Science of the Total Environment 925 (2024) 171718

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Exploring invasiveness and versatility of used microhabitats of the globally invasive *Gambusia holbrooki*

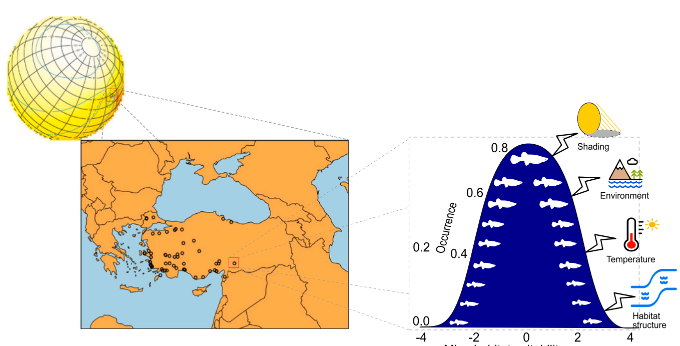
Irmak Kurtul[a,b,*,1], Ali Serhan Tarkan[b,c,d,**,1], Hasan Musa Sarı[a], Phillip J. Haubrock[e,f,g], Ismael Soto[f], Sadi Aksu[h], J. Robert Britton[b]

[a] *Marine and Inland Waters Sciences and Technology Department, Faculty of Fisheries, Ege University, İzmir, Türkiye*
[b] *Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Poole, Dorset, UK*
[c] *Department of Ecology and Vertebrate Zoology, Faculty of Biology and Environmental Protection, University of Lodz, Lodz, Poland*
[d] *Department of Basic Sciences, Faculty of Fisheries, Muğla Sıtkı Koçman University, Muğla, Türkiye*
[e] *Department of River Ecology and Conservation, Senckenberg Research Institute and Natural History Museum Frankfurt, Gelnhausen, Germany*
[f] *Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, University of South Bohemia in České Budějovice, Vodňany, Czech Republic*
[g] *CAMB, Center for Applied Mathematics and Bioinformatics, Gulf University for Science and Technology, Kuwait*
[h] *Vocational School of Health Services, Eskişehir Osmangazi University, Eskişehir, Türkiye*

HIGHLIGHTS

- Mosquitofish threatens endemic species globally.
- A high versatility is crucial for establishment and spread.
- Ecological versatility in microhabitat utilization increases invasiveness.
- Understanding microhabitat versatility can aid management.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Shuqing Zhao

Keywords:
Ecological valence
Microhabitat preference
Habitat management
Poeciliidae

ABSTRACT

Non-native species can lead to severe impacts on invaded ecosystems, including the decline of ecosystem function through deleterious impacts on species diversity. The successful establishment of non-native species in new environments is the first barrier a species must overcome, ultimately depending on its ability to either cope with or adapt to local site-specific conditions. Despite the widespread distribution and ecological consequences of many freshwater invaders, site-specific and climatic preferences are often unknown. This is also the case of the Eastern mosquitofish *Gambusia holbrooki*, a global invader considered as a pervasive threat to endemic species.

* Correspondence to: I. Kurtul, Marine and Inland Waters Sciences and Technology Department, Faculty of Fisheries, Ege University, İzmir, Türkiye.
** Correspondence to: A.S. Tarkan, Department of Ecology and Vertebrate Zoology, Faculty of Biology and Environmental Protection, University of Lodz, Lodz, Poland.
E-mail addresses: ikurtul@bournemouth.ac.uk (I. Kurtul), ali.serhan.tarkan@biol.uni.lodz.pl (A.S. Tarkan).
[1] These authors contributed equally.

https://doi.org/10.1016/j.scitotenv.2024.171718
Received 5 December 2023; Received in revised form 11 March 2024; Accepted 12 March 2024
Available online 13 March 2024
0048-9697/© 2024 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC license (http://creativecommons.org/licenses/by-nc/4.0/).

Here, we determined the ecological features and preferred site-specific conditions of *G. holbrooki* in Türkiye, which spans a wide range of diverse biogeographically distinct ecosystems by surveying populations from 130 localities in 2016 and 2017. *Gambusia holbrooki* were detected by hand-net in 48 of these sites (19 lotic, 29 lentic). It showed a preference for shallow waters with medium sized rocks, and abundances differed spatially across a latitudinal gradient and was influenced predominantly by variations in pH. The only other factors predicting its presence were low current velocities and gravel substrate, highlighting its ecological versatility in utilising a wide range of microhabitats. Bioclimatic models suggest that *G. holbrooki* is found in areas with a wide average annual temperature ranging from 10 to 20 °C, but with temperature not being a limiting factor to its invasion. *Gambusia holbrooki* shows a preference for xeric freshwater ecosystems and endorheic basins, as well as temperate coastal rivers, temperate upland rivers, temperate floodplain rivers and wetlands, and tropical and subtropical coastal rivers. These results, particularly the wide occurrence with only few limiting factors, emphasise the invasion potential of mosquitofish and should substantiate the need for localised invasive species management and conservation efforts, particularly in smaller or insular areas where mosquitofish and endemic fish species co-exist.

1. Introduction

Freshwater habitats are increasingly threatened by a myriad of anthropogenic activities, such as pollution, over-exploitation, and the introduction of non-native species (Friberg et al., 2011; Olden et al., 2022). Biological invasions, the intentional or accidental introductions of non-native species outside their natural bounds, often followed by their respective establishment and spread, threatens freshwater biodiversity through, for example, increased predation pressure and interspecific competitive interactions (Gozlan et al., 2010; Tarkan et al., 2015; Britton, 2023).

To develop an invasive population in a new environment, an introduced species must establish and, depending on definition, disperse and/or cause a measurable impact in the recipient ecosystem (Gozlan et al., 2010; Soto et al., 2024). Successful establishment is often accompanied by an adaptation to new environmental conditions that enable the exploitation of local resources (i.e. food, shelter; Fausch et al., 2001; Guo, 2006). Understanding how non-native species adapt to site-specific microhabitat conditions (small areas of habitat that differ in characteristics from the surrounding habitat) in novel environments can indicate the extent of their ecological versatility (Top et al., 2016). However, assessing the ecological requirements of the species in new habitat areas is limited to regions with very large and diverse climatic structures. It is therefore crucial to utilize bioclimatic and environmental data to determine the geographical areas where a potentially very harmful invasive species can occur (Elith et al., 2010; Pili et al., 2020).

Two of the most notorious invasive non-native species in freshwater ecosystems are the Eastern and Western mosquitofish *Gambusia holbrooki* and *Gambusia affinis*. These global invaders were originally introduced as biological control agents for mosquitoes in tropical and temperate areas, starting in the 1900s (Krumholz, 1948; Moyle, 2002; Walton et al., 2012), with negative consequences on native biodiversity reported (Pyke, 2008). Established populations of *G. holbrooki* are now present in at least 89 countries, with their invasion success generally attributed to high ecological and niche versatility, although these are rarely described (Feder et al., 1984; Kurtul et al., 2022). Mosquitofish invasions are often characterised by the formation of highly abundant populations early in the invasion process (Pyke, 2008), which impact the native fish fauna through asymmetric competitive interactions, predation of eggs and larvae, and aggressive interactions (i.e. fin-nipping) (Yoğurtçuoğlu and Ekmekçi, 2014; Yoğurtçuoğlu et al., 2020). Early studies indicated these invasive populations had trophic and habitat interactions with native fish species of the families Cyprinidae, Cyprinodontidae, and Gobiidae, which are all characterised by small body sizes and include a high number of endemic species (Howe et al., 1997; Ivantsoff and Aarn, 1999). However, a recent study by Santi et al. (2020) on wild-caught *G. holbrooki* from several European countries revealed a homogenous genetic structure, indicating a single introduction and showing genetic impoverishment compared to their native counterparts and phenotypic versatility. Accordingly, *G. holbrooki* is considered one of the '100 worst invasive species of the world' (Lowe et al., 2000; ISSG, 2013).

Across the invaded range, populations of *G. holbrooki* have established in lakes, ponds, lowland rivers, and swamps (Pyke, 2005). Within these differing ecosystems, they often occur in high abundances in the littoral zone, especially where there is dense vegetation (Lee and Burgess, 1980), as this provides refugia and foraging areas (Zarev, 2012). Their limnophilic characteristics mean populations are rarely found in high river flows (Meffe, 1984). They are however tolerant to low levels of oxygen (Cech et al., 1985), high salinity levels (Alcaraz and García-Berthou, 2007; Ruiz-Navarro et al., 2011), a wide pH gradient (Walton et al., 2012), and a broad range of water temperatures (4 to 42 °C; optimum between 31 and 35 °C; Pyke, 2005). In the Iberian Peninsula, temperature, elevation, and accumulated flow most strongly influenced *G. holbrooki* distribution, with the fish being more abundant downstream in warmer waters (Murphy et al., 2015). The progression of its invasions post-establishment (i.e. invasion dynamics in terms of abundance growth) were however strongly influenced by predominantly natural abiotic factors rather than biotic (e.g. predation pressure) and anthropogenic (e.g. exploitation) factors (Lloyd, 1987; Murphy et al., 2015). Species of the genus *Gambusia* sp. have been the subject of several past studies, including species distribution and ecological niche models (Jourdan et al., 2021). While the macro- and meso-habitat preferences of *G. holbrooki* have therefore been widely recognised (see Pyke, 2005), substantial knowledge gaps remain on their preferred site-specific conditions. Accordingly, understanding the relationship between microhabitat use (i.e. the use of a distinct, small-scale area offering unique environmental conditions) and local spatial distribution could provide important insights into mosquitofish invasion ecology (Pyke, 2008).

