma Thermal Power Plant<sup>51</sup> as a point source of pollution. In addition, the discharge of wastewater from industrial establishments,

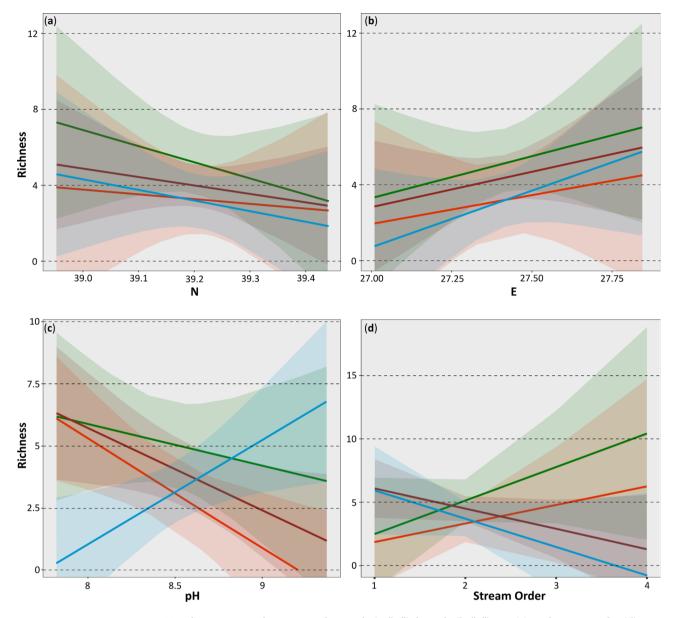


**Fig. 3.** Effects of spatial gradients on diversity metrics. Direction and strength of spatial trends based on geographical coordinates: (a) species richness, (b) Pielou's evenness, and (c) Shannon diversity. Red arrows indicate the influence of longitude ("N" axis) and blue arrows indicate the influence of latitude ("E" axis) on each diversity metric. Arrows represent the directionality of spatial correlation in multivariate space.

olive oil enterprises in the region, and the increase in fertilisers and pesticides used in agricultural areas likely contribute to riverine pollution<sup>63</sup>. Finally, there is also widespread metal and sediment pollution caused by mining actions<sup>64</sup>. These sources suggest widespread and increasing pollution as a threat within the basin, likely exacerbated by high evaporation rates and modified flows.

Moreover, the introduction of non-native species like the Rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) in the Sevişler and Kestel reservoirs, among other non-native species, have likely impacted the natural fauna, causing unforeseeable and yet unquantified costs<sup>12,65</sup>. Apart from *O. mykiss*, we specifically noted four non-native species in our study: *Gambusia holbrooki*, *Atherina boyeri*, *Carassius gibelio* and *P. parva*, underscoring the growing concern about non-native species in the river basin and their potential effects on the ecosystem. However, considering the reproductive and invasive potentials of the species listed here, they may become dominant in the environment following environmental or climatic changes. Non-native species such as *C. gibelio* and *A. boyeri*, which were not seen in river drainages until the early 2000s, have begun to appear in the region within a short period of about 20 years; thus are spreading and deemed as invasive. Considering that human-mediated transport has been occurring much more rapidly in recent years, the entry of new non-native species into the basin is also likely<sup>36</sup>. Therefore, it is important to closely monitor the natural fish populations of the basin, which host numerous endemic species, to ensure their sustainability.

Numerous species endemic to the Anatolian region, including Aegean chub Squalius fellowesii, Anatolian stone loach Oxynoemacheilus theophilii, Aegean scraper Capoeta bergamae, Anatolian barbel Barbus pergamonensis, Alburnus attalus, and Aegean spined loach Cobitis fahireae, can be found in the Bakırçay River<sup>36</sup>. Three IUCN Red List species; Chondrostoma holmwoodii (VU), A. attalus (EN), and Anguilla anguilla (CR) can also be found in the river but are threatened due to widespread pollution from various sources<sup>36</sup>. Moreover, A. anguilla is the most relevant species for the regional fisheries from an economic standpoint but is endangered due to overfishing and



**Fig. 4**. Trends in species richness across longitude ( $\mathbf{a}$ ; "N"), latitude ( $\mathbf{b}$ ; "E"), pH ( $\mathbf{c}$ ), and Stream Order ( $\mathbf{d}$ ) broken down by season (spring: green; summer: red; autumn: brown; winter: blue).

environmental degradation<sup>36,66</sup>. The river's biodiversity should be protected and subject to regular (i.e. annual) monitoring of fish distributions and abundances (both native and invasive species) to track community changes. To address the unique threats posed by pollution and habitat destruction, however, effective management strategies should be developed and put into practice<sup>67</sup>. These measures could include introducing sustainable fishing methods, strengthening habitat connectivity to support the migration of economically significant and endangered species, and improving water quality through pollution control measures. In addition, regional research organisations and agencies should collaboratively develop and implement regulations targeted at lowering pollution coming from domestic, industrial, and agricultural sources. Prioritising restoration initiatives will help restore damaged ecosystems, manage invasive species and preserve the integrity of the basin.

