Susceptibility of European freshwater fish to climate change: species profiling based on life-history and environmental characteristics

Running head: European freshwater fish and climate change

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Abstract

Climate change is expected to strongly affect freshwater fish communities. Combined with other anthropogenic drivers, the impacts may alter species spatio-temporal distributions, and contribute to population declines and local extinctions. To provide timely management and conservation of fishes, it is relevant to identify species that will be most impacted by climate change and those that will be resilient. Species traits are considered a promising source of information on characteristics that influence resilience to various environmental conditions and impacts. To this end, we collated life history traits and climatic niches of 443 European freshwater fish species and compared those identified as susceptible to climate change to those that are considered to be resilient. Significant differences were observed between the two groups in their distribution, life-history and climatic niche, with climate-change susceptible species being distributed within the Mediterranean region, and being characterized by greater threat levels, lesser commercial relevance, lower vulnerability to fishing, smaller body and range size, and warmer thermal envelopes. Based on our results, we establish a list of species of highest priority for further research and monitoring regarding climate change susceptibility within Europe. The presented approach represents a promising tool to efficiently assess large groups of species regarding their susceptibility to climate change and other threats, and to identify research and management priorities.

Introduction

As ectothermic organisms, fishes are intimately linked to local climatic conditions through physiological mechanisms that delimit tolerance or resilience (Comte & Olden, 2017a). Zoogeography of fishes is therefore greatly influenced by the average and spread of temperatures experienced in a given watershed (Pörtner & Farrell, 2008; Isaak & Rieman, 2013). Relative to seas and oceans, freshwater habitats are more drastically impacted by changes to climate, especially due to changes to temperature and flow, and climate change is projected to strongly affect freshwater fish communities (O'Reilly et al., 2003; Buisson et al., 2008; Graham & Harrod, 2009; Harrod, 2016; Radinger et al., 2017). Combined with other anthropogenic impacts (e.g. land use change and thermal pollution; Radinger et al., 2016; Raptis et al., 2017), climate change will restrict or redraw thermal envelopes, contribute to population declines and local extinctions, and result in shifts in the distribution of species (Ficke et al., 2007; Woodward et al.; 2010; Booth et al., 2011; Filipe et al., 2013). Riverine fish species losses due to climate change and reduced water discharge are predicted to reach 75% in some river basins, such as those of rivers Parnaíba (Brazil), Saloum (Senegal) and Cauvery (India; Xenopoulos et al., 2005). Phenological changes in fish behaviour (Otero et al., 2014; Dempson et al., 2017; Hovel et al., 2017) have been also detected and emphasize the powerful changes imposed by a changing climate. In Europe, there is a broad range of climatic conditions experienced across the landscape and a diverse ichthyofauna distributed throughout the lakes and rivers (Ficke et al., 2007). Within the IUCN (International Union for Conservation of Nature and Natural Resources) Red List, as many as 33% of European freshwater fish species are recognized as threatened by climate change (IUCN, 2017).

Efforts to preserve ecosystem integrity must focus on maintaining species richness and diversity to ensure that the services provided by freshwater ecosystems are maintained. Conservation is often limited by funding and therefore must undergo triage to identify priorities and allocate resources efficiently (McDonald-Madden et al., 2011). To provide timely management and conservation and allocate resources efficiently, it is important to identify those species that will be most impacted by climate change and those that might be rather resilient. Species traits are considered as a promising source of information on characteristics that influence resilience to various environmental conditions and impacts (Jiguet et al., 2007; Comte & Olden, 2017b). Species traits represent any morphological, physiological or phenological feature that is measurable at the individual level of a species (Floeter et al., 2018). Trait-based evaluation has been demonstrated to be linked to the risk status of species and can be used to investigate mechanisms that contribute to imperilment, make predictions about unassessed species, or rank and prioritize species based on their relative risk (Olden et al., 2007; Bland & Böhm, 2016; Kopf et al., 2017; Comte & Olden, 2018).

The aim of the present study was to assess various ecological and life-history characteristics of European freshwater fish species, and to identify traits that are characteristic of those that are susceptible to the effects of climate change. Based on an automated scraping of online trait databases with species-specific data on life history, distribution, climatic niches, threat and economic status, and calculation of climate envelopes using IUCN range maps overlaid on climate maps, we compared species identified as susceptible to climate change with those that are considered to be resilient. We also established a list of European species of highest priority for further research and monitoring regarding climate change susceptibility. The method allows to extrapolate results and characterize rare and less studied species, with scarce autecological information. Results of the study will advance our understanding of projected climate change effects on the European freshwater fish fauna.

Materials and methods

Dataset

Our analysis comprised comparisons of in total 443 European freshwater fishes between those that were categorized as threatened by climate change (n=148) within the IUCN Red List Database (IUCN, 2017) and those without climate change listed as a threat (n=295). Categorization of species according to their susceptibility to climate change within this database is based on threat assessment and expert judgement by IUCN species experts (Freyhof & Brooks, 2011; IUCN, 2017). A list of native European freshwater fish species belonging to 25 families, mainly to Cyprinidae (45%) and Salmonidae (20%), was obtained from the IUCN Red List database (IUCN, 2017). It included both exclusively freshwater species, as well as those that partly enter brackish and saltwater. Obtained data also comprised IUCN Red List classification and maps of their distributional range within Europe.