In Türkiye, *G. holbrooki* is considered as the first non-native fish intentionally introduced into freshwater ecosystems (Tarkan et al., 2015). It has since spread to six distinct geographic areas in the country, including a wide range of water bodies (Kurtul et al., 2022). The first official introduction of *G. holbrooki* dates back to 1960 into the Çukurova basin (Bahadıroğlu and Büyükçapar, 1997), where their release was for biocontrol of malaria (Geldiay and Balık, 1996). Although the species is widely distributed, information on key drivers contributing to its invasion success in Türkiye remain limited, including the species' microhabitat use and spatial distribution (e.g. Top et al., 2016). To fill this critical knowledge gap, we aimed to identify the microhabitat preferences and ecological niche models of *G. holbrooki*, using the diverse Turkish freshwaters as study area. Objectives were to (1) quantify the range of microhabitats used by *G. holbrooki* in Turkish freshwaters, (2) identify whether *G. holbrooki* expresses strong preferences for specific microhabitats, and (3) assess habitat characteristics that facilitate and inhibit the presence of *G. holbrooki* (4) determine the potential distribution of *G. holbrooki* in current and future climatic conditions. We predict that *G. holbrooki* populations use a wide range of microhabitats

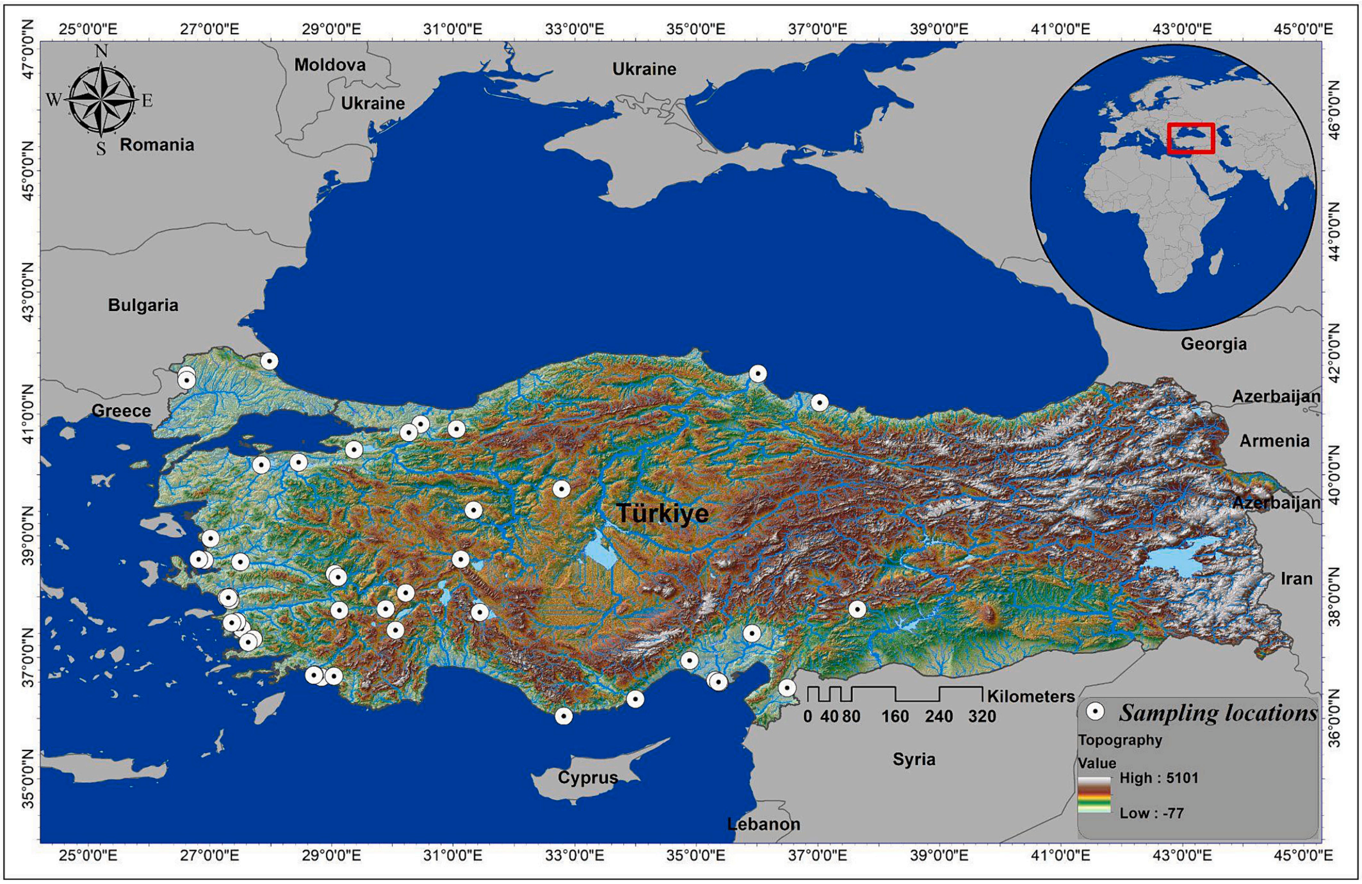


Fig. 1. Locations of sampling sites in this study where *Gambusia holbrooki* had been found (red squares) in Türkiye.

but show preferences for combinations of features while also demonstrating high tolerance to environmental factors, which also explain its widespread geographical distribution.

2. Materials and methods

2.1. Study area and sampling

Türkiye, a peninsula bordered by the sea on its north, west, and south sides, features xeric and endorheic basins. These basins supply freshwaters that include both lentic (such as ponds, lakes, and wetlands) and lotic (including temperate floodplain and coastal rivers) habitats (Tarkan et al., 2015). *Gambusia holbrooki* samples were collected across six geographical regions (Aegean, Mediterranean, Central Anatolia, Marmara Region, Black Sea Region, Southeastern Anatolia), covering all 11 ecoregions in Türkiye (Abell et al., 2008) (Table S1; Fig. 1).

Between April 2016 and November 2017, *G. holbrooki* was sampled from 130 sites across Türkiye. These sites were specifically chosen for their potential to reflect the primary water resources in the country and were identified based on their susceptibility to *Gambusia* invasions, as outlined by Kurtul (2018). The selection process aimed to cover all pertinent water resources and ecoregions comprehensively. For the sampling, a point abundance sampling (PAS) method was employed. This technique involves estimating species distribution and abundance by counting individuals at predetermined points (Nelva et al., 1979). Sampling was conducted using a micro-mesh hand-net, characterised by a net opening of 1.2 mˆ2 and a mesh size of 500 μ. Each site visit included multiple sweeps to ensure thorough sampling, varying between 16 and 20 sweeps, with the exception of one location (Berdan River) where only 12 sweeps were used, with similar sweeping times in each (i.e. 15–20 s; Table S1). This method was considered to provide reproducible and quantifiable samples of *G. holbrooki* and was efficient at capturing specimens across the species' entire size range (Copp, 1989). The sampled areas were located in the littoral zone, approximately 3 m from the bank in the case of lakes and covered a 300-m stretch in streams. Sampling was conducted in habitats accessible and shallower than 1.5 m in depth due to their accessibility. This is congruent with the known habitat use of *G. holbrooki* (Pyke, 2008) but may have influenced the study's results by preventing the sampling of deeper water habitats.

At each site, the following microhabitat variables were measured using a portable measuring device (WTW Multiparameter): water temperature (to 0.1 °C), dissolved oxygen (to 0.1 mg/L), pH, salinity (to 0.1 ‰) and conductivity (to 0.001 μS/cm). Additionally, the following physical characteristics were measured following Beyer et al. (2007) and Top et al. (2016, 2019): Depth (nearest cm), measured using a scaled pole; substratum composition (silt <0.06 cm, sand 0.06–0.2 cm, gravel >0.2–4 cm, gravel >4–6.4 cm, rock >6.4–10 cm, rock >10 cm); distance from the bank (DFB, nearest cm); distance from the nearest vegetation (DNV, nearest cm); percentage of woody structure (WM, ligneous material and roots), submerged aquatic vegetation (SAV); current velocity (measured using a pole as: no current when no ripple effect around the pole was visible; medium (0–5 $\mathrm{cm\,s^{-1}}$) if a gentle ripple effect around the pole was visible; fast (5–10 $\mathrm{cm\,s^{-1}}$) if an elevated ripple effect around the pole was visible); turbidity (assessed visually as: low, medium, high); light intensity (at the surface of water: shade or sun) (Table S2a, b).

