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Research Article

Trophic interactions and climate-driven range dynamics of native and invasive catfish in freshwater ecosystems

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Abstract

Invasive species and climate change are among the most significant drivers of biodiversity loss in freshwater ecosystems, yet their combined effect on predator-prey dynamics remains insufficiently characterised. Here, we assess the trophic interactions and climate-driven range dynamics of two large-bodied catfish—the non-native African catfish, *Clarias gariepinus* and the native Wels catfish, *Silurus glanis*—in a thermally stable freshwater system in Türkiye. Using comparative functional response experiments and stable isotope analysis, we quantified predation patterns on a native prey species, *Alburnus escherichii* and a widespread non-native prey, *Carassius gibelio*. Both predators exhibited feeding efficiency on the native prey, with *C. gariepinus* demonstrating consistently greater consumption rates and potential ecological impact, particularly under warmer conditions. Ecological niche models projected range expansion for both catfish species under future climate scenarios, with increasing habitat overlap that may elevate the likelihood of interspecific interactions and exacerbate predation pressure on native fish communities. Our findings demonstrate how warming conditions can reinforce the ecological impacts of an invasive predator while altering its spatial interactions with native species, underscoring the urgent need to integrate experimental, field-based, and modelling approaches to anticipate climate-amplified invasion risks in freshwater ecosystems.

Key words: *Clarias gariepinus*, Conservation management, Eurasia, Invasive species, *Silurus glanis*

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Introduction

Biological invasions can cause measurable and cascading changes to both abiotic and biotic components of the introduced environment (Carneiro et al. 2025; South et al. 2025). The impact of invasive species is especially significant in freshwater ecosystems, where the interconnected nature of water bodies enables their spread across various regions (Reid et al. 2019). Additionally, human activities such as commerce and recreation can unintentionally promote the dispersal of invasive species within these environments (Haubrock et al. 2022). Predicting ecological outcomes is of utmost importance to create suitable mitigation interventions and direct resources towards the most potentially damaging invasions. Invasive species compete with native species for resources, which can lead to competitive exclusion or alteration in food-web structure including shifts in dietary breadth, niche expansion, or niche constriction (Bøhn et al. 2008; Britton et al. 2018; Dominguez-Almela et al. 2021). Such ecological shifts can ripple through food webs, affecting energy flow and ecosystem stability (Ricciardi et al. 2013; Gallardo et al. 2016; Carneiro et al. 2025). Intraspecific competition further influences trophic interactions, as resource scarcity may drive dietary diversification (Svanbäck and Bolnick 2006). Despite efforts to assess these risks, predicting invasion outcomes and ecological impact remains challenging due to context-dependent variability (Dick et al. 2017; Catford et al. 2022).

Context dependence is a major challenge in invasion science (Catford et al. 2022), whereby the interactions between biotic and abiotic environments can modulate outcomes either directly or indirectly. Biotic interactions are governed by contexts such as prey abundance which modulates a consumer's functional response (i.e. density dependent predation; Dick et al. 2017). Interspecific interactions between novel and native species may also be constrained by predator/prey naivete or phylogenetic relatedness (Ricciardi et al. 2013). The strength of these interactions can then be moderated further by a suite of abiotic variables. For example, environmental changes driven by climate change can facilitate the persistence, expansion and ecological effects of invasive populations by altering thermal regimes, hydrological cycles, and habitat suitability (Emiroğlu et al. 2023; Haubrock et al. 2024). Measuring these responses can be a complex process due to logistical constraints, multiple interacting variables and maintaining ecologically realistic experimental setups. Therefore, impact assessments are often carried out across short timescales in experimentally simplistic ways or through computer modelling approaches, with limited ground truthing of whether results are scalable to natural systems. This constrains our ability to accurately predict when, where, and how a species may cause negative ecological impact, the mechanisms by which the impact is conferred, and upon which taxa.

To address these challenges recent advances have incorporated experimental and field-based approaches in a scalable manner (i.e. lab, mesocosm, field). Dominguez-Almela et al. (2021) combined comparative functional response (CFR) analyses and stable isotope analyses (SIA) from mesocosms to predict ecological impact and interspecific interactions of two cyprinids under climate warming scenarios. Similarly, Mofu et al. (2019) used CFR and field surveys assessing relative abundance to predict ecological impact of non-native fish compared to native species under thermal change and consumer density. CFR experiments assess the feeding efficiency of invasive versus native species across varying prey densities, offering insights into resource acquisition and potential competitive advantages (Dick et al. 2013; 2014; 2017). However, as controlled aquaria experiments may oversimplify natural food web dynamics, mesocosm and field studies provide a broader ecological context. Stable isotope analysis (SIA; δ13C, δ15N) complements these experiments by quantifying dietary shifts, trophic interactions, and niche alterations in invaded ecosystems (Tran et al. 2015; Britton et al. 2018). Integrating these experimental and field-based approaches enhances our ability to predict and mitigate the ecological impacts of invasive species more effectively.

This combination approach has conceptual advances but still falls short in incorporating the spatio-temporal context of invasion dynamics. As an invasive species spreads across suitable range, the ecological niche may contract or expand depending on consumer and resource ecology and predicted shifts in environmental and climate related variables (Guareschi et al. 2024). Species distribution modelling has been combined with economic impact assessment to extrapolate potential damages and management costs of non-native species (Soto et al. 2025). However, this has not been combined with ecological impact assessment, most likely due to the complexity of predicting biotic interaction strength. Nonetheless, if ecological impact can be quantified, spatial mapping of overlapping ranges can be used to prioritise assessment and management locations. Furthermore, human dimensions—such as angler-driven translocations and socio-economic motivations for stocking—may also strongly influence future distributions but remain largely underexplored in mechanistic impact frameworks.