### Conclusion

This study examined spatial and seasonal patterns of fish abundance and diversity in an anthropogenically impacted river, revealing relatively high biodiversity—including native, endemic, and non-native species. Importantly, our results indicate that spatial and seasonal patterns in species occurrences and catch rates are strongly associated with gradients in physicochemical variables such as pH and stream order. While we observed differences in the relative occurrences of native and non-native species across sites and seasons, the data do not support robust conclusions regarding long-term changes in fish community structure. Moreover, our results identified pH and stream order as significant predictors of fish assemblage structure, highlighting the importance of these environmental parameters in shaping community composition. Furthermore, the study

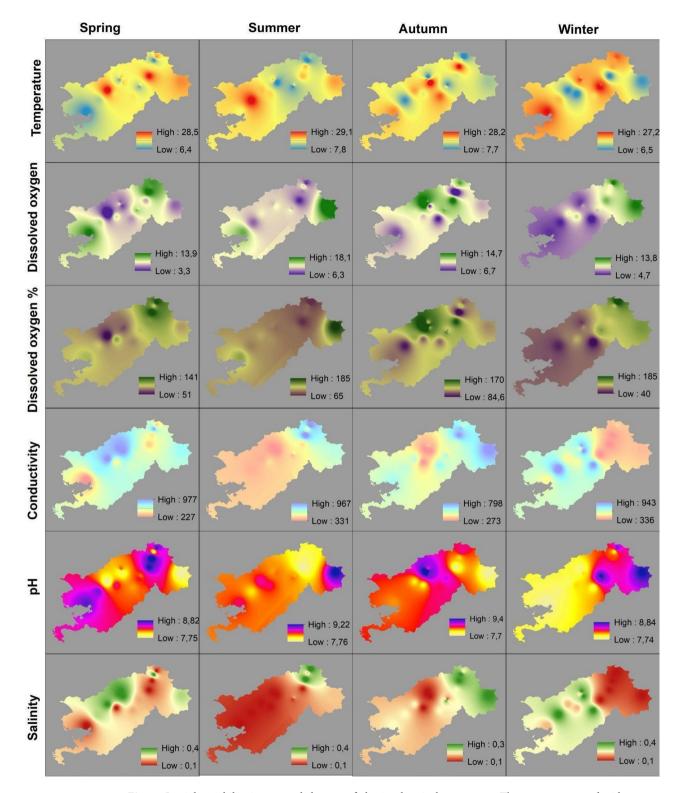


Fig. 5. Spatial variability in seasonal changes of physicochemical parameters. The map was created with ArcGIS Pro 3.4.

observed a marked shift in the ratio between native and non-native species over time, with non-natives becoming increasingly prominent in areas subject to greater anthropogenic pressure. We recommend regular monitoring and targeted mitigation of pollution in the Bakırçay River drainage, as ongoing anthropogenic pressures from settlements, agriculture, and industry are already impacting water quality and ecosystem health and are likely to intensify. Continuous monitoring over space and time is crucial to track these effects and future work should further explore how physicochemical and habitat gradients drive species distributions and abundance. Steps should be taken to increase ecosystem/community resilience and conserve endemic species and biodiversity by, for example, reducing industrial waste inputs and particularly during times when fishes may be most sensitive (e.g. spawning, migration etc.).

### Data availability

The data that support the findings of this study are available from the first author (Irmak Kurtul) upon reasonable request.

