Predicting how climate change and globally invasive piscivorous fishes will interact to threaten populations of endemic fishes in a freshwater biodiversity hotspot

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Abstract

Freshwater ecosystems are highly vulnerable to the detrimental impacts of both biological invasions and climate change. Piscivorous alien fishes drive populations of small-bodied native fishes to extinction and warming is already driving extreme temperature events in lakes and rivers globally. Here, we use Ecological Niche Modelling (ENM) to predict how climate change will alter the geographical space of six alien fishes and five native fish genera (which include multiple endemic species) in Turkey, a hotspot of freshwater fish diversity. The models predicted that the geographical space of the alien fishes already present in Turkey would generally increase (including pikeperch *Sander lucioperca* and perch *Perca fluviatilis*), but with the most substantial increases in largemouth bass *Micropterus salmoides*, a species not yet present in Turkey but that is invasive in countries nearby and is highly popular for sport angling. For the native fish genera, general predictions were for reduced geographical space, especially in the south and east of the country, suggesting the endemic species will become increasingly imperilled in future. Their populations will also be at increasing risk of deleterious impacts from the alien piscivores, as the predictions were also for increasing overlaps in the geographical space of both the alien fishes and native fish genera. These predictions suggest that the conservation of these endemic species need to consider measures on preventing both the introduction of alien species (e.g. largemouth bass) and the further dispersal of extant alien species (e.g. pikeperch), as well as habitat interventions that will limit the effects of climate change on their populations. These results also indicate that the combination of climate change and alien invasions could have substantial impacts on this – and similar – hotspots of freshwater diversity.

Keywords: Ecological Niche Modelling, Biological Invasions, Freshwater conservation, Impact risk

Introduction

Freshwater ecosystems are highly vulnerable to the detrimental impacts of climate change (Woodward et al. 2010), with warming already driving extreme temperature events in lakes and rivers around the world (Gudmundsson et al. 2021; Piccolroaz et al. 2020). These are coupled with extreme low flow events in rivers, which have globally been experiencing substantial declines in their fish diversity and population abundances (Su et al. 2021). Contemporary climate change is resulting in many species in the northern hemisphere shifting their distributions to areas of higher latitude (Jaric et al. 2019). However, the climate-driven dispersal of riverine fishes is inherently limited by natural and anthropogenic physical boundaries, resulting in species not shifting their distributions at a pace sufficient to track the rate of warming (Comte et al. 2013). Consequently, climatically vulnerable riverine fishes must also adapt *in situ* within communities where all species are responding to the altered conditions (Piccolroaz et al. 2020).

Where climate is a primary driver of species distributions (Hampe et al. 2004), predicting changes in their distributions requires consideration of both current and future climate scenarios (Heikkinen et al. 2006). This is more complex in regions where alien species are frequently introduced and translocated. This is because when these introductions are successful due to the effects of climate change (e.g., due to warming), it is highly likely that the integration of the alien species into the community will result in ecological impacts on native fishes that exacerbate the impacts already being caused by warming (Radinger et al. 2019; Radinger & Garcia-Berthou 2020). Moreover, warming temperatures might also release the thermal constraints on some warm-water alien fishes that are already present in temperate freshwaters, facilitating their establishment in areas where the current thermal regime inhibits this (Rahel and Olden 2008). This is already evident in England and Wales for some alien freshwater fish species, including common carp *Cyprinus carpio*, which are now increasingly developing invasive populations through warmer summer temperatures (Skeate et al. 2022). Predicting which of these persistent alien species will go on to develop invasive populations is important for implementing preventative measures to minimise impacts on native species (Spear et al. 2021; Iacarella et al. 2015). These measures are especially important to implement in regions where the assemblages include endemic species that are already threatened by other environmental changes, such as habitat fragmentation (Beatty and Morgan 2013).

Predatory invasive species have been identified as a major driver of species extinctions, with invasive predatory mammals implicated in the extinction or endangerment of 738 vertebrate species (Doherty et al. 2016). In freshwaters, invasive piscivorous fishes are a key driver of fish diversity loss (Britton 2022). For example, invasive peacock basses (*Cichla* spp.) are implicated in the substantial declines (> 90 %) in the diversity and abundance of native and endemic fishes in some hydro-electric reservoirs in southern Brazil (Pelicice and Agostinho 2009; Leal et al. 2021). Largemouth bass *Micropterus salmoides*, a widely introduced invasive sport fish, has similarly been associated with large declines in populations of small-bodied, native prey fishes (Gratwicke and Marshall 2001), including causing extinctions (Hickley et al. 2015). Moreover, depending on the species and ecosystem, impacts of alien piscivorous fishes are often predicted to negatively affect prey populations more severely than native fishes due to substantially higher attack and consumption rates (Alexander et al. 2014). Correspondingly, in regions where these alien fishes have been introduced and are persisting but are not yet invasive due to thermal constraints, there is high concern that these species will subsequently develop invasive populations that then have deleterious impacts on native and endemic fish populations (Britton et al. 2010).