In the laboratory, juvenile specimens were distinguished from adults by checking the gonopodium (Kurtul et al., 2022). All captured adults were euthanized (anaesthetic overdose: phenoxyethanol) (Misawa et al., 2014) and fixed in 4 % formaldehyde. *Gambusia holbrooki* was distinguished from its congener *G. affinis* by the species-specific characteristic of the former, involving the serration of the posterior edge of the joints

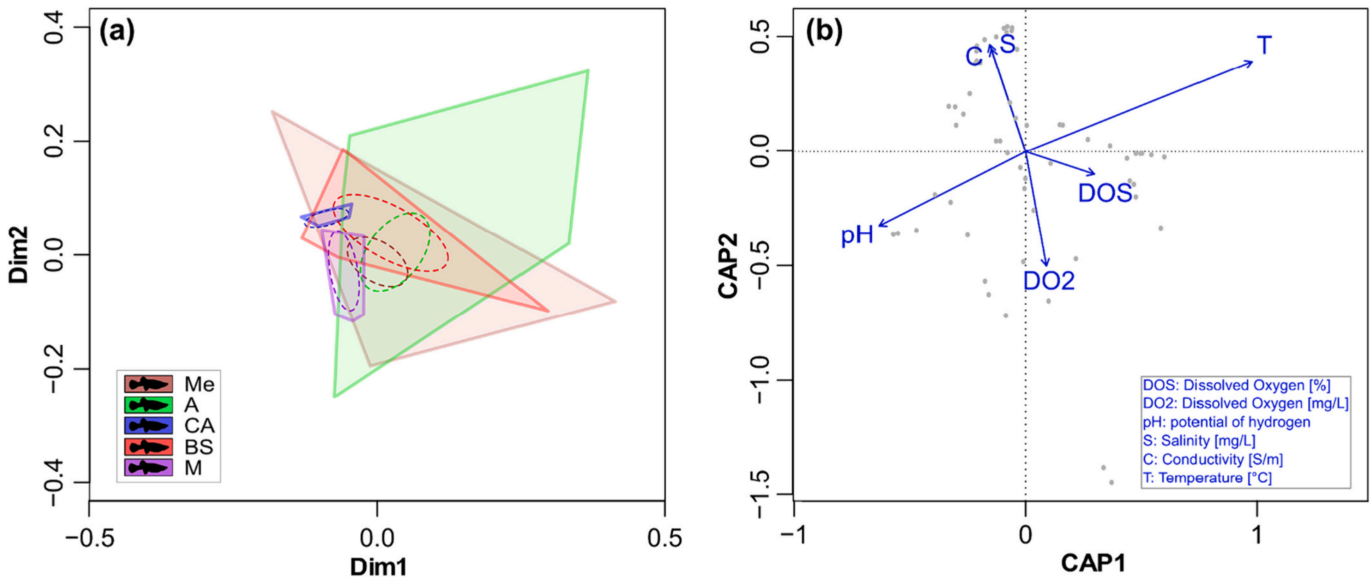


Fig. 2. Ordination of environmental conditions at the sampled sites by region (a) and trends in environmental factors over space (b) (Me: Mediterranean Region, A: Aegean Region, CA: Central Anatolia Region, BS: Black Sea Region, M: Marmara Region).

of the first elongate anal fin rays in males (Berg, 1965; Rauchenberger, 1989; Özuluğ et al., 2005).

2.2. Data analyses

2.2.1. Identifying patterns

The adult data from PAS were used in two subsequent ways: (*i*) as adult catch per unit effort (CPUE; number of adult *G. holbrooki* captured per cumulative fishing time; Table S3); and (*ii*) as presence/absence of adult *G. holbrooki*. We visually examined the distribution of CPUE values by generating a histogram, allowing assessments of the distribution pattern, revealing that the CPUE data for adult *G. holbrooki* was normally distributed, confirming the suitability of the statistical analyses. For (*i*), initial analyses tested the association between *G. holbrooki* CPUE and the environmental data (water temperature, pH, salinity, conductivity, dissolved oxygen) in a Permutational Multivariate Analysis of Variance (PERMANOVA; with 9999 permutations). In the analysis, *G. holbrooki* CPUE was the fixed factor, and the six environmental variables were independent variables using a Bray-Curtis dissimilarity measure. We then used a canonical discriminant analysis of the principal coordinates (CAP) using the *capscale* function in conjunction with environmental fitting relying on the *envfit* function of the vegan R package (Oksanen, 2012) to visualise particular patterns of spatial variation (based on each site's coordinates) in environmental variables. Based on a Spearman rank correlation coefficient with the first CAP axis (where $r > 0.3$) we then applied a PERMANOVA to test for significance.

For testing the presence/ absence of *G. holbrooki* (*ii*), the random forest algorithm of the *rfsrc* function of the randomForestSRC R package (Ishwaran et al., 2022) and a Generalized Additive Models (GAMs) using the *gam* function of the MASS R package was used (Ripley et al., 2013). The response variable was *G. holbrooki* presence/absence, with the predictor variables the same as for CPUE (excluding altitude, longitude, and latitude as these cannot predict microhabitat preference). Those predictors identified as most informative were then included in the GAMs using a binomial family (with logit link), with GAMs used as they allow the modelling of complex, non-linear relationships between environmental variables and species behaviour, so providing a more accurate representation of the underlying ecological processes at play (Wood et al., 2017). All analyses were performed in R version 4.2.3 (R Core Team, 2023).

2.2.2. Drivers of changes in CPUE

To identify the most important drivers of the Catch Per Unit Effort (CPUE), we ran a random forest using the *rfsrc* function of randomForestSRC R package. Variable importance in a Random Forest (RF) is determined by measuring the decrease in prediction accuracy when a particular variable is randomly permuted while keeping other variables unchanged (i.e. the higher the decrease in accuracy, the more important the variable that is considered). Here, we used a total of 2000 decision trees and five nodes. The out-of-bag (a measure of the goodness of fit of the model) reported a value of 0.1, while the out-of-bag performance error as measure of the model's predictive accuracy was 2.59.

To identify relevant predictors and to describe their effect on the occurrence of *G. holbrooki*, we considered the following variables: velocity, altitude, submerged aquatic vegetation, pH, longitude, substrata, latitude, water temperature, salinity, dissolved oxygen saturated, turbidity, distance from the bank, reeds, shade/sun, distance to nearest vegetation, depth, dissolved oxygen, specific conductivity, and woody material. Including those predictors identified as most informative, we ran GLMMs using the *glmmTMB* function of the glmmTMB R package (Magnusson et al., 2017), using a negative binomial family as being the most suitable choice for count data. To account for overdispersion and for potential interactions between site:environment (i.e. repeated measures), we included ecosystem type (lotic vs. lentic) as random effect.

2.2.3. Environmental variables and scenarios

Climate data for 1981–2010 encompassed 19 bioclimatic (bio1–19, temperature, precipitation) variables downloaded from CHELSA version 2.1 at a spatial resolution of 30 arc sec min (~1 km at the equator; Karger et al., 2017). Hydrological, physiographic, land cover and soil data were obtained from HYDROATLAS (Linke et al., 2019; Lehner et al., 2022) using the ArcGIS version 10.8.2 conversion toll feature. For this, we used the artificial intelligence model (MaxEnt; Maximum Entropy) which generates habitat projections through scenarios based on existing data (Phillips et al., 2017). These projections are designed to simulate various possible scenarios, such as shared socio-economic pathways (e.g., SSPs), climate change scenarios, or shifting land use patterns. The modelling process incorporates these scenarios to capture a range of environmental and socio-economic factors that may affect species distributions. As a result, this approach allows for the examinations of the potential distribution patterns for species, thereby informing conservation and management strategies.

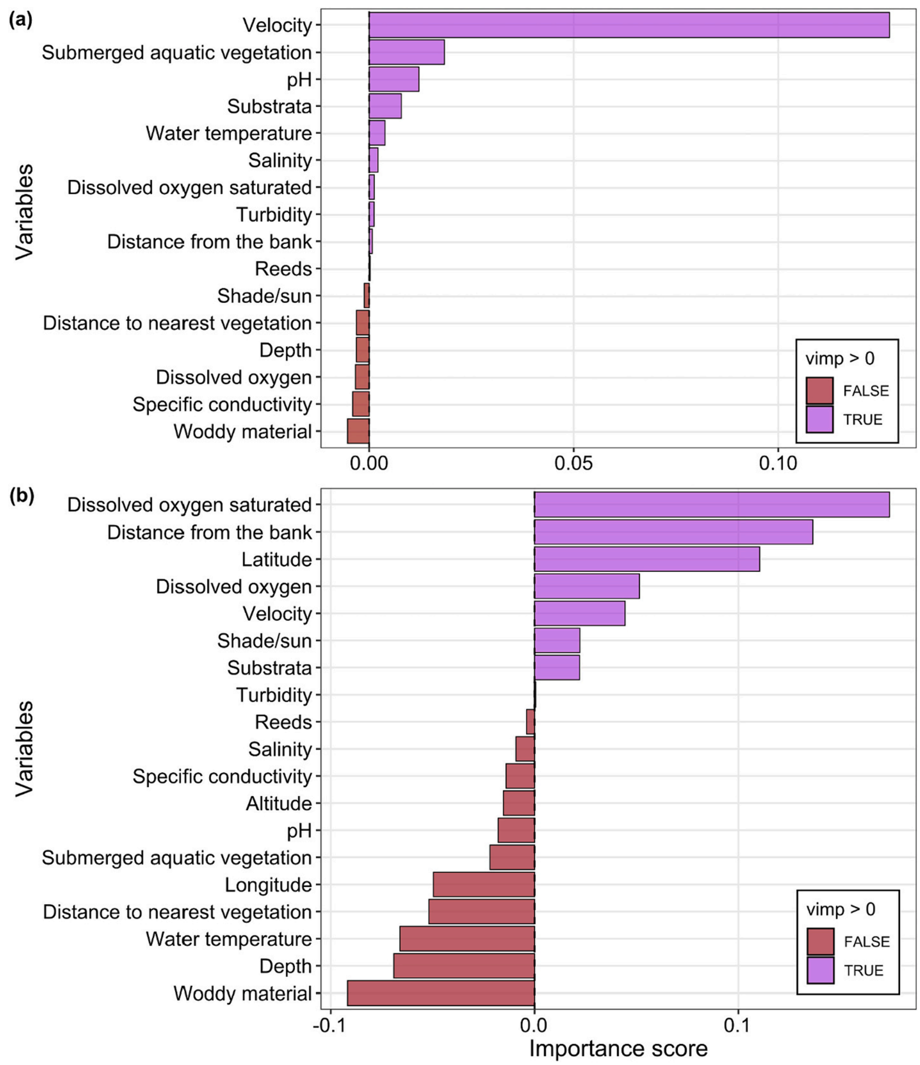


Fig. 3. Relative variable importance assessed by the applied random forest for site-specific conditions' relevant variables (a) and their influence on the CPUE for *Gambusia holbrooki* abundances (b), affecting the presence of *G. holbrooki*. The considered variables include velocity, altitude, submerged aquatic vegetation, pH, longitude, substrata, latitude, water temperature, salinity, dissolved oxygen saturation, turbidity, distance from the bank, reeds, shade/sun, distance to nearest vegetation, depth, dissolved oxygen, specific conductivity, and woody material. Purple indicates positive effects, while red indicates negative effects.