Received: 29 December 2024; Accepted: 1 August 2025

Published online: 13 August 2025

### References

- 1. Parvez, M. T. et al. Fish diversity decline in the lower gangetic plains: a victim of multiple stressors. *Biodivers. Conserv.* **32**, 341–362. https://doi.org/10.1007/s10531-022-02505-7 (2023).
- 2. Carosi, A., Lorenzoni, F. & Lorenzoni, M. Synergistic effects of climate change and alien fish invasions in freshwater ecosystems: a review. Fishes 8 (10), 486. https://doi.org/10.3390/fishes8100486 (2023).
- 3. Ruaro, R. et al. Non-native fish species are related to the loss of ecological integrity in Neotropical streams: a multimetric approach. *Hydrobiologia* 817, 413–430. https://doi.org/10.1007/s10750-018-3542-y (2018).
- 4. Albert, J. S. et al. Scientists' warning to humanity on the freshwater biodiversity crisis. *Ambio* **50** (1), 85–94. https://doi.org/10.100 7/s13280-020-01318-8 (2021).
- 5. Cantonati, M. et al. Characteristics, main impacts, and stewardship of natural and artificial freshwater environments: consequences for biodiversity conservation. *Water* 12 (1), 260. https://doi.org/10.3390/w12010260 (2020).
- 6. Byers, J. E. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos* **97** (3), 449–458. https://doi.org/10.1034/j.1600-0706.2002.970316.x (2002).
- 7. Fedorenkova, A., Vonk, J. A., Breure, A. M., Hendriks, A. J. & Leuven, R. S. Tolerance of native and non-native fish species to chemical stress: a case study for the river rhine. *Aquat. Invasions.* 8, 231–241. https://doi.org/10.3391/ai.2013.8.2.10 (2013).
- 8. Paker, H. Politicizing the Environment: the Ecological Crisis of Turkey. Turkey in Transition: Politics, Society and Foreign Policy (Peter Lang. 2020).
- 9. Giannetto, D. & Innal, D. Status of endemic freshwater fish fauna inhabiting major lakes of Turkey under the threats of climate change and anthropogenic disturbances: A review. *Water* 13 (11), 1534. https://doi.org/10.3390/w13111534 (2021).
- Freyhof, J., Kaya, C. & Ali, A. A critical checklist of the inland fishes native to the Euphrates and Tigris drainages. In: (ed Jawad, L. A.) Tigris and Euphrates Rivers: their Environment from Headwaters to Mouth, Aquatic Ecology Series, 11 (Springer, Cham; https://doi.org/10.1007/978-3-030-57570-0\_35 (2021).
- 11. Çevik, C. et al. A review of plastic pollution in aquatic ecosystems of Turkey. *Environ. Sci. Pollut Res.* **29** (21), 26230–26249. https://doi.org/10.1007/s11356-021-17648-3 (2022).
- 12. Tarkan, A. S. et al. Economic costs of Non-Native species in türkiye: A first National synthesis. *J. Environ. Manag.* 358, 120779. https://doi.org/10.1016/j.jenvman.2024.120779 (2024).
- 13. Freyhof, J., Yoğurtçuoğlu, B., Jouladeh-Roudbar, A. & Kaya, C. *Handbook of Freshwater Fishes of West Asia* (DeGruyter, 2025). (in press).
- 14. Turan, D., Kaya, C., Ekmekçi, F. G. & Doğan, E. Three new species of *Alburnoides* (Teleostei: Cyprinidae) from euphrates river, Eastern anatolia, Turkey. *Zootaxa* 3754 (2), 101–116. https://doi.org/10.11646/zootaxa.3754.2.1 (2014).
- 15. Turan, D., Aksu, İ., Oral, M., Kaya, C. & Bayçelebi, E. Contribution to the trout of euphrates river, with description of a new species, and range extension of *Salmo munzuricus* (Salmoniformes, Salmonidae). *Zoosyst Evol.* **97** (2), 471–482. https://doi.org/10.3897/zs e.97.72181 (2021).
- 16. Turan, D., Kaya, C. & Kottelat, M. The trouts of the upper Kura and Aras rivers in turkey, with descriptions of three new species (Teleostei: Salmonidae). *Zootaxa* 5150 (1), 43–64. https://doi.org/10.11646/zootaxa.5150.1.2 (2022).
- 17. Freyhof, J. & Yoğurtçuoğlu, B. A proposal for a new generic structure of the killifish family aphaniidae, with the description of *Aphaniops teimorii* (Teleostei: Cyprinodontiformes). *Zootaxa* **4810** (3), 421–451. https://doi.org/10.11646/zootaxa.4810.3.2 (2020).
- 18. Kaya, C. Spirlins of the Southern black sea basin, with the description of a new species (Teleostei: Leuciscidae). Zootaxa 4763 (3), 419–428. https://doi.org/10.11646/zootaxa.4763.3.6 (2020).
- Kaya, C., Yoğurtçuoğlu, B. & Freyhof, J. Oxynoemacheilus amanos, a new nemacheilid loach from the Orontes river drainage (Teleostei: Nemacheilidae). Zootaxa 4938 (5), 559–570. https://doi.org/10.11646/zootaxa.4938.5.3 (2021).
- 20. Kaya, C., Kurtul, I., Aksu, İ., Oral, M. & Freyhof, J. Oxynoemacheilus chaboras, a new loach species from the euphrates drainage in Türkiye (Teleostei, Nemacheilidae). Zoosyst Evol. 100 (2), 457–468. https://doi.org/10.3897/zse.100.118612 (2024).
- 21. Docherty, C. Establishment, spread and impact of Prussian Carp (*Carassius gibelio*), a new invasive species in Western North America. MSc Thesis, University of Alberta, Edmonton, AB, Canada, 79. (2016).
- 22. Gozlan, R. E., Andreou, D., Asaeda, T., Beyer, K., Bouhadad, R., Burnard, D., Robert Britton, J. (2010). Pan-continental invasion of *Pseudorasbora parva*: towards a better understanding of freshwater fish invasions. *Fish and Fisheries*, 11(4), 315–340. https://doi.org/10.1111/j.1467-2979.2010.00361.x.
- 23. Srean, P. Understanding the Ecological Success of Two Worldwide Fish Invaders (Gambusia Holbrooki and Gambusia affinis) (Universitat de Girona, 2015).
- 24. Su, G. et al. Human impacts on global freshwater fish biodiversity. *Science* 371 (6531), 835–838. https://doi.org/10.1126/science.a bd3369 (2021).
- 25. Ekardt, F. et al. Legally binding and ambitious biodiversity protection under the CBD, the global biodiversity framework, and human rights law. Environ. Sci. Eur. 35, 80. https://doi.org/10.1186/s12302-023-00786-5 (2023).
- Willis, K. J. et al. How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. *Philosophical Trans. Royal Soc. B: Biol. Sci.* 362 (1478), 175–187. https://doi.org/10.1098/rstb.2006.1977 (2007).
- 27. Tickner, D. et al. Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. *BioScience* **70** (4), 330–342. https://doi.org/10.1093/biosci/biaa002 (2020).
- 28. Yen, J. D. et al. Underlying trends confound estimates of fish population responses to river discharge. Freshw. Biol. 66 (9), 1799–1812. https://doi.org/10.1111/fwb.13793 (2021).
- 29. Danacıoğlu, Ş. Bakırçay Havzası'nda ekolojik risk karakterizasyonuna dayalı havza yönetimi. PhD Thesis, Balıkesir University. [In Turkish] (2017).
- 30. Partigöç, N. S. & Dinçer, C. The Multi-Disaster risk assessment: A-GIS based approach for Izmir City. *Int. J. Eng. Geosci.* 9 (1), 61–76. https://doi.org/10.26833/ijeg.1295657 (2024).
- Balık, S. Batı Anadolu Tatlısu Balıklarının Taksonomisi ve Ekolojik Özellikleri Üzerine Araştırmalar. PhD Thesis, Ege University (1974).