Climatically constrained but persistent alien species could thus potentially develop invasive populations in future. This can be predicted by climate change models to project shifts in the suitable thermal habitat of these species and hence predict their future distributions (Ruiz-Navarro et al. 2016a). When these predictions in shifting geographical space are completed for multiple species across large spatial areas, including endemic and native species, the extent of the spatial overlap in their geographical spaces can predict the extent to which these species are likely to coexist in future (Ruiz-Navarro et al. 2016b). Where an invading species is predicted to expand its geographical space and the extent of its co-existence with endemic species of diminishing geographical space, deleterious impacts on those endemics would then be predicted through both sub-optimal thermal regimes and increased predation pressure (Pysek et al. 2017). The identification of areas of high endemism that coincide with areas of highest invasion risk from persistent alien species can then be prioritised for immediate management actions to reduce these risks. Consequently, the aim of this study was to predict, in a freshwater biodiversity hotspot of high endemism, how climate change will alter the climate space for a range of high impacting alien piscivorous fishes, and overlay these predictions on those of threatened native fish genera. We posit that the geographical space for the alien piscivores will expand through warming to overlap the future distribution areas of the native fish genera, increasing their future interactions that will potentially result in substantially decreased fish diversity and endemism.

Material and Methods

The full roadmap on which analyses were based is summarized in Fig. 1

Study area and fish species

The focal area of study was the country of Turkey, a hotspot of freshwater fish diversity and endemism (Fricke et al. 2007), which has a distinct ichthyofauna that comprises of species present from both Europe and Asia (Smith and Darwall 2006; Cuttelod et al. 2009). To date, 384 freshwater fish species have been recorded from Turkey, of which 208 (54%) are endemic and 15 (4%) are alien (Çiçek et al. 2020). The country's latitudinal and longitudinal dimensions result in substantial differences in regional climates and so its climate change projections, with these coupled with the presence of large trans-boundary river systems that elevate the risk of introductions of alien fishes from both Asia and Europe. The risk of alien fish introductions is further elevated by government authorized aquaculture and stocking programmes based on both cage aquaculture and capture fisheries, with these acting as major introduction vectors (Tarkan et al. 2015).

There were six alien fish species selected for use here based on their current and likely coexistence with assemblages of native fish genera (Table S1); these were all of the order Perciformes: ruffe *Gymnocephalus cernua*, pumpkinseed *Lepomis gibbosus*, largemouth bass *Micropterus salmoides*, European perch *Perca fluviatilis*, Chinese sleeper *Perccottus glenii* and pikeperch *Sander lucioperca*. All of these fishes are piscivorous and the majority have deleterious and top-down impacts on small-bodied prey fish populations. Largemouth bass and Chinese sleeper have yet to be introduced, ruffe is present in the European regions only, with the remaining species all present across the country with populations either stable (pikeperch) or increasing (perch and pumpkinseed). All of these are temperate species, except for *L. gibbosus* and *G. cernua* that have wide temperature tolerances (4-30°C). Occurrence data were collected and modelled at genus-level for the native and endemic species that were all genera within the Cyprinidae family: *Alburnoides*, *Alburnus, Barbus, Gobio* and *Squalius*, within which there are numerous endemic species (Table S2). All modelled species were endemics of restricted distribution belonging to native fish genera and were all temperate.

Fish distribution data

Data on the occurrences of the selected alien fishes were obtained from a combination of sampling (for the species already present within Turkey) and global databases (e.g. the Global Biodiversity Information Facility (GBIF, https:// www. gbif. org/) (Table S3), where all records were non-duplicates. The corresponding occurrence unpublished data for native fish genera were obtained from only sampling programmes completed between 2002 and 2021 (Fig. S1) and from literature review. The reviewed literature covered peer-reviewed scientific papers and grey literature (e.g. checklists, institutional reports, conference proceedings), and covered the same time period as the sampling period. These data were then supplemented by data-mining online (e.g. geo-referenced images of alien fishes on social media sites). To sufficiently remove duplicates and avoid sampling bias, the records were rarefied spatially at 5 km intervals by using SDMtoolbox (Brown et al., 2017) in ArcGIS version 10.8.1 (ESRI, 2020). For alien species, the total number of occurrence records were: perch: 1679; ruffe: 1859; Chinese sleeper: 812; largemouth bass: 1788; pikeperch: 3230; and pumpkinseed: 1162. For the native fish genera, the total number of occurrence records were *Squalius*: 739; *Alburnoides*: 139; *Gobio*: 100; and *Alburnus*: 513. Note that for all of the native species of Table S1, their data were used at the genera level for the predictive modelling. This was because there were too few occurrence points for many of the endemic species to be useful at that taxonomic level and, given the high ecological and morphological characteristics of these species at the genus level, their occurrence data were able to be combined without compromising the relevance of the outputs.

Climate data

The climate data used were 19 bioclimate variables (Table S4), downloaded from WorldClim database version 2.1 (Fick and Hijmans 2017), and that had a spatial resolution of 2.5' (~4.63

km at the equator). These data were then clipped to the study area and their correlations tested in order to reduce the multicollinearity; where variables were highly correlated ($r \geq 0.7$), one of these variables was removed based on the relevancy of the variable to distribution of modelled species from the SDM toolbox (Brown et al. 2017). This resulted in 8 climate variables being used for both sets of species (Table S5). It acknowledged, however, that the retained climate variables are unlikely to be the only determinants of the distribution of these species (Pont et al. 2006), with other abiotic and biotic variables likely to also be influential, although they could not be incorporated into the models used (Wu et al. 2019).