We specifically created a hydroclimatic model to determine which environmental conditions affect the species distribution. In the model, Türkiye was projected using the world distribution of the species, and it was aimed to determine the relationship between the environmental factors affecting the global distribution of the species and the micro-habitat distribution in Türkiye. The study also calculated Levins' B1 (inverse concentration) and B2 (uncertainty values) using ENMTools v1.3 (Warren et al., 2008). The Levins' B2 value ranges from 0 to 1, with values near 0 indicating narrow niches and near 1 indicating broader niches (Cai et al., 2021; Slatyer et al., 2013; Evans and Jacquemyn, 2022).

3. Results

Out of 130 sampling sites, *G. holbrooki* was recorded from 48 sites using hand-net sampling (CPUE: 0.33–8.1; Table S1). The maximum number of females sampled (as cumulative number across all sampled points) was 95 individuals in Kocacay River (CPUE: 8.1). The maximum total number of males sampled in a water body was 67 in Kocacay River (CPUE: 8.1). No males were captured in 9 water bodies (Table S1). No adults were found in Lake Kocagöl (Muğla), Sarıçay River, Söke-Milas water resources, and Bakırçay River. The minimum length of females was 13.67 mm (Sarısu River) and maximum length 57.21 mm (Pınarbaşı water resources), whereas for males, minimum length was 16.64 mm (Güllük Lagoon) and maximum length 32.94 mm (Gebekirse Lake). CPUE (individual/net sweep) ranged from 0.33 (ind./net) (Berdan River) to 5.95 (ind./net) (Miliç River) (Table S1).

3.1. *Identifying patterns*

Although we found no considerable spatial divergence between abundance values when separated by region (Fig. 2a), we found a considerable gradient in water temperatures (8.0–32.7 °C), pH (6.75–9.00), salinity (0.0–25.7 ‰), and conductivity (202–40,300 μS/cm) across the sites (Figs. 2b; S1). Although the performed CAP did not find any significant differences in predictors across regions or ecosystem types (both $p > 0.05$; Fig. 2a), it indicated a weak correlation ($r_{sp} \leq 0.7$) between all predictors over space (i.e. the first axis), suggesting spatially differentiating trends (Table S4a). The CAP also identified temperature and pH as significant factors in shaping the ordination ($p < 0.05$; Table S4b, c). The applied PERMANOVA identified that only pH differed significantly across samples ($F = 1.37$, $p < 0.05$; Table S4d).

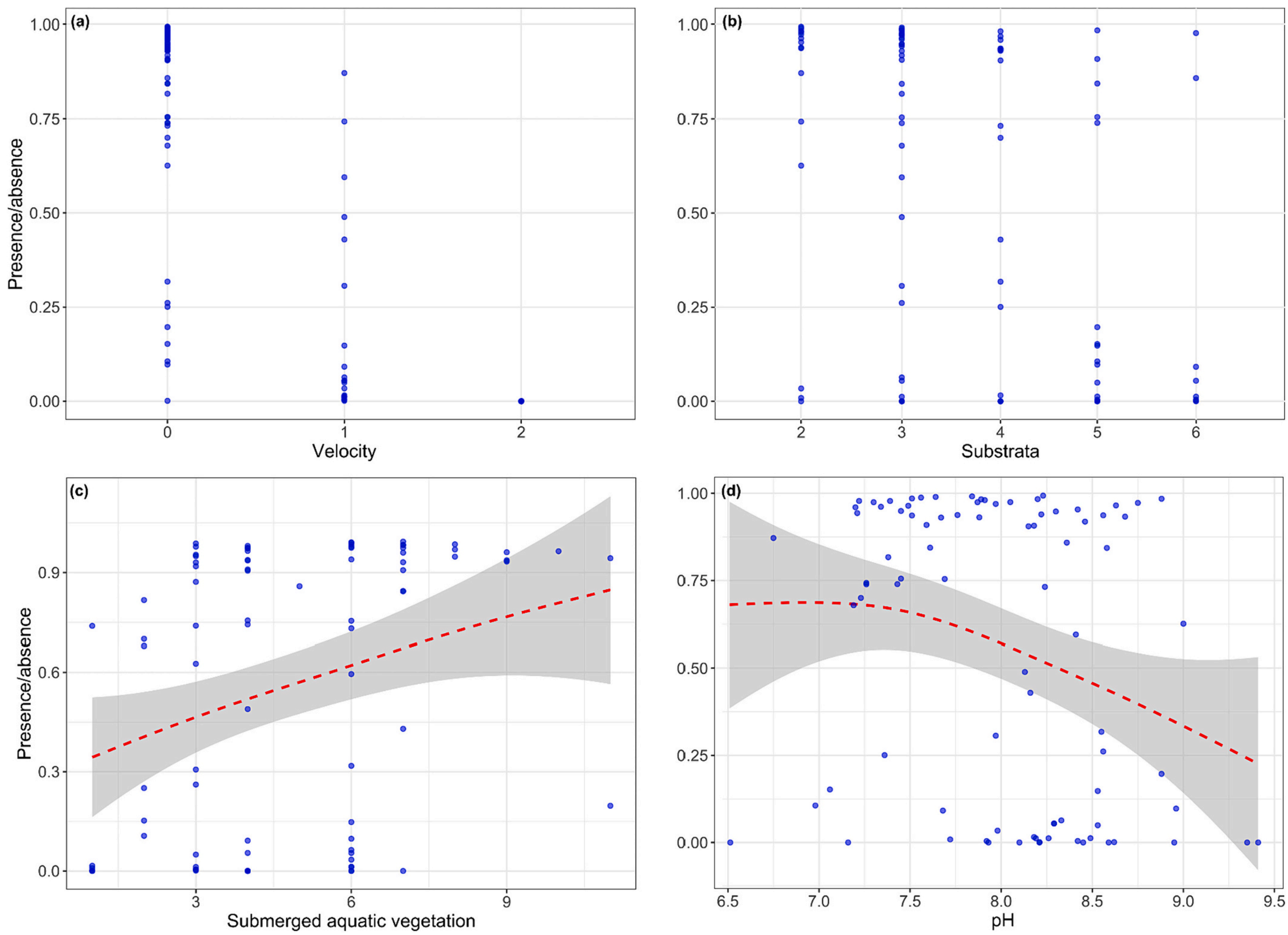


Fig. 4. Model response of GAMs for each of the variables identified in the Random Forest Dashed (velocity; (a); substrate, (b); submerged aquatic vegetation, (c); pH, (d)). Dashed lines indicate non-significant trends. Grey area denotes confidence intervals.

3.2. Microhabitat conditions

The random forest identified that velocity, submerged aquatic vegetation, pH, and substrate type substrata were the most important variables in predicting the presence of *G. holbrooki* (Fig. 3a). Based on our GAMs, velocity 1 (i.e. stagnant, low current, high current) and substrata 5 (depending on the size of the particles in the ground structure: >6.4 cm = large stones) had a significant effect on the presence of *G. holbrooki*, meaning that higher currents and large stones lead to a decrease in its presence (Fig. 4; Table S5).

3.3. Drivers of changes in CPUE

The variables that best explained changes in the CPUE of *G. holbrooki* and so used in Generalized Linear Mixed Models (GLMMs) were dissolved oxygen, distance from the bank, latitude, water temperature, water depth, and woody material (Fig. 3a). The applied GLMM identified that only latitude was a significant predictor, having a positive effect on CPUE values ($p < 0.001$; Fig. 5a; Table S6). All other included predictors (woody material, water temperature, depth, distance from the bank, dissolved oxygen; Fig. 5b–f) were not significant predictors of CPUE values.

3.4. Ecological niche model

Modelling results indicate that *G. holbrooki* occurs in regions with an average annual temperature of 10–20 °C and average temperature of the wettest quarter of 10 °C. Among the lithological classes, *G. holbrooki* prefers regions with unconsolidated sediments (SU) and carbonate sedimentary rocks (SC). It prefers xeric freshwater ecosystems and endorheic basins, temperate coastal rivers, temperate upland rivers, temperate floodplain rivers and wetlands, and tropical and subtropical coastal rivers. *Gambusia holbrooki*'s occurrence across different habitats in Türkiye was comparable to its versatile occurrence in its native region or globally (Table S7). The suitability (niche breadth) of possible habitats for the species in Türkiye (B1 = 0.57 and B2 = 0.96) is considerably higher than globally (B1 = 0.13 and B2 = 0.90).