Large-bodied, predatory, freshwater fish have the capacity to severely deplete native prey populations through predation and compete for resources with functional analogues. Generally, these species are prized by recreational anglers and aquaculture ventures due to fast growth, large biomass, and voracity, thus they are often moved between waterbodies (Vitule et al. 2006; South et al. 2022; Haubrock et al. 2022). One such species is the sharptooth catfish *Clarias gariepinus* (Burchell, 1822), a subtropical species of African origin that has been introduced globally for aquaculture due to its rapid growth, disease resistance, and tolerance of high stocking densities (Lal et al. 2003; Vitule et al. 2006). *Clarias gariepinus* is a highly adaptable and opportunistic generalist feeder capable of attaining large sizes (commonly > 100 cm and occasionally up to ~ 170 cm TL) (Vitule et al. 2006; Low et al. 2022). A broad thermal tolerance, the ability to breathe atmospheric oxygen and disperse overland have facilitated the establishment of *C. gariepinus* in numerous freshwater habitats (Verreth et al. 1993; Booth et al. 2010; Woodford et al. 2024). These traits raise significant concerns for invaded ecosystems, where *C. gariepinus* has been associated with native fish displacement, food web disruptions, and the transmission of parasites and diseases (Khan and Panikkar 2009; Kadye and Booth 2012a; Tepe et al. 2013; Low et al. 2022). In Türkiye, *C. gariepinus* may also pose competitive threats to the functionally analogous native Wels catfish *Silurus glanis* Linnaeus, 1758. Once widespread, and ecologically significant, *S. glanis* populations are now declining due to overfishing, pollution, drought, and habitat alterations, despite its status as a damaging invasive species outside of Türkiye (Copp et al. 2009). Although both species have attracted considerable research attention as charismatic, large non-native invasive species (Copp et al. 2009; Low et al. 2022), there is limited data regarding the actual ecological impacts of either species. Climate change projections indicate that *S. glanis* could persist or even expand its range northward (Rahel and Olden 2008), potentially interacting with or competing against invasive *C. gariepinus* in overlapping habitats. Thus, understanding the dynamics between these two large-bodied predators is essential for assessing future threats to native biodiversity.

Here, we used a nested and three-pronged approach to test ecological impact hypotheses and determine the possible ecological impacts posed by non-native *C. gariepinus* on the native *S. glanis* via competition, as well as predation on native - bleak *Alburnus escherichii* Steindachner, 1897 and non-native - gibel carp *Carassius gibelio* (Bloch, 1782) prey. These two prey species were selected based on their ecological relevance in the only known Turkish freshwater system where both non-native *C. gariepinus* and native *S. glanis* co-occur. In this river section, *A. escherichii* represents the dominant native prey species, while *C. gibelio* is a widespread invasive cyprinid found across the country. Previous studies have identified members of the genus *Alburnus* as key prey for *S. glanis* in natural habitats (e.g., Alp 2017), further supporting the inclusion of *A. escherichii* in this study. Including *C. gibelio*, which often coexists with both predator species and has established robust populations in degraded or disturbed environments, provides an opportunity to assess differential predation patterns on native versus non-native prey. First, CFR experiments were used to compare laboratory-derived metrics of predatory pressure and potential competition asymmetry to provide a baseline expectation of what might be occurring in natural systems. Stable isotope analyses were used to quantify trophic niche overlap in wild populations. Finally, ecological niche modelling was applied to predict the potential range changes for both predators under current and projected climate conditions to assess implications for native species and identify areas of concern. For the CFR and SIA results we hypothesize that (i) both *C. gariepinus* and *S. glanis* exert stronger predation pressure on the native *A. escherichii* than on the non-native *C. gibelio*, (ii) *C. gariepinus* will outperform *S. glanis* in ecological interactions, exhibiting higher prey consumption rates and overall ecological impact, iii) there will be niche overlap between *C. gariepinus* and *S. glanis* (iv) climate models will predict range expansion for both species, but with increasingly overlapping niches that may intensify interspecific competition and amplify threats to native fish communities. Thus, we evaluate the consistency of results and inferences across a spectrum of complexity and provide future projections of habitat suitability and co-occurrence with relative prey, as well as hotspots of potential risk across Europe.

Materials and methods

Study area

The Sakarya River is Turkey's third-longest river, stretching 810 km and draining a catchment area of 56,504 km^2—approximately 7% of the country's total surface area (Şengörür and İsa 2001; Emiroğlu 2011). Originating from springs on the Balat Plateau in the Emir Mountains, northeast of Afyonkarahisar, its primary spring zone is located near Sakaryabaşı, about 5 km southeast of the Çifteler district in Eskişehir Province. This spring zone includes three major springs—two cold-water and one hot-water—forming the headwaters of the Sakarya River. The Sakarya River system is sustained by multiple tributaries, including the Porsuk, Kirmir, Seydisuyu, Mudurnu, Göksu, and Ankara streams, as well as the limnocrene Sakaryabaşı springs (Emiroğlu 2011; Köse et al. 2015; Aksu et al. 2018). However, its longitudinal connectivity has been significantly fragmented by four major dams—Sarıyar, Kargın, Gökçekaya, and Yenice—impeding fish migrations and altering flow regimes. The basin is also subject to intense anthropogenic pressures, including industrial discharge, agricultural runoff, and expanding urban wastewater inputs (Çiçek et al. 2013; Köse et al. 2014). Within this river system, the Eminekin region was selected as the focal study site (Suppl. material 1: fig. S1). This area includes a water impoundment structure that regulates water levels seasonally—retaining water in summer for irrigation and releasing it in winter. The Eminekin site is characterized by helophytic vegetation along its riparian margins and hot-water springs maintaining temperatures between 18–24 °C (Emiroğlu 2011). During summer, water depth can reach up to 10 meters. The site supports a range of human uses, including a research facility operated by Ankara University's Faculty of Agriculture, a municipal drinking water source, and a public swimming area established around one of the springs. This combination of hydrological regulation, thermal influence, and multi-use management makes Eminekin a unique and ecologically relevant location within the broader Sakarya River system for investigating freshwater ecological dynamics. This section of the river includes non-native species such as *C. gariepinus*, *C. gibelio*, and Nile tilapia *Oreochromis niloticus*, as well as the native species, with *A. escherichii* being most abundant. Other native species present, although much less common and abundant, include *Cobitis simplicispina*, *Oxynoemacheilus angorae*, *Alburnoides kosswigi*, *Barbus escherichii*, *Capoeta baliki*, *Anatolichthys villwocki*, *Vimba vimba*, *Cyprinus carpio*, and *Squalius pursakensis*.

Sample collection, laboratory processing and data analyses

Comparative functional response experiments

Laboratory experiments were designed to test whether results from simplistic setups can be scaled to the field stable isotope data. Therefore, the use of fish as prey in this study was a deliberate and ecologically relevant choice, as both predator species under investigation—*C. gariepinus* and *S. glanis*—are known to exert significant predatory pressure, primarily on native and often endemic freshwater fishes.