The climate change projections used were for the years 2050 (2041-2060) and 2100 (2081-2100), using the lower and the upper limits of the Shared Socioeconomic Pathways (SSPs; SSP126 and SSP585) that were obtained from eight different global climate models (GCMs): BCC-CSM2-MR (Wu et al. 2019), CNRM-CM6-1 (Voldoire et al. 2019) CNRM-ESM2-1 (Seferian et al. 2019), CanESM5 (Swart et al. 2019), IPSL-CM6A-LR (Boucher et al. 2020), MIROC-ES2L (Tachiiri et al. 2019), MIROC6 (Shiogama et al. 2019), MRI-ESM2-0 (Yukimoto et al. 2019). These models represent a gradual decrease in CO_2 emissions and largely higher CO_2 respectively, and were used at a resolution of 2.5 (CarbonBrief 2016; https://www.worldclim.org/data/worldclim21.html). SSPs were used in the 6th Assessment Report by the Intergovernmental Panel on Climate Change (IPCC 2017), with these data from Phase 6 of the Combined Model Comparison Project (CMIP6) (Eyring et al. 2016; CarbonBrief 2016). The selection of CMIP6 models over CMIP5 models was primarily through their higher equilibrium climate sensitivity (ECS) (Carbonbrief, 2016), where model averages with low, medium and high ESC values were used.

Geographical space modelling

Predicted changes in the geographical space of the alien fishes and native fish genera were determined in bioclimate ensemble (i.e. consensus) (Marmion et al. 2009), as ensemble models overcome the variability of predictions that might occur between single models (Ruiz-Navarro et al. 2016b). Predictions of current and future fish species distributions were from 10 algorithms in the *biomod2* package (Thuiller et al. 2014) in R 2020: (1) generalized linear models (GLM), (2) Generalized Boosting Model (GBM), (3) random forests (RF), (4) generalized additive models (GAM), (5) classification tree analysis (CTA), (6) multivariate adaptive regression splines (MARS), (7) artificial neural networks (ANN), (8) Maximum entropy (MAXENT.Phillips.2), (9) BIOCLIM (SRE) and (10) Flexible Discriminant Analysis (FDA). Evaluation of the models used the area under the ROC curve ('AUC)' and the true skill statistic (TSS). AUC values range between 0 and 1, where 1 indicates 100 % accuracy and values ≤ 0.5 indicate predictive discrimination that is no better than a random guess (Ruiz-Navarro et al. 2016a). TSS values also vary between 0 and 1, with higher values indicating higher predictive ability, with values <0.2 having no predictive ability (TSS < 0.2) (Ben Rais Lasram et al. 2010; Lin et al. 2019). The variable importance of the included predictors in the ensemble model of each species were defined using the variables importance function. Model evaluation also used Cohen's Kappa (Heidke skill score) (KAPPA), using an 80:20 split of training to test data (Allouche et al. 2006). We created a community of different algorithms by calculating the weighting of the single models that had a ROC (or AUC) value higher than 0.7. The model outputs of the distribution-climate modelling for each alien species and native genus for each climate change projection was the simulated extent of the spatial area of Turkey and Europe (as calibration areas) that populations of these fishes occupy in current climate conditions, and their predicted spatial distribution under each climate change projection. These outputs, therefore, indicate the extent of simulated current versus predicted projection for each species. If a single model had a ROC assessment point below 0.7 then it was removed from the ensemble model. However, it was not case for the present study (*cf.* Table 1). In the study, pseudo-absence points were used as much as the occurrence point. Each pseudo absence point was randomly generated with 3 replicates.

The habitat suitability area of each species was determined by using the minimum threshold value of 0.1 (as the minimum for each species in the ArcMap version 10.8.1), obtained after the modeling of all species. The compatibility area was calculated by the controlled classification (maximum likelihood classification) method in ArcMap after .shp values were converted to a polygon file. Polygon data of alien species and native fish genera were combined separately using the 'merge function' in ArcMap. Comparisons in overlapping habitats were completed between alien and endemic fish species across Turkey based on all examined scenarios. It was calculated as the number of overlapping squares in the new predicted range of species and this was represented as percent of overlapping range suggesting interaction probability (0-25.0% = 1, 25.1-50.0% = 2, 50.1-75.0 = 3, 75.1-100% = 4).

Results

Ensemble model predictions

Amongst the native genera, the *Alburnoides* genus and *Squalius* genus were predicted to have substantial reductions in their geographical space under future conditions (Fig. S2-7; Table 2). In the alien fishes, there were species-specificity in their predicted geographical spaces with, for example, the widest geographical space for ruffe being in current conditions (Table 2, Fig. S2), whereas for largemouth bass and pumpkinseed it was in future conditions (SSPs 585_2100 and SSPs 126_2100 respectively; Table 2, Fig. S3, S4). In general, the alien fishes with patterns of increased geographical space under the projected scenarios had increases that were in more southerly and easterly directions, whereas the native genera had predictions in these directions of decreasing geographical space (Table 2). The climate variables that contributed most to the predictions of shifts in geographical space are provided in Fig. 2.