The GLMM testing the microhabitat preferences of *G. holbrooki* indicated that across the sampling sites, "rock substrata > 6.4-10 cm" and "fast velocity: elevated ripple effect around the pole -5 - 10 cm s^{-1}" negatively affected the presence of *G. holbrooki* ($p < 0.05$, Table S7). Comparing the data collected in this study with the as suitable identified area indicated that occurrences (Fig. 6a) fell well within the as suitable identified areas covering almost the entirety of Türkiye (Fig. 6a), with higher abundances also overlapping with highly suitable regions (Fig. 6b).

4. Discussion

Non-native fish species are known for their adverse effects on invaded ecosystems (Pyke, 2008). *Gambusia holbrooki*, arguably among the most infamous invasive fish species (ISSG, 2013), is known for its

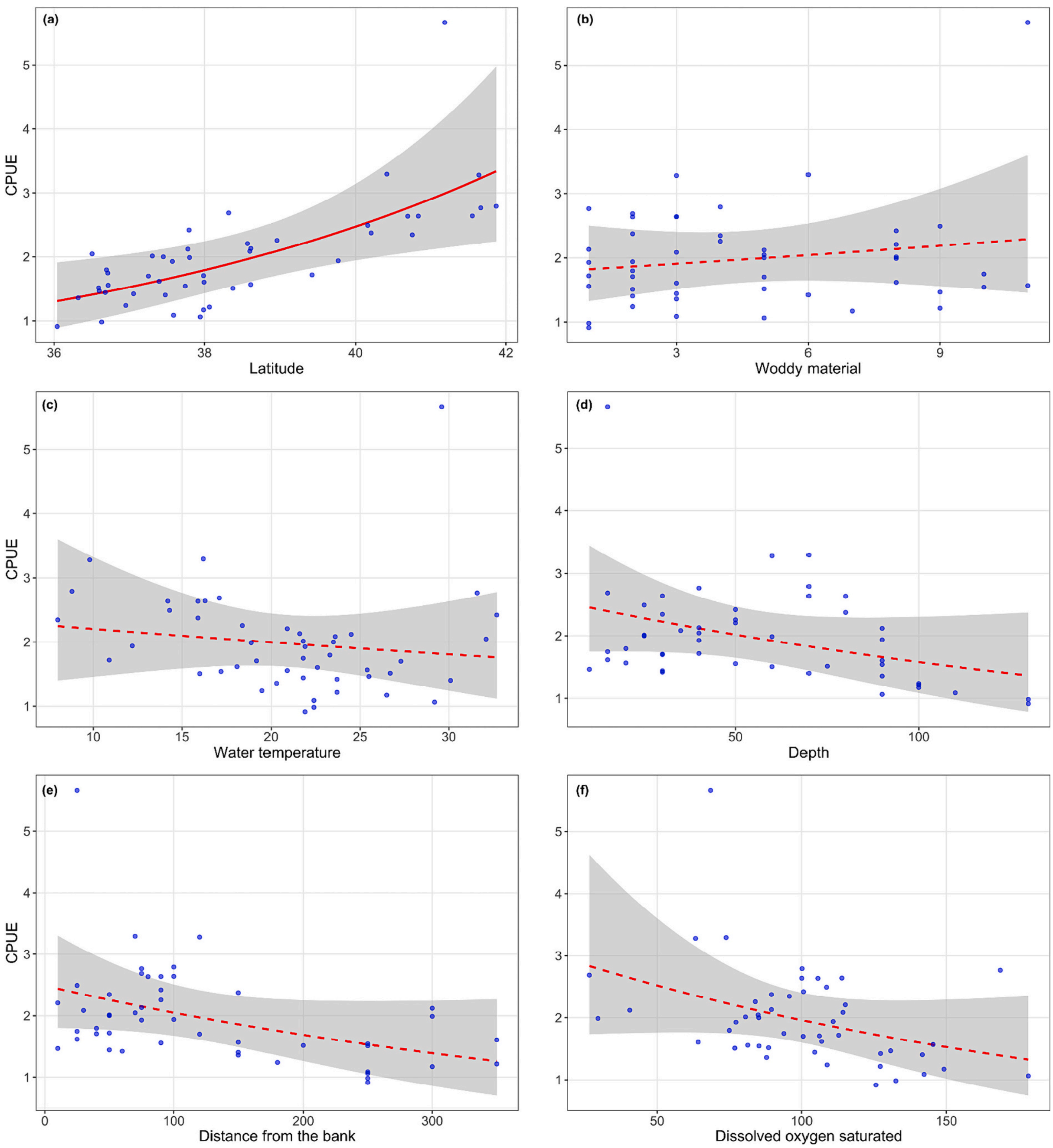


Fig. 5. Model response of GLMM for each of the variables identified in the Random Forest (latitude, (a); woody material (b); water temperature, (c); depth, (d); distance from the bank, (e); dissolved oxygen saturated, (f)). Dashed lines indicate non-significant trends, while the solid line indicates a significant effect of the predictor. Grey area denotes confidence intervals.

remarkable capacity to thrive in different environments due to their ability to tolerate a wide range of environmental parameters and express high behavioural versatility that, in entirety, facilitate its invasiveness (Arthington, 1991; Pen et al., 1993). Investigating the factors (i.e. site-specific conditions) affecting its presence and abundance here revealed that the environmental tolerances of *G. holbrooki* were mainly influenced by low current velocities and substrate as determinants of its establishment, with higher pH and water temperatures being prerequisites for higher abundances. These findings are congruent with all our predictions, revealing important insights into the ecology of this global invader.

Understanding a species' invasion risk and factors determining the possibility of an invader to establish is of utmost importance for mitigating its potential impacts (Britton et al., 2011). Our study results also support previous research on *G. holbrooki*, highlighting its high ecological versatility and niche variability. Previous studies highlighted considerable phenotypic plasticity in response to habitat change (e.g. embryo fat content was found to increase in competitive habitats and body shape differed across habitats; Santi et al., 2020) and reported *G. holbrooki's* preference for warm and slow-flowing freshwater environments with abundant aquatic vegetation (Casterlin and Reynolds, 1977; Pen and Potter, 1991). Other studies (e.g. Marshall and Elliot, 1998; Pires et al., 1999; Vlach et al., 2005) identified substrate type (except for rock >6.4–10 cm) as a strong variable determining the habitat preferences of *G. holbrooki*, while a recent study indicated the importance of plastic phenotypes (Santi et al., 2020). Our microhabitat analyses similarly revealed that *G. holbrooki* were predominantly found in stagnant water bodies with gravel substrates. This unexpected finding

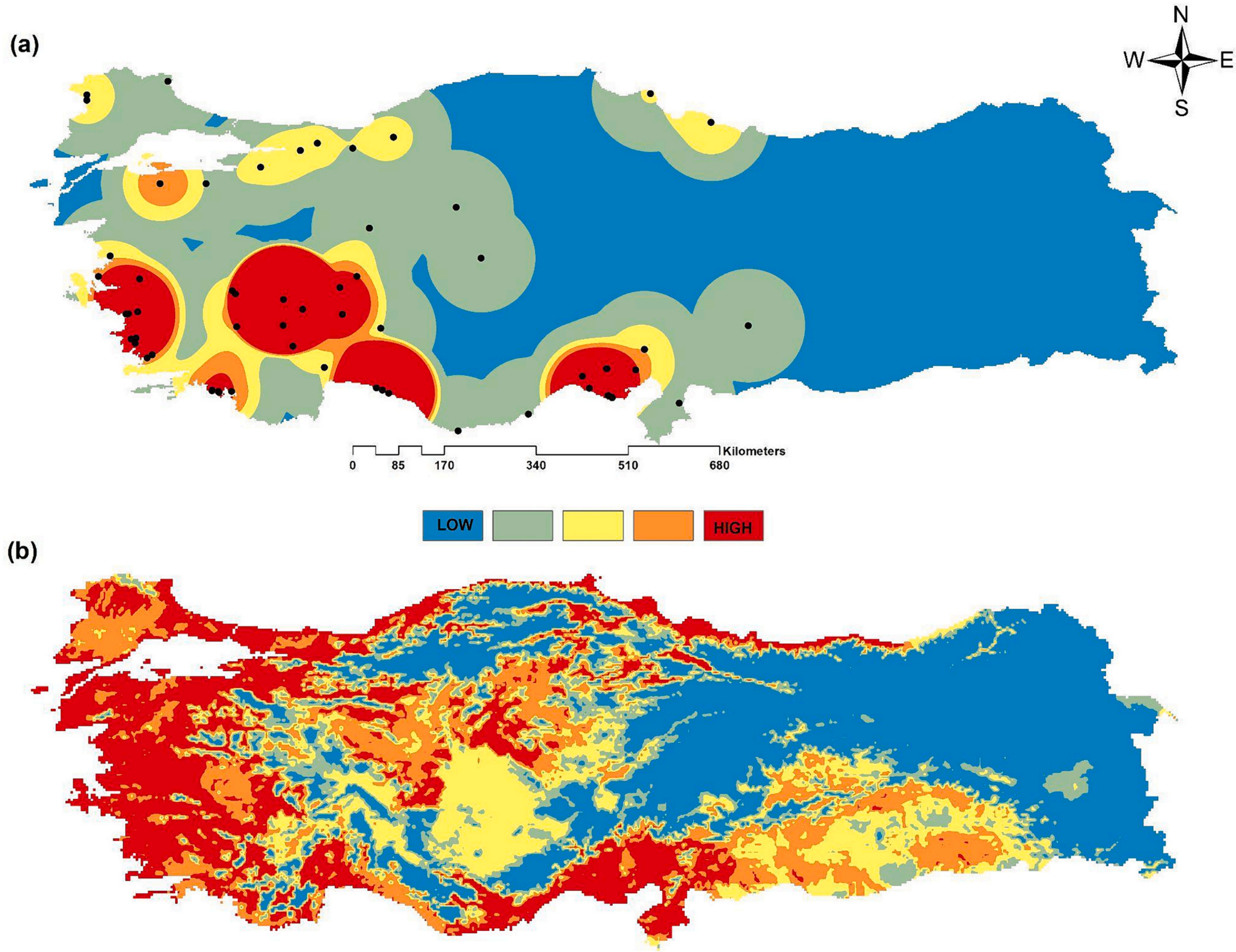


Fig. 6. Density map of the abundance of *G. holbrooki* in Türkiye, where red zones indicate higher abundance and blue zones indicate lower abundance (a). Ecological niche model for Türkiye, where red indicates areas of high suitability and blue indicates areas of low suitability (b).