- 32. Kuru, M. et al. Türkiye'de Bulunan Sulak Alanların Ramsar Sözleşmesi Balık Kriterlerine Göre Değerlendirilmesi. T.C. Çevre Bakanlığı Çevre Koruma Genel Md (Projesi,, 2001). Kesin Rapor, 289 s, Ankara. [In Turkish].
- 33. Çoker, T. & Akyol, O. Çandarlı Körfezi (Ege Denizi) Balıkları. Türk Bilimsel Derlemeler Dergisi 5 (1), 5-9. [In Turkish] (2012).
- 34. Ekmekçi, F. G. & Kırankaya, Ş. G. Distribution of an invasive fish species, *Pseudorasbora parva* (Temminck & schlegel, 1846) in Turkey, *Turk. I. Zool.* 30 (3), 329–334 (2006).
- 35. Özuluğ, M. & Freyhof, J. Rediagnosis of four species of *Alburnus* from Turkey and description of two new species (Teleostei: Cyprinidae). *Ichthyol. Explor. Freshw.* **18** (3), 233–246 (2007).
- 36. İlhan, A., Sarı, H. M. & Kurtul, I. Bakırçay Nehri (Kuzey ege, Türkiye) Balık faunası [Fish fauna of Bakırçay Stream (North Eagean, Turkey)]. Ege J. Fish. Aquat. Sci. 37 (3), 309–312. https://doi.org/10.12714/egejfas.37.3.14 (2020).
- 37. Freyhof, J. & Yoğurtçuoğlu, B. Luciobarbus Lydianus and L. kottelati, two synonyms of L. graecus (Teleostei: Cyprinidae). Zootaxa 5415 (3), 466–476. https://doi.org/10.11646/zootaxa.5415.3.6 (2024).
- 38. Pike, C., Crook, V. & Gollock, M. Anguilla anguilla. The IUCN red list of threatened species 2020: e.T60344A152845178. (2020). h ttps://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T60344A152845178.en. Accessed on 04 June 2024.
- 39. Freyhof, J. Alburnus attalus. The IUCN red list of threatened species: e.T19018221A19222743. (2014). Accessed on 04 June 2024.
- Freyhof, J. Chondrostoma holmwoodii. The IUCN red list of threatened species: e.T4787A19006425. Accessed on 04 June 2024. 2014.
- 41. Güçlü, S. S. & Küçük, F. The ichthyofauna of Gediz river (Turkey): taxonomic and zoogeographic features. *Annu. Res. Rev. Biol.* **6** (3), 202–214 (2015).
- 42. Cantrell, D. L. et al. The use of kernel density Estimation with a bio-physical model provides a method to quantify connectivity among salmon farms: Spatial planning and management with epidemiological relevance. Front. Vet. Sci. 5, 269. https://doi.org/10.3389/fyets.2018.00269 (2018).
- 43. Aksu, S., Başkurt, S., Emiroğlu, Ö. & Tarkan, A. S. Establishment and range expansion of non-native fish species facilitated by hot springs: the case study from the upper Sakarya basin (NW, Turkey). *Oceanol. Hydrobiol. Stud.* 50 (3), 247–258. https://doi.org/10. 2478/oandhs-2021-0021 (2021).
- 44. Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M. B. BIOMOD-a platform for ensemble forecasting of species distributions. *Ecography* 32 (3), 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x (2009).
- 45. Emiroglu, Ö. et al. Predicting how climate change and globally invasive piscivorous fishes will interact to threaten populations of endemic fishes in a freshwater biodiversity hotspot. *Biol. Invasions.* 25 (6), 1907–1920. https://doi.org/10.1007/s10530-023-0301 6-4 (2023)
- 46. Ruiz-Navarro, A., Gillingham, P. K. & Britton, J. R. Predicting shifts in the climate space of freshwater fishes in great Britain due to climate change. *Biol. Conserv.* 203, 33–42. https://doi.org/10.1016/j.biocon.2016.08.021 (2016).
- 47. Lin, C. T. & Chiu, C. A. The relic trochodendron Aralioides Siebold & zucc. (Trochodendraceae) in taiwan: ensemble distribution modeling and climate change impacts. Forests 10 (1), 7. https://doi.org/10.3390/f10010007 (2019).