All experimental fish were collected from the field (Çifteler). Upon arrival at the laboratory, fish were measured for initial body mass and length: *C. gariepinus* (230–410 g, 330–410 mm), *S. glanis* (220–330 g, 300–380 mm), *A. escherichii* (12–21 g, 111–136 mm), and *C. gibelio* (14–37 g, 89–125 mm). They were then acclimated for 40 days at 21 °C under a 16:8 h light-dark cycle. Outside of experiments, fish were housed in 90 L flow-through stock tanks and maintained on a diet of crushed pelletized fishmeal. For CFR experiments, catfish species were presented with *A. escherichii* and *C. gibelio* as prey in 90 L tanks at 21.5 °C (reflecting the average temperature of their collection sites) following a 24-hour period where food was withheld. Prey densities were set at 1, 2, 4, 8, 16, 32, and 64 fish, with a 24-hour exposure period. The number of fish consumed was recorded, with three replicates per prey density per species.

The CFR parameters, attack rate (a) and handling time (h), were estimated for each species and temperature using maximum likelihood estimation (MLE) within the Random Predator Equation, implemented in the R package "*Frair*" (Pritchard et al. 2017) in R 4.5.1 (R Core Team 2025). This equation assumes a Type II functional response (eqn 1) and non-replacement of prey, expressed as:

$$N_e = N_0\,(1 - \exp(a(N_e h - T))) \qquad \text{eqn 1}$$

where N_e is the number of prey consumed, N_0 is the initial prey density, a represents the attack parameter, h is the handling parameter, and T is the total experimental duration. To visualize uncertainty, 2000 non-parametric bootstraps were used to generate empirical 95% confidence intervals around the functional response curves. These curves can be considered a population level phenomenological comparison between treatments where lack of overlapping is regarded as statistically significant. We used Z-tests implemented in the frair::frair_compare function to assess statistical differences in *a* and *h* between species (Pritchard et al. 2017; Cuthbert et al. 2019). Maximum feeding estimate (1/*h*) was calculated for each predator - prey treatment. To assess drivers of ecological impact (i.e. *a* or *h*), we calculated the Functional Response Ratio (FRR) as FRR = *a*/*h*, where *a* is the attack rate and *h* is the handling time derived from the functional response curve (Cuthbert et al. 2019).

Isotope data

To assess the ecological niche and interspecific interactions of invasive *C. gariepinus* and native *S. glanis* we conducted stable isotope analysis. Sampling was conducted in July 2022 during summer. Fish were collected using electrofishing, both with a backpack unit (SAMUS 1000) and from a boat (LANJING LJ-4085NP-24V IGBT NC Fish Shocker). In total, 15 specimens of each species of *C. gariepinus*, *S. glanis*, *A. escherichii* and *C. gibelio* were collected for stable isotope analysis, with *A. escherichii* and *C. gibelio* considered as important fish prey. Muscle tissue samples were taken from all individuals of each fish species for stable isotope analysis. The tissue was carefully cleaned to remove fat, skin, scales, and bones before being stored at −20 °C.

Samples were dried for 48 hours at 60 °C in separate glass trays, then finely ground into a powder using an agate mortar and pestle. The processed samples were analyzed using a Thermo Finnigan Delta Plus Advantage isotope ratio mass spectrometer at the Biological and Chemical Research Centre in Warsaw, Poland. Isotope compositions were expressed in ‰ using the δ notation: $\delta^{13}C$ or $\delta^{15}N = ((R_{sample} / R_{standard}) - 1) \times 1000$, where R represents the $^{13}C{:}^{12}C$ or $^{15}N{:}^{14}N$ ratios. Vienna Pee Dee Belemnite served as the standard for carbon, while atmospheric N_2 was used for nitrogen. The $\delta^{15}N$ values were converted to trophic position (TP) to provide a more ecologically meaningful metric, using the following equation:

$$TP_i = (\delta^{15}N_i - \delta^{15}N\_base) / 3.4 + 2 \qquad \text{eqn 2}$$

where TP_i is the trophic position of the individual fish, $\delta^{15}N_i$ is the nitrogen isotope value of that individual, $\delta^{15}N\_base$ is the average value for primary consumers (i.e., the baseline invertebrates), 3.4‰ represents the average enrichment in $\delta^{15}N$ per trophic level, and 2 corresponds to the assumed trophic position of the baseline organism (Post 2002).

To evaluate isotopic niche overlap between the two species, we applied three complementary methods. First, we tested for significant differences in $\delta^{15}N$ and $\delta^{13}C$ values using a permutational univariate analysis of variance (PERANOVA), based on Euclidean distance with 9,999 permutations, implemented via the "*adonis2*" function in the vegan R package (Oksanen 2012). Second, we quantified isotopic niche overlap using standard ellipse areas (SEA), estimated via maximum likelihood. Both 40% and 95% SEA values (applying SEAc where needed to correct for small sample sizes) were derived and niche overlap expressed as the proportion of shared ellipse area relative to each species' total niche area. This was performed using the "*SIBER*" R package (Jackson et al. 2011).

Ecological Niche Modelling (ENM)

Environmental niche modelling was used to determine future spatial extent of species overlap to upscale impact assessment (both predation and competition) of non-native predator *C. gariepinus* on native functional analogue *S. glanis* and native and non-native fish prey. Therefore, this study focused on the natural distribution range of *Alburnus* species and non-native distribution range of *C. gibelio* to predict hotspots of impact.

Species occurrence records were obtained from the Global Biodiversity Information Facility (GBIF; GBIF.org, 2022; GBIF.org, 2025a, 2025b, 2025c) and supplemented by field sampling (Suppl. material 1: fig. S2). To ensure spatial accuracy, the dataset was cleaned using the "*CoordinateCleaner*" package (Zizka et al. 2019), which removes records from institutions or museums, zero coordinates, and other common spatial anomalies. Additional manual filtering was performed to exclude records with missing coordinates, outliers, and potentially erroneous data points. To reduce spatial autocorrelation, a spatial thinning procedure was applied in ArcGIS Pro 3.4 (Esri 2025) using the *SDMtoolbox* 2.0 plugin (Brown et al. 2017).

Nineteen bioclimatic variables and one elevation raster were retrieved from the WorldClim 2.1 database (Fick and Hijmans 2017), all at a spatial resolution of 2.5 arc-minutes (~5 km). Raster layers were cropped to the extent of the study area (West: -20°, East: 80°, South: 20°, North: 75°) and resampled to align with the elevation layer. Grid cells with missing environmental values were excluded from further analysis. Future climate projections were obtained from CMIP6 models under two Shared Socioeconomic Pathways (SSP1-2.6 and SSP5-8.5) for the time periods 2041–2060 and 2081–2100 (Eyring et al. 2016). Models were selected based on their demonstrated reliability in simulating freshwater ecosystem dynamics and hydrological processes (Suppl. material 1: table S1).