Overlapping geographical space for alien and native fish genera

The geographical space overlaps of alien largemouth bass and the native *Alburnoides* genus was at the highest probability in the 585_2100 scenario and it was generally above 2 (i.e. more than 50% probability). The other native genera were generally less affected by the geographical space increases of the alien species (interaction probability ≤2), other than for the *Gobio* genus that had more than 50% encountering probability with alien perch and pikeperch in the 126_2050 scenario (Table 3). The highest extent of geographical space overlaps between all of the alien species and the native genera, and thus where there is the highest risk of deleterious impacts on the endemic species, was in the 126_2100 scenario, followed by the 126_2050, 585_2050 and 585_2100 scenarios. These predictions suggest that the risk of ecological impacts will be higher in future, with this risk elevated above current conditions in all of Turkey except for eastern areas (Fig. 3). However, all scenarios predicted that the native genera would have a high risk of impacts from alien percids (Fig. 3, S2-7).

Discussion

The Ecological Niche Modelling (ENM) that were applied to different climate change projections for both modelled native genera and invasive freshwater fishes in Turkey predicted that their shifts on geographical space were species-specific, with a general pattern of increases for the alien species and decreases for the native genera. For the alien species, predictions ranged from relatively small increases in geographical space (Chinese sleeper) to relatively large (largemouth bass), and where changes in the annual range of temperature was the most important variable in the ensemble model predictions. This was in contrast to the native genera, where the combination of precipitation in the driest month and annual mean temperature was most influential. Notwithstanding, it is considered likely that the distributions of these alien species are likely to shift through a combination of anthropogenic-mediated dispersal (usually between catchments) and natural dispersal (within catchments) (Tarkan et al. 2015), although the models were limited to only two dispersal scenarios (no dispersal/ full dispersal). Thus, future predictive models should be developed to also include the influence of hydrological connectivity (Dominguez Almela et al. 2020; 2022).

There are a number of factors that are already altering the composition of riverine fish communities in Turkey, including river impoundments (such as the presence of weirs that impede migratory species), introductions of alien species (Tarkan et al. 2015), pollution, and habitat modification (Aksu 2020; 2021). However, these generally influence fish population abundances, community structure and trait expression, rather than presence (Tarkan et. al. 2012). In general, ENM is considered as suitable for predicting how climate change will influence the distributions of fish species in marine and freshwater ecosystems (Rahel and Olden 2008; Jones et al. 2013; Elliott et al. 2015), especially where the distributions of these species are strongly temperature driven and so influenced by latitudinal and altitudinal gradients (Chen et al. 2011; Forister et al. 2010). However, species-specific characters (physiological tolerance, resilience) and sensitivity to environmental changes can also have a crucial role for the direction and magnitude of range shifts (Comte and Grenouillet 2015). Here, more complex, interactive relationships between explanatory environmental factors (e.g. temperature versus precipitation) for the species concerned and their temporal pattern (i.e. size of distributional ranges) would need consideration (Conti et al. 2015). For all native genera, predictions suggested some temperature thresholds might exist, given their predicted expansions of geographical space under low emission projections, but constrictions under high emissions. A recent meta-analysis suggested that the ability of species distribution models, such as ENM, to predict occurrence can be low, with predictions being best used as hypotheses to test with independent data, especially when being used to inform conservation decisions (Lee-Yaw et al. 2021). In the context of the present study, the spatial extent of Turkey and the complexity of the fish communities present mean that the application of the ENM to inform conservation decisions could be considered as appropriate, given the difficulties of obtaining independent data over and above that already applied here.

The most substantial predicted shifts in geographical space were for the alien species in the eastern and southern parts of Turkey, especially for largemouth bass and Chinese sleeper (as they are currently not present there), but also for pumpkinseed, perch and pikeperch that are already present. For largemouth bass, these predictions are consistent with those in the Korean peninsula and South Africa, where mean annual temperature and the maximum temperature of the warmest month were the most influential climate variables (Mamun et al. 2018; Khosa et al. 2019). The range sizes of all of the alien species and native genera modelled either remain unchanged or reduced under scenarios of no dispersal, but reductions were only evident in the native genera under the full dispersal scenario. These reduced geographical spaces in the native genera are consistent with some recent studies in Iran suggesting that some important habitats of endemic *Alburnus* and *Albornoides* species will become unsuitable in next decades (Esmaeili et al. 2018; Yousefi et al. 2020) due to changes in annual precipitation temperatures.