may be explained by localised environmental modifications or unique ecological characteristics of the sampled sites (Kurtul, 2018), where gravel substrate has been introduced or naturally occurs in ways not typically associated with stagnant water bodies, potentially affecting the habitat preferences of *G. holbrooki*.

Current velocity and substrate type are crucial determinants for the establishment of non-native fish species (Caiola et al., 2014), as they influence habitat suitability, feeding opportunities, competitive advantage, predator avoidance, reproductive success, physiological adaptations, and the potential for successful colonisation or invasion in a new environment. Climate change effects, such as warmer temperatures and reduced river flows resulting from drought, thereby contribute to the expansion into increasingly suitable habitats, thus facilitating the invasion of *G. holbrooki* (Murphy et al., 2015). Although our analysis accounted for water temperature as a variable, recognizing its potential influence on the distribution of invasive fish species (Kurtul and Sarı, 2019), our results suggest that temperature alone may not be a facilitating factor for the future distribution of *G. holbrooki* in Türkiye, indicating a notable tolerance of the species to higher temperatures (Pyke, 2008). The significant determinant of higher abundances was found to be an increase in latitude, specifically populations situated in the North of Türkiye. This latitude effect might not solely reflect climatic conditions, such as temperature, but could also represent other underlying factors. For instance, higher latitudes may be associated with greater local propagule pressure due to variations in habitat connectivity or freshwater ecosystem types that favour *G. holbrooki*'s proliferation (Xiong et al., 2019). Additionally, latitude could be indicative of regional differences in economic activities, urbanisation, and human presence, which might influence habitat suitability through mechanisms such as increased nutrient runoff or habitat modifications (Gosselin and Callois, 2018). These findings underscore the complex interplay between various environmental and anthropogenic factors in shaping the distribution and spread of invasive populations of species like *G. holbrooki* amidst climate change (Hulme, 2017). The ongoing rise in temperatures and the impacts of drought conditions on river flows further complicate this dynamic, potentially making more areas suitable habitats for *G. holbrooki* (Carosi et al., 2021; Ramírez et al., 2018).

We also found that pH was a potential factor – albeit being non-significant – influencing the relative presence/absence of *G. holbrooki*, which was corroborated by ecological niche modelling suggesting that Unconsolidated Sediments (SU) and Carbonate Sedimentary Rocks (SC) rocks were also relevant factors. This suggests that *G. holbrooki* populations may be influenced by variations in pH levels within their habitats, with a higher pH being a barrier. Changes in pH can occur naturally but also because of human activities, such as pollution or runoff from agricultural practices (Wang et al., 2017). Acidic or alkaline conditions can directly affect the physiology, behaviour, and reproductive success of aquatic organisms, including fish species (Novo et al., 2015). The specific reasons behind the relationship between pH and abundances of *G. holbrooki* in our study may require further investigation. It is, however, possible that *G. holbrooki* has a certain tolerance range for pH levels and thrive under specific conditions (Walton et al., 2012). Alternatively, *G. holbrooki* might adapt to certain pH ranges (pH range: 6.75 to 10.85), contributing to their invasion success through successful establishment and higher relative abundance in certain habitats.

The applied ecological niche model revealed significant suitable habitats extending beyond the regions and sites where samples were collected across Türkiye. This expansive range suggests that the species may have the potential for wider distribution within the country. Furthermore, the ecological niche model corroborated earlier models, highlighting that current velocity and substrate composition are pivotal determinants of habitat suitability for the species. Given that these environmental conditions are prevalent throughout Türkiye, it raises concerns about the species' propensity to spread. The findings underscore the importance of monitoring and implementing measures to manage potential expansion.

4.1. Global distribution

Due to the wide tolerance and its diverse habitat use, *G. holbrooki* is able to occur across wide environmental gradients (Kurtul et al., 2022). The spatial expansion of *G. holbrooki* poses a challenge for native species and ecosystems, as their competitive prowess and potential disruption threaten to upset the ecological balance of native fish populations (Pyke, 2008). Concomitantly, this invasion by *G. holbrooki* is unlikely to be hindered by minimal differences in microhabitat characteristics. Globally and especially in Türkiye, *G. holbrooki* demonstrates remarkable ecological versatility, establishing populations in a wide range of freshwater habitats (Santi et al., 2020). In Türkiye, our findings indicate that suitable habitats for *G. holbrooki* are widespread across the country, with a notable preference for xeric freshwater ecosystems, endorheic basins, and various riverine and wetland environments. This pattern echoes the species' versatility in habitat selection, similarly, observed in its native range in North America (Matthews and Marsh-Matthews, 2011).

In its native North American habitat, *G. holbrooki*, along with other species of mosquitofish (Rauchenberger, 1989; Scharpf, 2008), exhibits a broad ecological range that spans from the southern tropical swamps to the temperate regions of New Jersey (Vidal et al., 2010). This extensive distribution highlights the species' ability to thrive in diverse environmental conditions, from warm, subtropical waters to cooler, temperate ecosystems. The versatility of *G. holbrooki* is further underscored by its presence in varied aquatic environments including, but not limited to, stagnant and flowing waters, environments with varying degrees of salinity, and habitats with diverse substrate compositions. The wide-ranging adaptability of *G. holbrooki* even suggests a high level of ecological plasticity, which likely contributes to its establishment in non-native regions. This, coupled with its aggressive breeding and competitive behaviour (Rupp, 1996; Pyke, 2008; Ember, 2023), has facilitated its spread across different continents, including their notable presence in Türkiye. While future studies should investigate the niche conservatism in *G. holbrooki* (Wiens et al., 2010), the comparison between the habitats favoured by *G. holbrooki* in Türkiye and its broad ecological niche in North America and other invaded ranges underlines the species' global adaptability and the potential for similar ecological impacts in invaded regions.

CRediT authorship contribution statement

Irmak Kurtul: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Ali Serhan Tarkan:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Hasan Musa Sarı:** Supervision, Resources, Investigation, Data curation. **Phillip J. Haubrock:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Ismael Soto:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Sadi Aksu:** Visualization, Methodology, Investigation, Formal analysis. **J. Robert Britton:** Writing – review & editing, Validation, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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: 2015/SÜF/016). We thank TÜBİTAK BİDEB (2211 Program), which supported the first author during her PhD research. We thank TÜBİTAK BİDEB (2219 Program), which supported Irmak Kurtul and Ali Serhan Tarkan with one-year scholarships during their post-doc research in the United Kingdom.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.171718.

References

Abell, R., Thieme, M.L., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., Coad, B., Mandrak, N., Balderas, S.C., Bussing, W., Stiassny, M.L.J., Skelton, P., Allen, G.R., Unmack, P., Naseka, A., Sindorf, N., Robertson, J., Armijo, E., Higgins, J.V., Heibel, T.J., Wikramanayake, E., Olson, D., López, H.L., Reis, R.E., Lundberg, J.G., Pérez, M.H.S., Petry, P., 2008. Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. Bioscience 58, 403–414. https://doi.org/10.1641/B580507.

Alcaraz, C., García-Berthou, E., 2007. Life history variation of invasive mosquitofish (*Gambusia holbrooki*) along a salinity gradient. Biol. Conserv. 139 (1–2) https://doi.org/10.1016/j.biocon.2007.06.006 (83–92 pp.).

Arthington, A.H., 1991. Ecological and genetic impacts of introduced and translocated freshwater fishes in Australia. Can. J. Fish. Aquat. Sci. 48 (1), 33–43.

Bahadıroğlu, C., Büyükçapar, H.M., 1997. Sıtma ile biyolojik mücadelede sivrisinek balıkları (*Gambusia affinis*, Baird and Girard)'nın önemi. Ekol. Çev. Der. 22, 34–36 (In Turkish).

Berg, L.S., 1965. Freshwater Fishes of the U.S.S.R. and Adjacent Countries, , 4th editionVol. 3. Israel Program for Scientific Translations Ltd., Jerusalem, p. 510s.

Beyer, K., Copp, G.H., Gozlan, R.E., 2007. Microhabitat use and interspecific associations of introduced topmouth gudgeon *Pseudorasbora parva* and native fishes in a small stream. J. Fish Biol. 71, 224–238. https://doi.org/10.1111/j.1095-8649.2007.01677.x.