To address multicollinearity among environmental predictors, a two-step variable selection procedure was applied. First, Pearson correlation coefficients were calculated for all variable pairs, and one variable from each pair with a correlation coefficient $|r| > 0.90$ was removed to reduce redundancy (Dormann et al. 2013). In the second step, a Variance Inflation Factor (VIF) analysis was conducted using the "*usdm*" package (Naimi et al. 2014), and variables with VIF values exceeding 10 were iteratively excluded until all retained predictors met the threshold.

Species Distribution Modelling (SDM)

Species distribution models (SDMs) were constructed using the "*BIOMOD2*" package (Thuiller et al. 2014) in R, with version 4.2–6-1 employed in combination with the terra package for raster processing. A total of 9 modelling algorithms were implemented, including Artificial Neural Networks (ANN), Flexible Discriminant Analysis (FDA), Generalized Additive Models (GAM), Generalized Boosted Models (GBM), Generalized Linear Models (GLM), Maximum Entropy (MAXENT and MAXNET), Random Forest (RF), and Extreme Gradient Boosting (XGBOOST).

Model validation was performed via five-fold cross-validation. Model performance was evaluated using the True Skill Statistic (TSS) and the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC). Only models with both TSS and AUC values greater than 0.6 were retained for the final ensemble predictions. Environmental variable extraction and raster manipulation were conducted using the "*dismo*" package (Hijmans et al. 2017).

Sympatry (Overlap) Analysis

To identify potential contact zones between species, habitat suitability rasters from individual SDMs were multiplied on a pixel-by-pixel basis following Emiroğlu et al. (2023). The resulting raster values were normalized to a scale of 0–100 and classified into five categories: 0–20%, 20–40%, 40–60%, 60–80%, and 80–100%. The proportion of pixels falling within each category was calculated and visualized using histograms to evaluate spatial overlap and degrees of sympatry.

Results

Comparative functional responses

All predator prey combinations resulted in significant Type II functional responses indicating high prey consumption at low prey densities (Table 1). Functional response curves of each predator diverged for both prey species, with impact on *A. escherichii* being the most pronounced for both (Fig. 1). Functional response curves for both predators feeding on the same prey overlapped considerably indicating similar predation efficiency (Fig. 1).

Prey consumption comparisons

There was no difference in attack parameters on *A. escherichii* compared to *C. gibelio* in either predator species (Table 2, Fig. 1). Handling time (*h*) was significantly longer for *C. gibelio* than for *A. escherichii* in both *C. gariepinus* and *S. glanis* (Table 2, Fig. 1), indicating that both predators required more time to subdue and consume the non-native prey.

Predator comparisons

Clarias gariepinus had a significantly higher attack rate than *S. glanis* when preying on *A. escherichii* (Table 2, Fig. 1), while no significant difference was observed for *C. gibelio* (Table 2, Fig. 1). Handling time differences between the species were not statistically significant for either prey ($P > 0.05$).

Functional Response Ratio

Clarias gariepinus exhibited a notably higher FRR when preying on *A. escherichii* (203.5) compared to *C. gibelio* (61.3), suggesting substantially greater predatory efficiency on the native prey (Table 2). Similarly, *S. glanis* also showed a higher FRR on *A. escherichii* (123.5) than on *C. gibelio* (49.0) (Table 2, Fig. 1).

Table 1. First order linear coefficient results from logistic regressions for the predator and prey combinations. All values indicate a Type II functional response.

Prey	Species	Linear coefficient	*P*
A. escherichii	*C. gariepinus*	-0.07	**< 0.0001**
	S. glanis	-0.06	**< 0.0001**
C. gibelio	*C. gariepinus*	-0.04	**< 0.0001**
	S. glanis	-0.03	**< 0.0001**

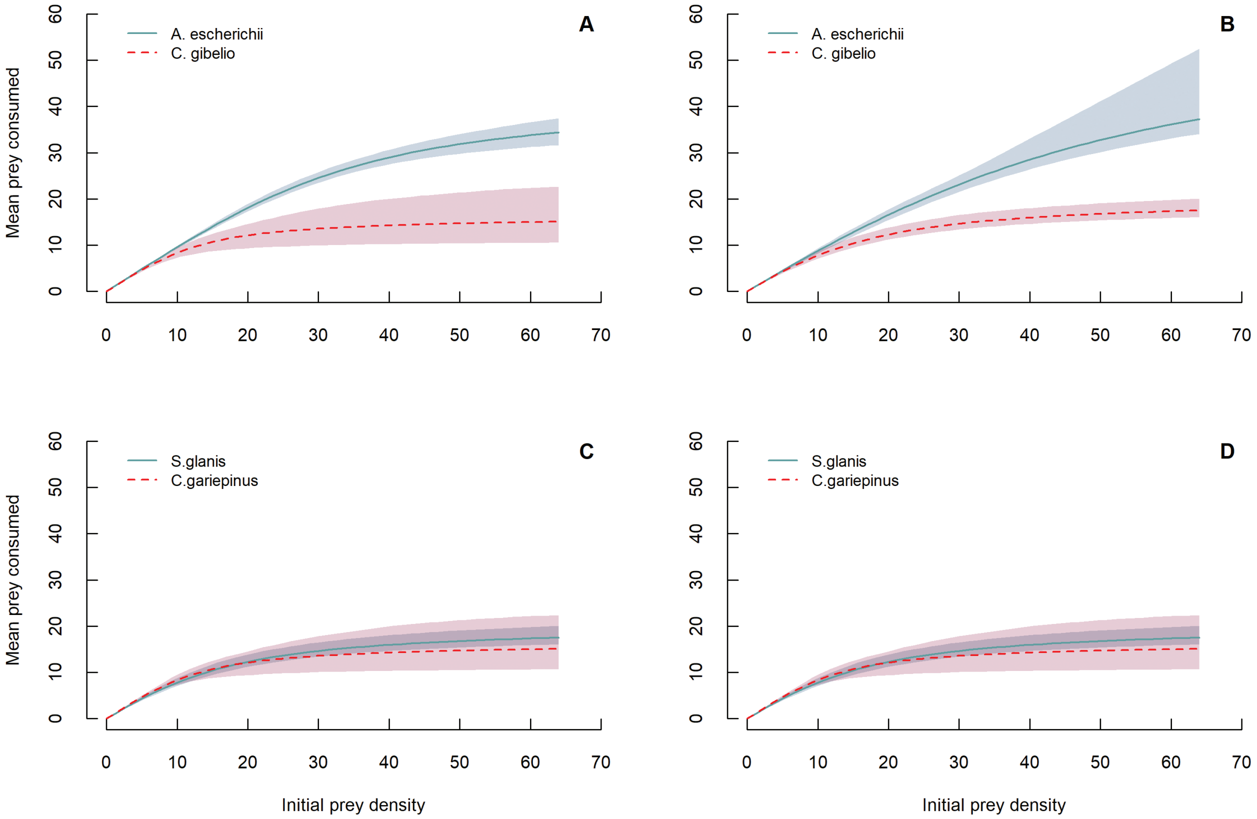

Figure 1. Comparative functional response curves for (**A**) *Clarias gariepinus* and (**B**) *Silurus glanis* feeding on *Alburnus escherichii* and *Carassius gibelio* as prey. Panels (**C**) and (**D**) show combined responses of both predators on *A. escherichii* and *C. gibelio*, respectively. Shaded areas around the curves represent 95% confidence intervals generated by bootstrapping.