All of the modelled alien species are piscivorous and so have high potential for causing deleterious, top-down effects on the native fish genera. Given that Turkey is a hotspot of freshwater fish diversity, with almost one-third of species present being local endemics (Çiçek et al. 2020), then these climate-based predictions are highly concerning in a conservation context. Although largemouth bass is currently not present in Turkey, it was the alien fish that presented the highest risk under the climate change scenarios as it had the highest predicted overlap in geographical space with the *Alburnoides* genus that comprises of many local endemics. Listed as one of the 100 worst alien species in the world (Lowe et al. 2000), the primary impact mechanism of largemouth bass is predation pressure exerted by established populations, which is usually sufficient to incur significant ecological impacts in invaded ecosystems. Reported impacts include significant declines in the native cyprinid fish species *Alburnus alborella* in Italy (Bianco and Ketmaier 2001), which belongs to a close genus with similar body sizes of fish species in *Alburnoides* genus, and also large declines in populations of similar small-bodied, native prey fishes in Southern Africa (Gratwicke and Marshall 2001). Indeed, largemouth bass is commonly considered as causing the displacement, declines and even extirpation of indigenous fish species, including cyprinids, soon after their establishment and invasion (de Leoan et al. 2000; Wittenberg 2005). Should they be introduced into Turkey then it is considered highly likely that this species could drive the extirpation of several threatened native endemics of the *Alburnoides* genus that already have a highly restricted distribution range. Our models also indicated some similar - but of lower magnitude - overlaps in geographical space of existing invaders in Turkey (pikeperch, perch and pumpkinseed) and native genera. Given that both pikeperch and perch predate on similar-sized cyprinid species to largemouth bass (Mustamaki et al. 2014; Nolan and Britton 2018) then they pose a more active threat to the endemic *Alburnoides* species, especially as they increasingly share geographical space in future.

Our results clearly suggest that conservation measures are necessary to prevent future impacts on the endemic fishes of Turkey from these alien piscivorous fishes. For species such as perch, pikeperch and pumpkinseed, policies and regulations require implementing for preventing their further dispersal through translocations. For largemouth bass and Chinese sleeper that are not present, but are present in countries nearby and, in the case of largemouth bass, is a popular sport fish, then there is a need for introduction prevention, including active surveillance of potential points of entry. Local populations of endemic and climate-vulnerable species could be managed actively, such as using managed relocations (MR) to safeguard the species in future, although care would be needed to prevent potential genetic issues through introducing fish between different watersheds (Griffiths et al. 2009). Given there is no such stocking practice on native endemic species in Turkey other than some native trout species (Akkan et al. 2016), *in situ* conservation management could also focus on habitat quality and quantity restoration, particularly in the areas where warming water temperatures (from air temperature increases) degrade the suitable habitats (e.g. Top et al. 2016).

In conclusion, predictions were for some marked changes in the geographical spaces of the modelled alien species and native genera of freshwater fishes in Turkey, with further predictions that these fishes will increasingly overlap in their geographical space in future, potentially leading to extirpations of endemic species. While some caution is suggested in these results, as they are based on ENM that does not consider other abiotic and biotic variables in their predictions, they nevertheless suggest that conservation measures require implementation to safeguard these endemic fishes. These measures should integrate strategies to prevent new introductions and translocations of alien species, and improve the status of endemic species through assisted translocation and habitat improvement to increase population resilience. While these results are important for conserving aquatic biodiversity in Turkey, they also highlight that similar issues are likely to be present in other biodiversity hotspots in the world affected by alien species and climate change.

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Author contributions

Özgür Emiroğlu: Conceptualization, Investigation, Data curation. **Sadi Aksu**: Methodology, Visualization, Writing – original draft. **Sercan Başkurt**: Writing – review & editing, Visualization. **Robert Britton**: Conceptualization, Writing – review & editing, Supervision. **Ali Serhan Tarkan**: Conceptualization, Methodology, Writing – original draft, review& editing.

Data availability

All data generated or analyzed during this study are included in this published article and are available from the corresponding author.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Consent to publication All authors have consented to publish this version of the manuscript.

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Table 1. The performance metrics of the ensemble distribution models per species. Area under curve (ROC), true skill statistic (TSS) and Cohen's Kappa (Heidke skill score) (KAPPA).

Species	TSS	ROC	KAPPA
Lepomis gibbosus	0.926	0.994	0.922
Gymnocephalus cernua	0.909	0.990	0.906
Micropterus salmoides	0.848	0.983	0.846
Perccottus glenii	0.910	0.991	0.905
Perca fluviatilis	0.950	0.996	0.942
Sander lucioperca	0.942	0.996	0.929
Alburnoides sp.	0.857	0.989	0.857
Alburnus sp.	0.986	0.996	0.986
Gobio sp.	0.949	0.993	0.950
Squalius sp.	0.885	0.987	0.885

594 **Table 2.** Distribution area % changes of species (from the number of pixels) according to future projections.