- 48. Oksanen, J. Constrained ordination: tutorial with R and vegan. R-packace Vegan. 1 (10), 1-9 (2012).
- 49. Oksanen, J. Vegan: an introduction to ordination. (2015).
- 50. Haubrock, P. J., Cuthbert, R. N. & Haase, P. Long-term trends and drivers of biological invasion in central European streams. *Sci. Total Environ.* 876, 162817. https://doi.org/10.1016/j.scitotenv.2023.162817 (2023).
- 51. Bates, D. et al. Package 'lme4'. Convergence 12 (1), 2 (2015).
- 52. IUCN [International Union for the Conservation of Nature]. IUCN Red List of threatened species. Version 2014.3. http://www.iucnredlist.org [20 February 2025].
- 53. Balık, S., Ustaoğlu, M. R. & Sarı, H. M. Kuzey Ege bölgesindeki Akarsuların faunası Üzerine Ilk Gözlemler. Su Ürünleri Derg. 16 (3–4), 289–299 (1999). [In Turkish].
- 54. Bell, D. T., Wilkins, C. F., van der Moezel, P. G. & Ward, S. C. Alkalinity tolerance of Woody species used in bauxite waste rehabilitation, Western Australia. *Restor. Ecol.* 1 (1), 51–58. https://doi.org/10.1111/j.1526-100X.1993.tb00008.x (1993).
- 55. Schindler, D. W. Effects of acid rain on freshwater ecosystems. Science 239 (4836), 149–157. https://doi.org/10.1126/science.239.4 836.149 (1988).
- 56. Soto, I. et al. Long-term trends in crayfish invasions across European rivers. Sci. Total Environ. 867, 161537 (2023).
- 57. Soto, I. et al. Tracking a killer shrimp: *Dikerogammarus villosus* invasion dynamics across Europe. *Divers. Distrib.* **29** (1), 157–172 (2023).
- Harrel, R. C., Davis, B. J. & Dorris, T. C. Stream order and species diversity of fishes in an intermittent Oklahoma stream. Amer Midl. Naturalist 428–436 (1967).
- 59. Stenger-Kovács, C., Tóth, L., Tóth, F., Hajnal, E. & Padisák, J. Stream order-dependent diversity metrics of epilithic diatom assemblages. *Hydrobiologia* 721, 67–75 (2014).
- 60. Best, J. Anthropogenic stresses on the world's big rivers. Nat. Geosci. 12 (1), 7-21. https://doi.org/10.1038/s41561-018-0262-x (2019).
- 61. Cooke, S. J., Paukert, C. & Hogan, Z. Endangered river fish: factors hindering conservation and restoration. *Endanger. Species Res.* 17 (3), 179–191. https://doi.org/10.3354/esr00426 (2012).
- 62. Schneider, S. H. F. Geoarchaeological Case Studies in the Bakırçay Valley Paleogeography and Human-environmental Interactions in the Chora of Pergamon in Western Turkey. PhD thesis. Freien Universität Berlin, 146 (2014).
- 63. Kaymakçı Başaran, A. Bakırçay deltası Kirlilik parametreleri ve Çandarlı Körfezi Ile Olan etkileşimi. Ege Üniversitesi Fen bilimleri enstitüsü (Doktora Tezi) 175 s. [In Turkish] (2004).
- Tomar, A. Toprak ve Su Kirliliği ve Su Havzalarının Korunması. TMMOB İzmir Kent Sempozyumu, 8–10 Ocak 2009, 333–345. [In Turkish] (2009).
- Ahmed, D. A. Recent advances in availability and synthesis of the economic costs of biological invasions. BioScience 73, 560–574. https://doi.org/10.1093/biosci/biad060 (2023).
- 66. Kurtul, I. et al. How fish populations in lake Bafa (Western Anatolia) respond to ecological shifts. Aquatic conservation. *Aquat. Conserv.: Mar. Freshw.* 34 (5), e4154. https://doi.org/10.1002/aqc.4154 (2024).
- Reid, A. J. et al. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biol. Rev. 94 (3), 849–873. https://doi.org/10.1111/brv.12480 (2019).