Table 2. Parameters of the comparative functional responses, with statistically significant differences in the parameters between species (α = 0.05) in bold. *a* = attack rate, *h* = handling time (B). *Z* and *P* values are statistical outputs from regression that indicate whether *a* and *h* differ significantly between the comparator species. FRR is the functional response ratio.

	A. escherichii / C. gibelio (C. gariepinus)	*A. escherichii / C. gibelio (S. glanis)*	*C. gariepinus / S. glanis (A. escherichii)*	*C. gariepinus / S. glainis (C. gibelio)*
a	4.07/3.68	2.47/2.45	4.07/2.47	3.68/2.45
Z	0.38	0.04	-2.09	-1.40
P	0.71	0.97	**0.05**	0.16
h	0.02/0.06	0.02/0.05	0.03/0.02	0.06/0.05
1/*h*	50/17	50/20	33/50	17/20
Z	-5.65	-5.10	-1.79	-1.39
P	**< 0.0001**	**< 0.0001**	0.07	0.17
FRR	203.5/61.3	123.5/49	135.7/123.5	61.3/49

Isotope analysis

Fish length and mass, and isotopic metrics of the studied species are summarized in Table 3. *Alburnus escherichii* and *C. gibelio* did not significantly differ in length (P = 0.12) but did in weight ($P < 0.05$). In contrast, *S. glanis* was significantly larger and heavier than *C. gariepinus* ($P < 0.01$). Trophic position (TP) was highest in *S. glanis*, followed by *C. gariepinus*, *A. escherichii*, and *C. gibelio*. δ^{13}C values were highest in *C. gariepinus* and *A. escherichii*, with *C. gibelio* showing the most depleted values. Significant positive relationships between TP or δ^{13}C and size (TL and W) were observed only in *S. glanis*.

Table 3. Summary of morphological and isotopic metrics with associated statistical comparisons among species.

Species	Mean TL (mm) ± SE	W (g) Mean ± SE	TP	δ^{13}C (‰)	δ^{15}N (‰)	TP–TL	TP–W	δ^{13}C–TL	δ^{13}C–W
C. gariepinus	360.7 ± 4.34	282.5 ± 11.14	3.30	-26.76	11.66	0.44	0.31	0.22	0.26
S. glanis	585.5 ± 10.71	1352.3 ± 86.93	3.57	-24.65	12.60	**0.01**	**0.001**	**0.01**	**0.01**
A. escherichii	117.5 ± 1.86	24.24 ± 0.90	2.89	-26.69	10.27	0.78	0.66	0.71	0.47
C. gibelio	110.8 ± 3.89	21.24 ± 2.28	2.83	-21.45	10.07	0.20	0.23	0.43	0.26

Significance *P* values in bold. SE = standard error; TL = total length; W = weight; TP = trophic position; δ^{13}C = carbon stable isotope ratio.

The isotopic niches of *C. gariepinus* and *S. glanis* were statistically differentiated for δ^{13}C (pseudo$F_{1,19}$ = 7.67, P = 0.009) but not for δ^{15}N (pseudo$F_{1,19}$ = 0.62, P = 0.47). Standard ellipse areas (SEA; maximum likelihood estimates) showed limited niche overlap between the two species. Using the 95% SEA, the overlap of *C. gariepinus* with *S. glanis* was 5.4% (Fig. 2). When considering the 40% SEA, the overlap estimate was very small (0.3%).

Ecological niche modelling

Bioclimatic variables were selected based on correlation analysis (Suppl. material 1: fig. S3). Model performance, evaluated via the True Skill Statistic (TSS), showed good fit across taxa: *Alburnus* sp. (TSS: 0.77–0.89), *C. gariepinus* (0.63–0.78), *C. gibelio* (0.77–0.94), and *S. glanis* (0.81–0.93) (Table 4). *Alburnus* sp., *C. gibelio* and *S. glanis* showed broad habitat suitability across Europe, with suitable areas also identified for *C. gariepinus* (Suppl. material 1: fig. S4).

For *Alburnus* sp., the strongest predictors were BIO3 (Isothermality), BIO7 (Annual Temperature Range), and BIO5 (Max Temperature of Warmest Month), underscoring its sensitivity to temperature structure. Suitability declined sharply when BIO3 exceeded ~40, indicating a preference for areas with distinct seasonal variation but low daily fluctuation (Suppl. material 1: fig. S5). *Clarias gariepinus* distribution was shaped mainly by BIO1 (Annual Mean Temperature), BIO3, and BIO7. Suitability increased above BIO3 ~50, highlighting its preference for thermally stable environments with moderate seasonal variability (Suppl. material 1: fig. S5).

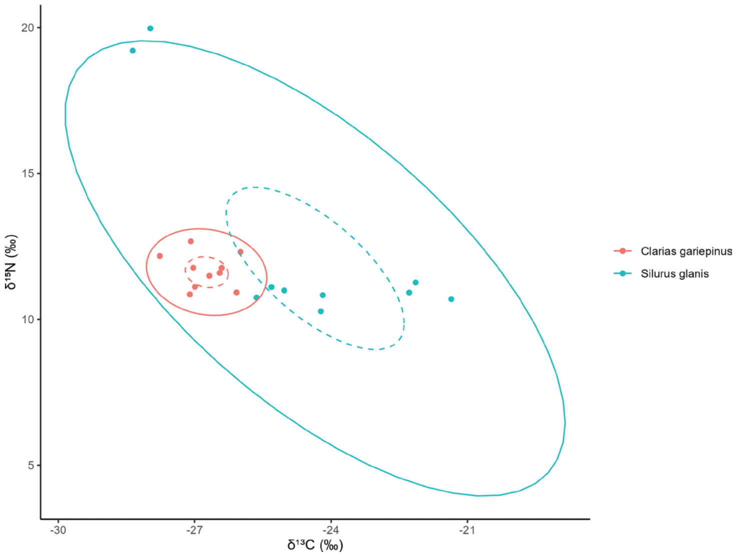

Figure 2. A Standard Ellipse Areas (SEA) for *C. gariepinus* and *S. glanis*: 95% (solid lines) and 40% (dashed lines).