Species	Scenario & Year	Species Range Change (%)	Current Range Size	Future Range Size (No Dispersal)	Future Range Size (Full dispersal)
Alburnoides sp.	SSPs_126_2050	-9.564	13457	9420	12170
Alburnoides sp.	SSPs_126_2100	-8.078	13457	9400	12370
Alburnoides sp.	SSPs_585_2050	-12.365	13457	8706	11793
Alburnoides sp.	SSPs_585_2100	-34.213	13457	6225	8853
Alburnus sp.	SSPs_126_2050	-22.932	10675	4675	8227
Alburnus sp.	SSPs_126_2100	-24.000	10675	4499	8113
Alburnus sp.	SSPs_585_2050	-35.007	10675	3309	6938
Alburnus sp.	SSPs_585_2100	-75.073	10675	249	2661
Gobio sp.	SSPs_126_2050	-46.158	13367	5223	7197
Gobio sp.	SSPs_126_2100	-47.026	13367	5145	7081
Gobio sp.	SSPs_585_2050	-65.901	13367	2553	4558
Gobio sp.	SSPs_585_2100	-93.304	13367	156	895
Squalius sp.	SSPs_126_2050	-33.156	10535	4384	7042
Squalius sp.	SSPs_126_2100	-33.175	10535	4402	7040
Squalius sp.	SSPs_585_2050	-44.357	10535	3262	5862
Squalius sp.	SSPs_585_2100	-80.522	10535	304	2052
G. cernua	SSPs_126_2050	-3.993	77715	48474	74612
G. cernua	SSPs_126_2100	0.382	77715	50143	78012
G. cernua	SSPs_585_2050	-23.957	77715	35192	59097
G. cernua	SSPs_585_2100	-23.957	77715	35192	59097
L. gibbosus	SSPs_126_2050	28.643	116492	92390	149859
L. gibbosus	SSPs_126_2100	31.443	116492	92855	153120
L. gibbosus	SSPs_585_2050	27.952	116492	81189	149054
L. gibbosus	SSPs_585_2100	-2.604	116492	49419	113458
M. salmoides	SSPs_126_2050	-7.422	47479	22459	43955
M. salmoides	SSPs_126_2100	-0.259	47479	23712	47356
M. salmoides	SSPs_585_2050	-9.103	47479	14984	43157
M. salmoides	SSPs_585_2100	-53.820	47479	816	21926
P. fluviatilis	SSPs_126_2050	25.593	78671	64586	98805
P. fluviatilis	SSPs_126_2100	33.662	78671	66682	105153

P. fluviatilis	SSPs_585_2050	43.859	78671	63050	113175
P. fluviatilis	SSPs_585_2100	47.066	78671	46955	115698
P. glenii	SSPs_126_2050	-42.301	33907	11255	19564
P. glenii	SSPs_126_2100	-39.281	33907	12760	20588
P. glenii	SSPs_585_2050	-51.635	33907	11081	16399
P. glenii	SSPs_585_2100	-99.997	33907	0	1
S. lucioperca	SSPs_126_2050	39.401	85214	63681	118789
S. lucioperca	SSPs_126_2100	46.012	85214	65069	124423
S. lucioperca	SSPs_585_2050	34.296	85214	56618	114439
S. lucioperca	SSPs_585_2100	20.184	85214	25408	68014

Table 3. The rate of niche overlap with native species of alien species in Turkey during the periods when alien species are most widely distributed. Degree of interaction (overlapping) probability are given in parenthesis and bold text.

	Alburnoides sp.			*Alburnus sp.*			*Gobio sp.*			*Squalius sp.*		
	O	A	E	O	A	E	O	A	E	O	A	E
GC_CURRENT	50.0 (**2**)	5.9	44.1	32.0 (**2**)	31.7	36.3	41.5 (**2**)	18.8	39.7	37.0 (**2**)	33.3	29.6
SL_126_2050	73.4 (**3**)	20.5	6.2	47.2 (**2**)	48.6	4.2	72.5 (**3**)	19.7	7.8	44.9 (**2**)	52.2	2.9
MS_585_2100	76.4 (**4**)	3.0	20.6	10.3 (**1**)	88.4	1.3	5.9 (**1**)	94.1	0.0	41.3 (**2**)	46.1	12.6
LG_126_2100	68.1 (**3**)	29.1	2.8	43.0 (**2**)	55.1	2.0	33.5 (**2**)	66.4	0.1	39.7 (**2**)	59.4	0.9
PF_126_2050	69.7 (**3**)	23.0	7.3	44.3 (**2**)	50.3	5.4	68.7 (**3**)	22.3	9.0	43.9 (**2**)	53.6	2.5
PG_126_2100	18.7 (**1**)	7.2	74.1	16.5 (**1**)	19.4	64.1	17.5 (**1**)	27.1	55.4	22.6 (**1**)	18.1	59.2

O: Overlapping, A: Alien, E: Endemic, GC: *Gymocephalus cernua*, SL: *Sander lucioperca*, MS: *Micropterus salmoides*, LG: *Lepomis gibbosus*, PF: *Perca fluviatilis*, PG: *Perccottus glenii*

Figure legends

Fig. 1. Processing methods in the roadmap of this study.

Fig. 2. The contribution rate of each environment variable to the modeling. Upper and lower panels denote endemics and alien species (ALBN: *Alnurnodies* sp., ALBS: *Alburnus* sp., GB: *Gobio* sp., SQ: *Squalius* sp., GC: *Gymocephalus cernua*, LG: *Lepomis gibbosus*, MS: *Micropterus salmoides*, PF: *Perca fluviatilis*, PG: *Perccottus glenii*, SL: *Sander lucioperca*). See Table S1 and S2 for explanations of environmental variables used.

Fig. 3. Prediction of overall niche overlap between assessed alien and native species in the borders of Turkey in different climate models when alien species would have the widest distribution.