### Acknowledgements

We are grateful to the Republic of Türkiye Ministry of Agriculture and Forestry for the research legal permission. We would like to express our appreciation to the Ege University Scientific Research Project Commission, which supported this study (BAP-Project No: 16/SÜF/038). We thank TÜBITAK BIDEB (2219 Program), which supported Irmak Kurtul and Ali Serhan Tarkan with one-year scholarships during their post-doc research in the United Kingdom, and Cüneyt Kaya in Czech Republic. Phillip J. Haubrock was supported by the Marie Skłodowska-Curie Postdoctoral Fellowship HORIZON-MSCA-2022-PF-01 (Project DIRECT; Grant No. 101203662) within the European Union's Horizon 2022 research and innovation programme.

### **Author contributions**

Irmak Kurtul: Conceptualization, Methodology, Writing – review & editing, Data curation. Phillip J. Haubrock: Conceptualization, Methodology, Visualization, Writing – review & editing. Cüneyt Kaya: Writing – review & editing, Data curation. Sadi Aksu: Conceptualization, Methodology, Writing – original draft. Ali İlhan: Investigation, Data curation. Hasan Musa Sarı: Investigation, Data curation. Cem Aygen: Investigation, Data curation. Ismael Soto: Methodology, Visualization, Writing – review & editing. Ben Parker: Methodology, Visualization, Writing – review & editing, Supervision. Ali Serhan Tarkan: Conceptualization, Writing – review & editing, Supervision.

### **Declarations**

### Competing interests

The authors declare no competing interests.

### Additional information

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1038/s41598-025-14709-2.

**Correspondence** and requests for materials should be addressed to I.K. or C.K.

Reprints and permissions information is available at www.nature.com/reprints.

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

**Open Access** This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <a href="https://creativecommons.org/licenses/by-nc-nd/4.0/">https://creativecommons.org/licenses/by-nc-nd/4.0/</a>.

© The Author(s) 2025