Table 4. Mean TSS and ROC values across species distribution models.

Species	Metric	ANN	FDA	GAM	GBM	GLM	MAXENT	MAXNET	RF	XGBOOST
Alburnus sp.	TSS	0.79	0.87	0.83	0.89	0.88	0.77	0.86	0.89	0.86
	ROC	0.92	0.96	0.96	0.98	0.98	0.91	0.97	0.98	0.97
S. glanis	TSS	0.88	0.87	0.83	0.91	0.88	0.81	0.89	0.93	0.87
	ROC	0.95	0.98	0.97	0.99	0.98	0.92	0.98	0.99	0.97
C. gariepinus	TSS	0.64	0.71	0.63	0.74	0.68	0.61	0.70	0.78	0.68
	ROC	0.88	0.93	0.90	0.95	0.92	0.86	0.93	0.97	0.92
C. gibelio	TSS	0.85	0.90	0.78	0.90	0.89	0.84	0.89	0.94	0.87
	ROC	0.95	0.98	0.94	0.99	0.98	0.93	0.99	1.00	0.98

For *S. glanis*, BIO1, BIO11 (Mean Temperature of Coldest Quarter), and BIO7 were most important. High sensitivity to cold-season temperatures and a preference for variable thermal regimes (suitability dropped when BIO3 exceeded ~45) indicate its ecological restriction to regions with marked seasonal change (Suppl. material 1: fig. S5). *Carassius gibelio*'s distribution was driven by BIO3, BIO5, and BIO19 (Precipitation of Coldest Quarter), favoring areas with broad annual but narrow daily temperature ranges (Suppl. material 1: fig. S5).

Habitat overlap analyses revealed the greatest shared suitability between *S. glanis* and both *Alburnus* sp. and *C. gibelio* (Table 5, Suppl. material 1: table S2, Fig. 3). *C. gariepinus* overlapped with *Alburnus* sp. and *S. glanis* across three suitability classes, extending to four classes with *Alburnus* sp. alone (Table 5). All species shared habitat in three common classes (Table 5; Suppl. material 1: fig. S3).

Discussion

Predicting ecological interactions from experimental studies has long been challenged by questions about how well simplified settings capture the complexity of natural systems. In this study, each methodological component—functional responses (FRs), stable isotope analysis (SIA), and ecological niche modelling (ENM/SDM)—provides a different line of evidence on predator foraging, trophic position, and spatial-climatic context. Rather than viewing these as providing a single deterministic prediction, our aim is to integrate them as complementary perspectives that together identify where interactions are most likely to occur, and which mechanisms may underpin them.

Our functional response experiments provide mechanistic insights into the feeding efficiencies of the two apex predators but do not, on their own, explain the observed trophic niche segregation. Instead, the narrower isotopic niche of *C. gariepinus* suggests that, under field conditions, the individuals sampled had a more specialized diet relative to *S. glanis*. Equivalent FR curves between both species indicate their broadly comparable consumer efficiency, which is consistent with competitive potential, while SIA shows minimal trophic niche overlap due to *C. gariepinus* exhibiting a more restricted niche. Furthermore, both species demonstrated a preference for native prey species *A. escherichii* over non-native *C. gibelio* in functional response analysis. This highlights the potential of both predators to destabilize *A. escherichii* populations, especially when co-occurring. Thereby, these results identify the mechanisms through which both predators could affect native prey when they co-occur.