Britton, J.R., 2023. Contemporary perspectives on the ecological impacts of invasive freshwater fishes. J. Fish Biol. 103 (4), 752–764. https://doi.org/10.1111/jfb.15240.

Britton, J.R., Gozlan, R.E., Copp, G.H., 2011. Managing non-native fish in the environment. Fish Fish. 12, 256–274. https://doi.org/10.1111/j.1467-2979.2010.00390.x.

Cai, Q., Welk, E., Ji, C., Fang, W., Sabatini, F.M., Zhu, J., 2021. The relationship between niche breadth and range size of beech (Fagus) species worldwide. J. Biogeogr. 48 (5), 1240–1253. https://doi.org/10.1111/jbi.14074.

Caiola, N., Ibáñez, C., Verdú, J., Munné, A., 2014. Effects of flow regulation on the establishment of alien fish species: a community structure approach to biological validation of environmental flows. Ecol. Indic. 45, 598–604. https://doi.org/10.1016/j.ecolind.2014.05.012.

Carosi, A., Ghetti, L., Lorenzoni, M., 2021. The role of climate changes in the spread of freshwater fishes: implications for alien cool and warm-water species in a Mediterranean basin. Water 13 (3), 347. https://doi.org/10.3390/w13030347.

Casterlin, M.E., Reynolds, W.W., 1977. Aspects of habitat selection in the mosquito fish *Gambusia affinis*. Hydrobiologia 55, 125–127. https://doi.org/10.1007/BF0002105.

Cech, J.J., Massingill, M.J., Vondracek, B., Linden, A.L., 1985. Respiratory metabolism of mosquitofish, *Gambusia affinis*: effects of temperature, dissolved oxygen, and sex difference. Environ. Biol. Fishes 13, 297–307.

Copp, G.H., 1989. Electrofishing for fish larvae and juveniles: equipment modifications for increased efficiency with short fishes. Aquacult. Fish. Manag. 20, 453–462. https://doi.org/10.1111/j.1365-2109.1989.tb00372.x.

Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. Methods Ecol. Evol. 1, 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x.

Ember, F., 2023. Dietary Overlap between the Non-native Mosquitofish (*Gambusia affinis)* and Native Common Bully (*Gobiomorphus cotidianus*): Evidence for Interspecific Competition? (Doctoral dissertation, The University of Waikato.

Evans, A., Jacquemyn, H., 2022. Range size and niche breadth as predictors of climate-induced habitat change in Epipactis (Orchidaceae). Front. Ecol. Evol. 10, 894616 https://doi.org/10.3389/fevo.2022.894616.

Fausch, K.D., Taniguchi, Y., Nakano, S., Grossman, G.D., Townsend, C.R., 2001. Flood disturbance regimes influence rainbow trout invasion success among five Holarctic regions. Ecol. Appl. 11, 1438–1455. https://doi.org/10.1890/1051-0761(2001)011[1438:FDRIRT]2.0.CO;2.

Feder, J.L., Smith, M.H., Chesser, R.K., Godt, M.J.W., Asbury, K., 1984. Biochemical genetics of mosquitofish. II. Demographic differentiation of populations in a thermally altered reservoir. Copeia 108–119. https://doi.org/10.2307/1445041.

Friberg, N., Bonada, N., Bradley, D.C., Dunbar, M.J., Edwards, F.K., Grey, J., Hayes, R.B., Hildrew, A.G., Lamouroux, N., Trimmer, M., Woodward, G., 2011. Biomonitoring of human impacts in freshwater ecosystems: the good, the bad and the ugly. In Advances in ecological research Academic press. 44, 1–68. https://doi.org/10.1016/B978-0-12-374794-5.00001-8.

Geldiay, R., Balık, S., 1996. Türkiye Tatlısu Balıkları Kitabı, II. Baskı. İzmir: Ege Üniversitesi Basım Evi, 532s (In Turkish).

Gosselin, F., Callois, J.M., 2018. Relationships between human activity and biodiversity in Europe at the national scale: spatial density of human activity as a core driver of biodiversity erosion. Ecol. Indic. 90, 356–365. https://doi.org/10.1016/j.ecolind.2018.03.010.

Gozlan, R.E., Britton, J.R., Cowx, I.G., Copp, G.H., 2010. Current knowledge on non-native freshwater fish introductions. J. Fish Biol. 76, 751–786. https://doi.org/10.1111/j.1095-8649.2010.02566.x.

Guo, Q., 2006. Intercontinental biotic invasions: what can we learn from native populations and habitats? Biol. Invasions 8, 1451–1459. https://doi.org/10.1007/s10530-005-5834-1.

Howe, E., Howe, C., Lim, R., Burchett, M., 1997. Impact of the introduced Poeciliid *Gambusia holbrooki* (Giarad, 1859) on the growth and reproduction of *Pseudomugil signifer* (Kner, 1865) in Australia. Mar. Freshw. Res. 48, 425–434.

Hulme, P.E., 2017. Climate change and biological invasions: evidence, expectations, and response options. Biol. Rev. 92 (3), 1297–1313. https://doi.org/10.1111/brv.12282.

Ishwaran, H., Lauer, M.S., Blackstone, E.H., Lu, M., Kogalur, U.B., 2022. Randomforestsrc: Random survival forests vignette. Random Forest SRC 15.

ISSG., 2013. "Global Invasive Species Database (Invasive Species Specialist Group)", http://www.iucngisd.org/gisd/100_worst.php (Erişim tarihi: 22 Temmuz 2016).

Ivantsoff, W., Aarn, N., 1999. Detection of predation on Australian native fishes by *Gambusia holbrooki*. Mar. Freshw. Res. 50 (5), 467–468. https://doi.org/10.1071/MF98106.

Jourdan, J., Riesch, R., Cunze, S., 2021. Off to new shores: climate niche expansion in invasive mosquitofish (*Gambusia* spp.). Ecol. Evol. 11 (24), 18369–18400. https://doi.org/10.1002/ece3.8427.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, P., Kessler, M., 2017. Climatologies at high resolution for the earth land surface areas. Sci. Data. 4, 170122 https://doi.org/10.1038/sdata.2017.122.

Krumholz, L.A., 1948. Reproduction in the western mosquitofish *Gambusia affinis* and its use in mosquito control. Ecological monographs 18, 1–43. https://doi.org/10.2307/1948627.

Kurtul, I., 2018. Investigation of the Distribution and Bio-Ecological Features of *Gambusia* (Mosquitofish) Species in Türkiye. Ege University Graduate School of Natural and Applied Sciences (PhD Thesis, 182 pp.).

Kurtul, I., Sarı, H.M., 2019. *Gambusia holbrooki* (Sivrisinek balığı)'nin Türkiye'deki Dağılımına Katkılar. LimnoFish 5 (3), 170–180. https://doi.org/10.17216/LimnoFish.519729.

Kurtul, I., Tarkan, A.S., Sarı, H.M., Britton, J.R., 2022. Climatic and geographic variation as a driver of phenotypic divergence in reproductive characters and body sizes of invasive *Gambusia holbrooki*. Aquat. Sci. 84, 29. https://doi.org/10.1007/s00027-022-00862-7.

Lee, D.S., Burgess, G.H., 1980. *Gambusia affinis* (Baird and Girard), Mosquitofish. In: Lee, D.S., et al. (Eds.), Atlas of North American Freshwater Fishes. N. C. State Mus. Nat. Hist., Raleigh, i-r, p. 538 (854 pp.).

Lehner, B., Messager, M.L., Korver, M.C., Linke, S., 2022. Global hydro-environmental lake characteristics at high spatial resolution. Sci. Data. 9, 351. https://doi.org/10.1038/s41597-022-01425-z.

Linke, S., Lehner, B., Ouellet Dallaire, C., Ariwi, J., Grill, G., Anand, M., Beames, P., Burchard-Levine, V., Maxwell, S., Moidu, H., Tan, F., Thieme, M., 2019. Global hydro-environmental sub-basin and river reach characteristics at high spatial resolution. Sci. Data. 6, 283. https://doi.org/10.1038/s41597-019-0300-6.

Lloyd, L., 1987. An alternative to insect control by "mosquitofish" *Gambusia affinis*. In: TD St. George, B.H. Kay and J. Blok, editors. Proceedings 4th Symposium on Arbovirus Research, Australia: Q.I.M.R. Brisbane, pp. 156–163.

Lowe, S., Browne, M., Boudjelas, S., De Poorter, M., 2000. 100 of the world's worst invasive alien species, a selection from the global invasive species database. Published by The Invasive Species Specialist Group (ISSG), a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), pp. 1–12.

Magnusson, A., Hans, S., Anders, N., Casper, B., Kasper, K., Martin, M., Koen van, B., Ben, B., Mollie, B., Maintainer, M.B., 2017. Package 'glmmtmb'. R Package Version 0 (2), 0 25.

Marshall, S., Elliot, M., 1998. Environmental influences on the fish assemblage of the Humber estuary. U.K. Estuar. Coast. Shelf Sci. 46, 175–184.

Matthews, W.J., Marsh-Matthews, E., 2011. An invasive fish species within its native range: community effects and population dynamics of *Gambusia affinis* in the Central United States. Freshw. Biol. 56 (12), 2609–2619. https://doi.org/10.1111/j.1365-2427.2011.02691.x.

Meffe, G.K., 1984. Effects of abiotic disturbance on coexistence of predator-prey fish species. Ecology 65, 1525–1534. https://doi.org/10.2307/1939132.