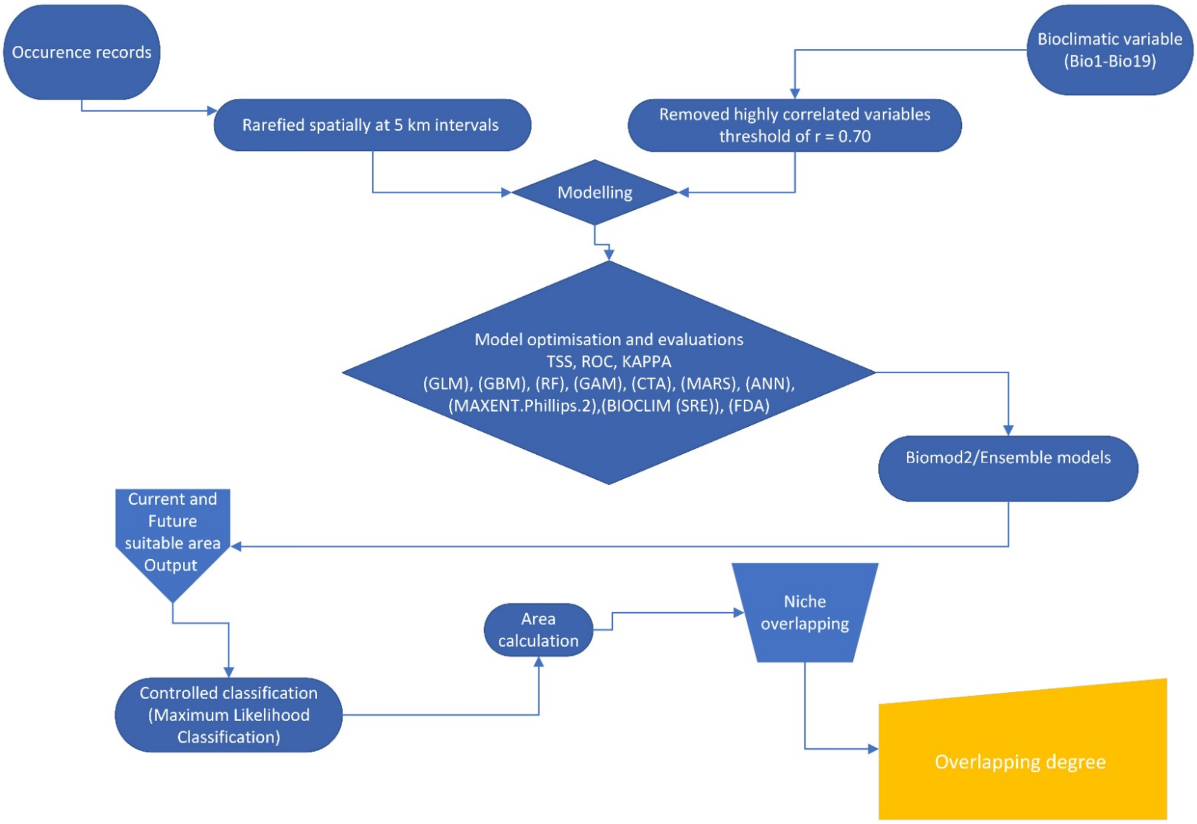
Occurence records
Bioclimatic variable (Bio1-Bio19)
Rarefied spatially at 5 km intervals
Removed highly correlated variables threshold of r = 0.70
Modelling
Model optimisation and evaluations
TSS, ROC, KAPPA
(GLM), (GBM), (RF), (GAM), (CTA), (MARS), (ANN), (MAXENT.Phillips.2),(BIOCLIM (SRE)), (FDA)
Biomod2/Ensemble models
Current and Future suitable area Output
Area calculation
Niche overlapping
Controlled classification (Maximum Likelihood Classification)
Overlapping degree

Fig. 1.