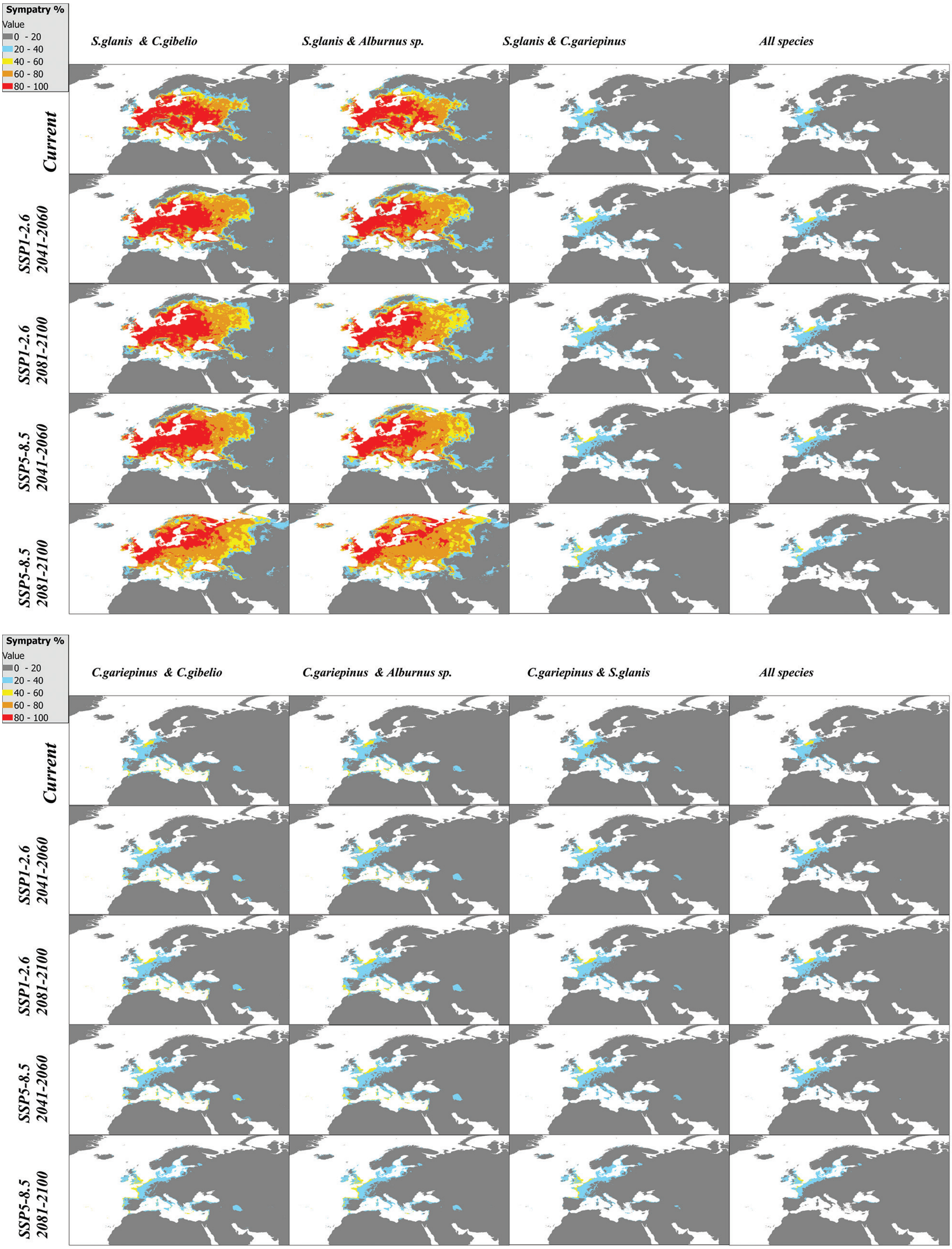

Figure 3. Prediction of overall niche overlap between *Silurus glanis* (top plot) and *Clarias gariepinus* (bottom plot) and other species assessed in current and different climate models.

Table 5. Projected habitat overlap (%) between *C. gariepinus*, *S. glanis*, *C. gibelio*, *Alburnus* sp. across five suitability classes under different climate scenarios.

Species Pair	Scenario	0–20%	20–40%	40–60%	60–80%	80–100%
C. gariepinus–*Alburnus* sp.	Present	92.0	6.9	1.1	0.0	0.0
C. gariepinus–*Alburnus* sp.	SSP1-2.6 (2040–2060)	91.2	7.6	1.2	0.0	0.0
C. gariepinus–*Alburnus* sp.	SSP1-2.6 (2080–2100)	90.7	8.0	1.3	0.0	0.0
C. gariepinus–*Alburnus* sp.	SSP5-8.5 (2040–2060)	90.8	8.0	1.2	0.0	0.0
C. gariepinus–*Alburnus* sp.	SSP5-8.5 (2080–2100)	91.5	7.7	0.9	0.0	0.0
C. gariepinus–*S. glanis*	Present	94.3	5.3	0.4	0.0	0.0
C. gariepinus–*S. glanis*	SSP1-2.6 (2040–2060)	93.6	5.9	0.5	0.0	0.0
C. gariepinus–*S. glanis*	SSP1-2.6 (2080–2100)	93.2	6.2	0.5	0.0	0.0
C. gariepinus–*S. glanis*	SSP5-8.5 (2040–2060)	93.1	6.4	0.5	0.0	0.0
C. gariepinus–*S. glanis*	SSP5-8.5 (2080–2100)	93.4	6.1	0.6	0.0	0.0
C. gariepinus–*C. gibelio*	Present	92.1	6.8	1.0	0.1	0.0
C. gariepinus–*C. gibelio*	SSP1-2.6 (2040–2060)	91.4	7.4	1.1	0.1	0.0
C. gariepinus–*C. gibelio*	SSP1-2.6 (2080–2100)	91.0	7.7	1.2	0.1	0.0
C. gariepinus–*C. gibelio*	SSP5-8.5 (2040–2060)	91.0	7.8	1.2	0.1	0.0
C. gariepinus–*C. gibelio*	SSP5-8.5 (2080–2100)	91.5	7.5	1.0	0.0	0.0
S. glanis–*Alburnus* sp.	Present	65.5	7.9	4.9	8.5	13.2
S. glanis–*Alburnus* sp.	SSP1-2.6 (2040–2060)	59.1	8.4	6.4	12.8	13.3
S. glanis–*Alburnus* sp.	SSP1-2.6 (2080–2100)	58.2	9.0	7.6	12.0	13.1
S. glanis–*Alburnus* sp.	SSP5-8.5 (2040–2060)	57.4	8.2	6.9	14.4	13.2
S. glanis–*Alburnus* sp.	SSP5-8.5 (2080–2100)	55.9	6.7	6.9	21.6	8.7
S. glanis–*C. gibelio*	Present	67.6	6.8	4.2	6.9	14.5
S. glanis–*C. gibelio*	SSP1-2.6 (2040–2060)	62.4	5.8	4.9	11.0	15.9
S. glanis–*C. gibelio*	SSP1-2.6 (2080–2100)	61.8	6.1	5.8	10.5	15.8
S. glanis–*C. gibelio*	SSP5-8.5 (2040–2060)	61.0	5.8	5.2	12.2	15.8
S. glanis–*C. gibelio*	SSP5-8.5 (2080–2100)	58.4	5.8	8.0	17.0	10.7
All species	Present	95.9	3.8	0.3	0.0	0.0
All species	SSP1-2.6 (2040–2060)	95.3	4.4	0.3	0.0	0.0
All species	SSP1-2.6 (2080–2100)	94.9	4.8	0.3	0.0	0.0
All species	SSP5-8.5 (2040–2060)	95.0	4.7	0.3	0.0	0.0
All species	SSP5-8.5 (2080–2100)	95.6	4.2	0.2	0.0	0.0

Determining the mechanism of ecological impacts is essential to predict outcomes of biological invasions (Carneiro et al. 2025). Niche constriction of invasive species when in sympatry with native analogues fits the niche variation, or trophic specialization hypothesis, where generalist species become more specialist to reduce competition (Mason et al. 2008; Britton et al. 2019; Dominguez-Almela et al. 2021). Lack of difference in functional response curves on either prey species indicated competitive ability between predators. Stable isotope analysis showed limited niche overlap between predator species despite similar trophic positions and no difference in δ^{15}N. *Silurus glanis* is predominantly a piscivore with some reliance on macroinvertebrates (Vagnon et al. 2022; Baer et al. 2025), in comparison, *C. gariepinus* exhibits considerable generalist omnivory with no specific dietary preference (Kadye and Booth 2012b; Low et al. 2022). This pattern suggests that when these predators co-occur, behavioural or dietary adjustments may reduce direct competitive interactions, as noted for *S. glanis* in interactions with northern pike *Esox lucius* Linnaeus, 1758 and channel catfish *Ictalurus punctatus* (Rafinesque, 1818) (Haubrock et al. 2020; Říha et al. 2025).

Both predator species exhibited consistently high predation pressure on *A. escherichii* rather than the non-native *C. gibelio* as supported by functional response derived evidence. This supports previous findings highlighting *Alburnus* spp. as principal prey for *S. glanis* (Alp 2017) and underscores the susceptibility of native cyprinids to heightened predation pressure in invaded systems (Tarkan et al. 2023a). The lower impact on *C. gibelio* was driven by longer handling times than for *A. escherichii* in both predators. This suggests that *C. gibelio* may benefit from a degree of predation refuge, potentially due to *C. gibelio* having a deeper bodied morphology (Tarkan et al. 2023b) and neither predator having eco-evolutionary experience with *C. gibelio*. Furthermore, *A. escherichii* has similar morphology to South African redfin minnows and barbs - *Psuedobarbus* spp., *Enteromius* spp., which have experienced population declines because of *C. gariepinus* invasions (Cambray 2003).