Misawa, A., Kada, S., Yoshida, M., 2014. Comparison of the mode of action of three anesthetic agents, 2-phenoxyethanol, MS-222, and eugenol on goldfish. Aquac. Sci. 62 (4), 425–432.

Moyle, P.B., 2002. Inland Fishes of California. University of California Press, Revised and expanded, Berkeley, p. 502s.

Murphy, C.A., Grenouillet, G., García-Berthou, E., 2015. Natural abiotic factors more than anthropogenic perturbation shape the invasion of eastern mosquitofish (*Gambusia holbrooki*). Freshw. Sci. 34 (3), 965–974. https://doi.org/10.1086/681948.

Nelva, A., Persat, H., Chessel, D., 1979. Une nouvelle méthode d'étude des peuplements ichtyologiques dans les grands cours d'aeu par échantillonnage ponctuel d'abodance. C R Acad Sci III Paris. 289, 1295–1298 (In French).

Novo, M., Cunha, L., Maceda-Veiga, A., Talavera, J.A., Hodson, M.E., Spurgeon, D., Bruford, M.W., Morgan, A.J., Kille, P., 2015. Multiple introductions and environmental factors affecting the establishment of invasive species on a volcanic island. Soil Biol. Biochem. 85, 89–100. https://doi.org/10.1016/j.soilbio.2015.02.031.

Oksanen, J., 2012. Constrained ordination: tutorial with R and vegan. R-packace Vegan 1 (10), 1–9.

Olden, J.D., Chen, K., García-Berthou, E., King, A.J., South, J., Vitule, J.R., 2022. Invasive species in streams and rivers. Enc. Inland. Waters. 2, 436–452. https://doi.org/10.1016/B978-0-12-819166-8.00083-9.

Özuluğ, M., Altun, Ö., Meriç, N., 2005. On the fish fauna of Lake İznik (Turkey). Turk. J. Zool. 29, 371–375.

Pen, L.J., Potter, I.C., 1991. Reproduction, growth and diet of *Gambusia holbrooki* (Girard) in a temperate Australian river. Aquat. Conserv.: Mar. Freshw. Ecosyst. 1, 159–172. https://doi.org/10.1002/aqc.3270010205.

Pen, L.J., Potter, I.C., Calver, M.C., 1993. Comparisons of the food niches of three native and two introduced fish species in an Australian river. Environ. Biol. Fishes 36, 167–182. https://doi.org/10.1007/BF00002797.

Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: An open-source release of Maxent. Ecography 40 (7), 887–893. ISO 690.

Pili, A.N., Tingley, R., Sy, E.Y., Diesmos, M.L.L., Diesmos, A.C., 2020. Niche shifts and environmental non-equilibrium undermine the usefulness of ecological niche models for invasion risk assessments. Sci. Rep. 10 (1), 1–18. https://doi.org/10.1038/s41598-020-64568-2.

Pires, A.M., Cowx, I.G., Coeldho, M.M., 1999. Seasonal changes in fish community structure of intermintent streams in the middle reaches of the Guadiana basin. Portugal. J. Fish. Biol. 54, 235–249. https://doi.org/10.1111/j.1095-8649.1999.tb00827.x.

Pyke, G.H., 2005. A review of the biology of *Gambusia affinis* and *Gambusia holbrooki*. Rev. Fish Biol. Fish. 15, 339–365. https://doi.org/10.1007/s11160-006-6394-x.

Pyke, G.H., 2008. Plague minnow or mosquitofish? A review of the biology and impacts of introduced *Gambusia* species. Ann. Rev. Ecol. Syst. 39, 171–191. https://doi.org/10.1146/annurev.ecolsys.39.110707.173451.

R Core Team, 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ramírez, A., Gutiérrez-Fonseca, P.E., Kelly, S.P., Engman, A.C., Wagner, K., Rosas, K.G., Rodríguez, N., 2018. Drought facilitates species invasions in an urban stream: results from a long-term study of tropical island fish assemblage structure. Front. Ecol. Evol. 6, 115. https://doi.org/10.3389/fevo.2018.00115.

Rauchenberger, M., 1989. Systematics and Biogeography at the Genus *Gambusia* (Cyprinodontiformes: Poeciliidae). The American Museum of Natural History Novitates, Newyork, p. 74s.

Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D., Ripley, M.B., 2013. Package 'mass'. Cran r 538, 113–120.

Ruiz-Navarro, A., Moreno-Valcárcel, R., Torralva, M., Oliva-Paterna, F.J., 2011. Life-history traits of the invasive fish *Gambusia holbrooki* in saline streams (SE Iberian Peninsula): does salinity limit its invasive success? Aquat. Biol. 13 (2), 149–161. https://doi.org/10.3354/ab00360.

Rupp, H.R., 1996. Adverse assessments of *Gambusia affinis*: an alternative view for mosquito control practitioners. J. Am. Mosq. Control Assoc. 12, 155–166.

Santi, F., Riesch, R., Baier, J., Grote, M., Hornung, S., Jüngling, H., Plath, M., Jourdan, J., 2020. A century later: adaptive plasticity and rapid evolution contribute to geographic variation in invasive mosquitofish. Sci. Total Environ. 726, 137908 https://doi.org/10.1016/j.scitotenv.2020.137908.

Scharpf, C., 2008. Annotated checklist of north American freshwater fishes, including subspecies and undescribed forms. Part IV: Cottidae through Percidae. Am. Curr. 34 (4), 1–44.

Slatyer, R.A., Hirst, M., Sexton, J.P., 2013. Niche breadth predicts geographical range size: a general ecological pattern. Ecol. Lett. 16, 1104–1114. https://doi.org/10.1111/ele.12140.

Soto, I., Balzani, P., Carneiro, L., Cuthbert, R.N., Macedo, R., Tarkan, A.S., Haubrock, P. J., 2024. Taming the terminological tempest in invasion science. Biol. Rev. https://doi.org/10.1002/BRV.13071.

Tarkan, A.S., Marr, S.M., Ekmekçi, F.G., 2015. Non-native and translocated freshwater fish species in Turkey. Fish. Mediterr. Environ. 3, 28. https://doi.org/10.29094/FiSHMED.2015.003.

Top, N., Tarkan, S., Vilizzi, L., Karakuş, U., 2016. Microhabitat interactions of non-native pumpkinseed *Lepomis gibbosus* in a Mediterranean-type stream suggest no evidence for impact on endemic fishes. Knowl. Manag. Aquat. Ecosyst. 417, 36. https://doi.org/10.1051/kmae/2016023.

Top, N., Karakuş, U., Tepeköy, E.G., Britton, J.R., Tarkan, A.S., 2019. Plasticity in habitat preferences of two native Ponto-Caspian gobies, *Proterorhinus semilunaris* and *Neogobius fluviatilis*: implications for invasive populations. Knowl. Manag. Aquat. Ecosyst. 420, 40. https://doi.org/10.1051/kmae/2019031.

Vidal, O., García-Berthou, E., Tedesco, P.A., García-Marín, J.L., 2010. Origin and genetic diversity of mosquitofish (*Gambusia holbrooki*) introduced to Europe. Biol. Invasions 12, 841–851. https://doi.org/10.1007/s10530-009-9505-5.

Vlach, P., Dušek, J., Švátora, M., Moravec, P., 2005. Fish assemblage structure, habitat and microhabitat preference of five fish species in a small stream. Folia Zool. 54 (4), 421–431.

Walton, W.E., Henke, J.A., Why, A.M., 2012. A handbook of global freshwater invasive species. In: Francis, Robert A. (Ed.), *Gambusia affinis* (Baird & Girard) and *Gambusia holbrooki* Girard (Mosquitofish), Chapter: 22. Earthscan, New York, pp. 261–272.

Wang, Q., Zhang, Q., Wu, Y., Wang, X.C., 2017. Physicochemical conditions and properties of particles in urban runoff and rivers: implications for runoff pollution. Chemosphere 173, 318–325. https://doi.org/10.1016/j.chemosphere.2017.01.066.

Warren, D.L., Glor, R.E., Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62, 2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Jonathan Davies, T., Grytnes, J.A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M., Stephens, P.R., 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecol. Lett. 13 (10), 1310–1324. https://doi.org/10.1111/j.1461-0248.2010.01515.x.

Wood, S., Scheipl, F., Wood, M.S., 2017. Package 'gamm4'. Am. Stat. 45 (339), 0–2.

Xiong, W., Tao, J., Liu, C., Liang, Y., Sun, H., Chen, K., Chen, Y., 2019. Invasive aquatic plant (*Alternanthera philoxeroides*) facilitates the invasion of western mosquitofish (*Gambusia affinis*) in Yangtze River. China. Aquat. Ecosyst. Health. Manag. 22 (4), 408–416. https://doi.org/10.1080/14634988.2019.1700090.

Yoğurtçuoğlu, B., Ekmekçi, F.G., 2014. Threatened fishes of the world: *Aphanius transgrediens* Ermin, 1946 (Cyprinodontidae). Croat. J. Fish. 72, 186–187. https://doi.org/10.14798/72.4.774.

Yoğurtçuoğlu, B., Uyan, U., Ekmekçi, F.G., 2020. The influence of environmental instability on the reproductive strategy of the critically endangered Acigol killifish (*Aphanius transgrediens*). J. Fish Biol. 97, 246–256. https://doi.org/10.1111/jfb.14358.

Zarev, V.Y., 2012. Some life-history traits of *Gambusia holbrooki* (Pisces: Poecilidae) from Bulgaria. Acta. Zool. Bulg. 64 (3), 263–272.