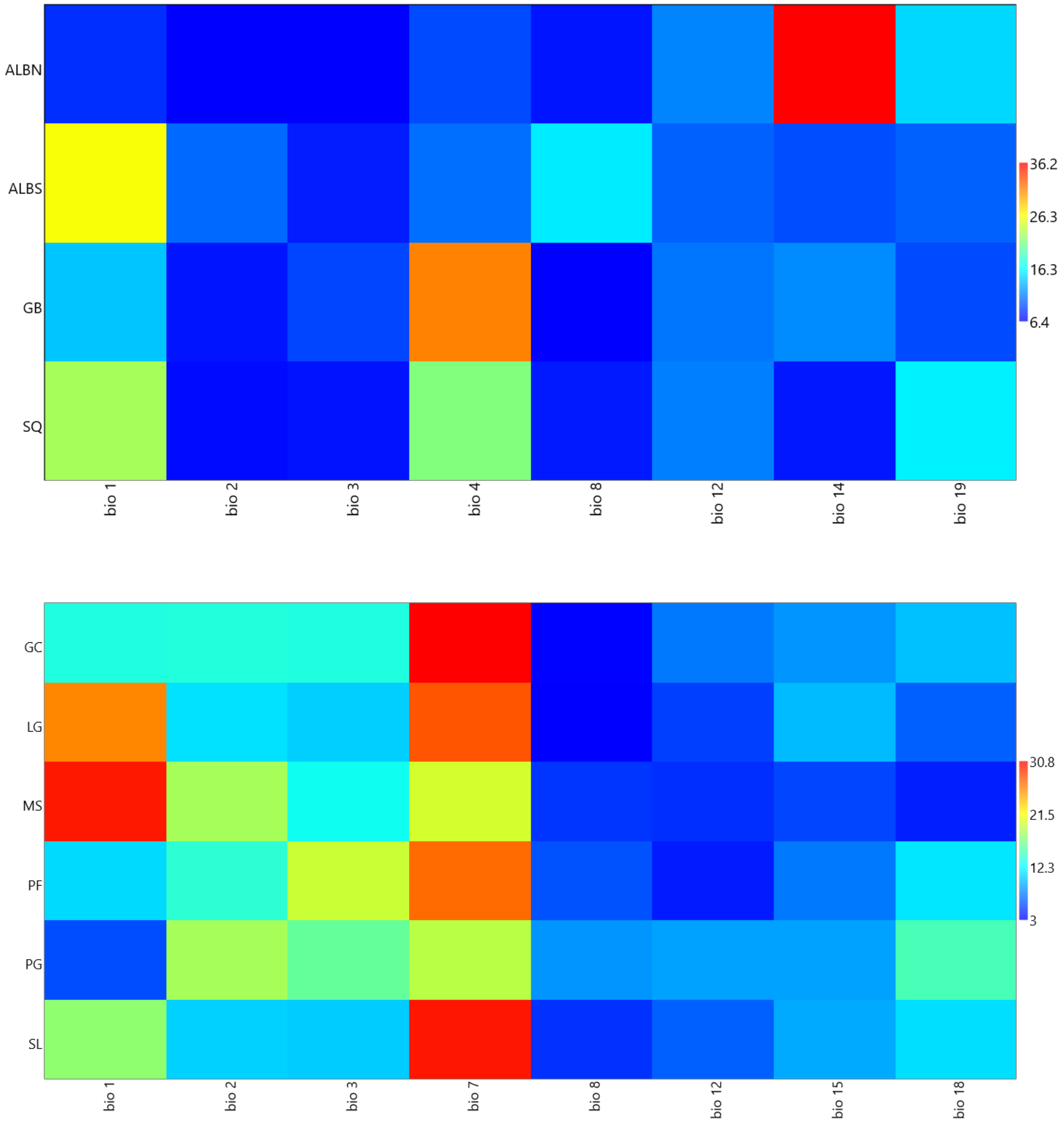
ALBN
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Fig. 2.

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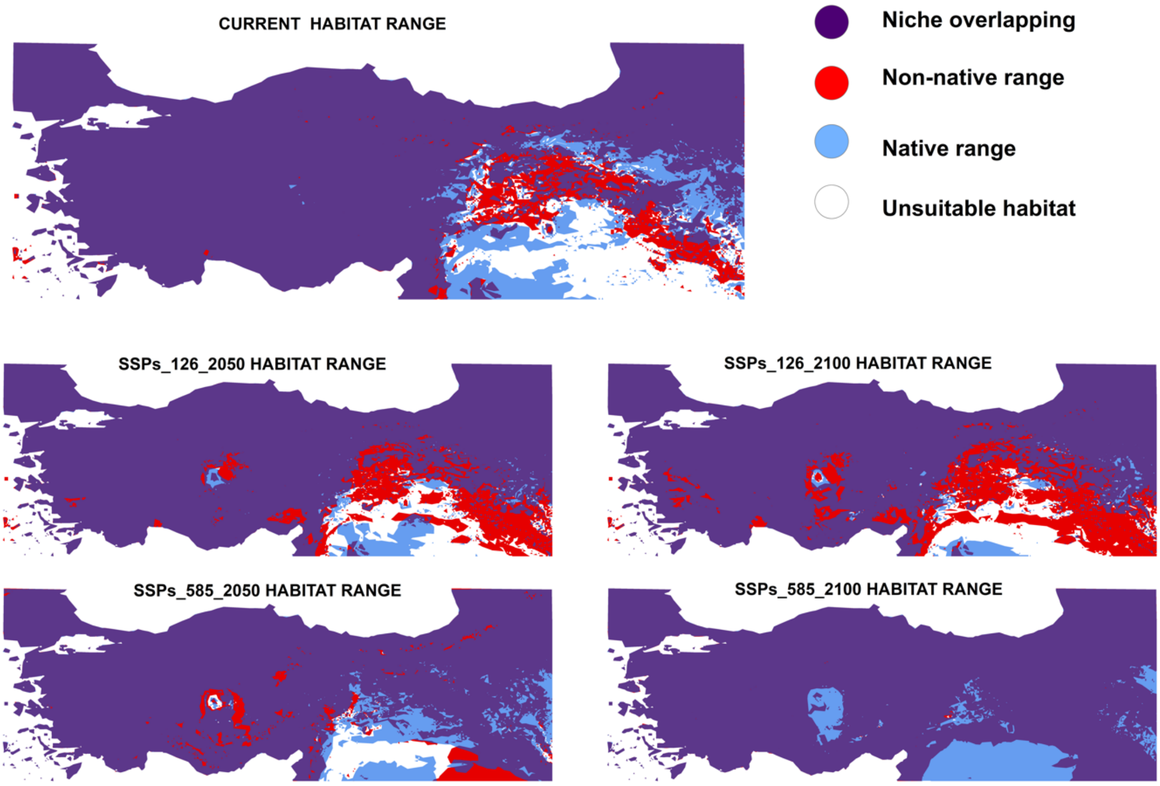

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666 **Fig. 3.**

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