Ecological niche modelling revealed divergent but overlapping habitat preferences, shaped primarily by key bioclimatic variables. While *C. gariepinus* favored thermally stable regions with moderate seasonal variability, *S. glanis* showed a clear preference for areas with more pronounced seasonal fluctuations and greater sensitivity to cold-quarter temperatures. Notably, *S. glanis* exhibited a much broader potential distribution across temperate zones, reflecting a closer climatic match to many habitats occupied by *Alburnus* spp. This suggests that *S. glanis* may pose a more pervasive and sustained predation threat to native *Alburnus* populations than *C. gariepinus*, whose range remains comparatively constrained by its reliance on warmer, more stable thermal regimes. Despite these ecological distinctions, climate projections indicate expanding and increasingly overlapping ranges for both predators, especially under warming scenarios. This aligns with Rahel and Olden (2008) and Emiroğlu et al. (2023), who highlight climate change as a key driver of range expansions among both invasive and native freshwater predators. However, we emphasize that these correlative models identify spatial and climatic contexts for possible interactions—they do not predict the outcomes of competition or predation. They do not incorporate behavioral plasticity, diet switching, or density-dependent processes, all of which are critical for determining realised interactions. Ideally, fully forecasting predator-prey or predator-predator dynamics under climate change would require individual-based models, multispecies mechanistic models, or dynamic trophic networks. Parameterizing such models would require empirical data on interaction strengths, habitat partitioning, and context-dependent feeding behavior that are currently unavailable but should be a research priority to develop and validate. For these reasons, our SDMs should be interpreted as identifying areas of heightened potential ecological risk, rather than deterministic predictions of interaction outcomes.

Our findings demonstrate the mechanisms which govern asymmetric ecological interactions in a fish community of native and invasive species. The ability of *C. gariepinus* to reduce trophic niche size can facilitate persistence in sympatry with *S. glanis* both now and in future range expansion scenarios. However, our analysis is limited as we were not able to sample stable isotopes from locations where the predators occur in alloaptry to confirm our hypothesis absolutely. Nonetheless, the combination of our results reinforces the notion that the additive pressure exerted by both *C. gariepinus* and *S. glanis* may compound threats to native cyprinid populations, underscoring the importance of integrated management strategies that address both non-native and native apex predators. Habitat suitability models further suggest that climate change will exacerbate invasion dynamics, emphasizing the urgency of incorporating climate-adaptive approaches into biosecurity planning (Gallardo et al. 2016; Aksu et al. 2024). To further understand the complexity of trophic interactions future research should incorporate multi-prey systems to better capture the complexity of trophic interactions and potential prey-switching behaviors that might emerge under varying prey availability. Moreover, while temperature emerged as a dominant driver in the niche models, other environmental factors—such as dissolved oxygen, habitat structure, water flow, and pollution levels—likely play critical roles in shaping predator distributions and interactions. These factors were beyond the scope of the present study but warrant detailed investigation to refine our understanding of invasion dynamics. Further, the human dimension is likely to be highly influential. Both *S. glanis* and *C. gariepinus* are valued by recreational anglers, and intentional or accidental introductions, translocations, and management practices driven by socio-economic motivations may significantly shape their future distributions (Tarkan et al. 2015; 2024; South et al. 2022). Additionally, while our controlled functional response trials provided valuable mechanistic insights, mesocosm or long-term field experiments are essential to validate these patterns in more complex, natural settings where indirect interactions, habitat heterogeneity, and temporal variability may significantly influence outcomes (Ricciardi et al. 2013; Dominguez-Almela et al. 2021).

From a regional conservation perspective, these results raise urgent concerns for Turkish freshwater systems. The establishment of *C. gariepinus* in these environments risks displacing native predators, destabilizing ecological balances, and accelerating biodiversity loss (Emiroğlu et al. 2018). Notably, findings from a recent study on the Upper Sakarya Basin demonstrate that even localized hot spring sources can facilitate the establishment and range expansion of non-native fish species. Despite thermal refugia being patchy, dispersal habitats are likely, especially during warmer months, and such connectivity is expected to become more pronounced and sustained under future climate conditions (Aksu et al. 2021). Historically, *S. glanis* has played a key role in structuring native fish communities, but its dominance is now challenged by the dual pressures of biological invasion and environmental change (Tarkan et al. 2015). It is uncertain what population level effects of interspecific competition by *C. gariepinus* may have on *S. glanis* and other native species, thus this should be a research priority. Conservation strategies should thus prioritize habitat restoration, vigilant monitoring of predator-prey dynamics, and stricter regulation of aquaculture and fish stocking practices to limit further spread of *C. gariepinus*. Adaptive management frameworks that integrate climate projections will also be essential to mitigate long-term risks, particularly as thermal regimes shift and expand potential overlap between these competing predators. In the broader European context, the dual invasive and native-invader roles of *S. glanis* highlight the complexities of managing apex predators across their native and non-native ranges (Copp et al. 2009). Integrated conservation policies must account for the compounded threats of invasive apex predators and climate change, underscoring the need for transboundary cooperation and data sharing.

In conclusion, our integrated approach highlights how combining mechanistic feeding trials, field-based trophic data, and climatic suitability modelling can reveal where and how ecological risks may emerge, even if interaction outcomes cannot yet be fully predicted. The combination of strong predatory impacts, overlapping ecological niches, and climate-driven range expansions suggests that freshwater ecosystems face mounting pressures from dual apex predator dynamics—posing new challenges for biodiversity conservation and fisheries management across Eurasia.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

The experiment and all regulated procedures were completed following ethical approval by the Animal Welfare and Ethical Review Board of Fisheries Faculty, Muğla Sıtkı Koçman University (No: E-38607093-604.01-301669).

Use of AI

No use of AI was reported.

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Author contributions

Sercan Başkurt and Ali Serhan Tarkan conceived the ideas and designed methodology; Sercan Başkurt, Özgür Emiroğlu, Sadi Aksu, Esengül Köse, Oğuzcan Mol, Emre Çınar collected the data; Ali Serhan Tarkan and Sadi Aksu analysed the data; Ali Serhan Tarkan and Josie South led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Tables and figures

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Supplementary material 2

Raw data

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