In addition, for each species we collated trait information related to their life history, ecology, fishery and threat status, and spatial and bioclimatic data variables (Table 1). Life-history data were obtained from the FishBase database (Froese & Pauly, 2017) by using the rfishbase R package (Boettiger et al., 2012, 2017). Traits with low data coverage (i.e. those that were available for less than 1% of all species) were excluded from the analysis. Bioclimatic spatial data were obtained from the MERRAclim database (Vega et al., 2017) and included 19 variables related to temperature and humidity (Table 1). Global Human Footprint map (map of anthropogenic impacts on the environment) was obtained from WCS and CIESIN (2005) and the spatial elevation data were obtained from USGS (2010). Based on the distributional range maps of each species (IUCN, 2017), mean values within each species' range were estimated for each of the spatial variables using the intersect tool in ArcGIS (version 10.5) and the *extract* function in the R (version 3.4.3; R Core Team, 2017) package raster (version 2.6-7; Hijmans, 2017). Range maps were also used to estimate the number of watersheds covered by each species based on WRI (2006), as well as the area and coordinates of the range centroid for each species. Descriptions of all variables used in the analysis, general descriptive statistics and information on data sources are presented in Supplementary material S1. The complete dataset is presented in Supplementary material S2.

Statistical Analysis

We calculated boosted regression trees (BRT) to evaluate the relationship between the membership of a species to the group of susceptible vs. non-susceptible species and the 45 explanatory variables. BRT are a statistical learning method that combines and averages (boosting) many simple single regression trees to form collective models of improved predictive performance (Elith et al., 2008). BRT can accommodate continuous and categorical variables, are not affected by missing values or transformation or outliers and are considered to effectively select relevant variables, identify variable interactions and avoid overfitting (Elith et al., 2008, Radinger et al., 2015).

Specifically, we first fitted an initial global BRT model (R package *dismo*, *gbm.step*, version 1.1-4; Hijmans et al., 2017) using the complete set of explanatory variables. An automatized stepwise backward selection of explanatory variables (*gbm.simplify*) was applied to eliminate non-informative variables based on model-internal cross-validation of changes in a models' predictive deviance (Hijmans et al., 2017). Thereafter, we calculated a final BRT model (*gbm.step*) based on the selected set of explanatory variables. For all BRT modeling steps, tree complexity and learning rate was set to 3 and 0.001, respectively, to achieve the recommended number of more than 1000 regression trees (Elith et al., 2008). All other model settings were set to default or were automatically adjusted by the boosting algorithm. We calculated a 10-fold cross validation of the BRT model as already implemented in the algorithm. In addition, we extracted the mean AUC (area under the receiver operating characteristic curve) as a measure of the model's predictive quality. The AUC is a thresholdindependent rank-correlation coefficient with high values typically indicating a strong agreement between the model prediction and, in this specific case, the membership of species to the susceptible vs. non-susceptible group (Hijmans & Elith, 2017).

The relative importance (%) of each explanatory variable in the final BRT model was quantified based on the number of times each variable was used for splitting, weighted by the squared improvement at each split and averaged over all trees (Elith et al., 2008). For BRT models with Gaussian distribution, the relative variable importance equals the reduction of squared error attributable to a given variable (Friedman, 2001; Greenwell et al., 2018). Differences between groups were also assessed by bootstrapping, by sampling each group independently and estimating the difference based on confidence intervals (functions *two.boot* and *boot.ci*, R package *simpleboot*, version 1.1-3; Peng 2008). Differences were considered to be significant if 95% confidence intervals did not overlap with zero.

Subsequently, species were ranked based on the subset of variables selected by the BRT analysis (i.e., those with >1% variable importance score), and weighed by the importance of each variable, in order to estimate their position along the climate change susceptibility continuum. For each species, the value of each variable was standardized based on its position between the minimum (t_{min}) and maximum values (t_{max}) observed in the dataset, with 0-1 possible range, and multiplied by the importance score (I_x) of the given variable:

$$R_{tx} = \frac{t_x - t_{min}}{t_{max} - t_{min}} \times I_x \qquad (1)$$

where R_{tx} represents the rank value of variable t in species x, and t_x is the value of variable t for species x. For variables where the lower endpoint (t_{min}) is associated with the climate change susceptibility, equation should be adjusted as follows:

$$R_{tx} = \frac{t_{max} - t_x}{t_{max} - t_{min}} \times I_x \qquad (2)$$

Summing of all ranking scores across all variables yielded the total species ranking score, which can range from 0 to 100, with higher values indicating stronger climate change susceptibility.

Results

Our analyses indicated substantial differences between climate change susceptible and non-susceptible species. The BRT analysis selected the 35 most relevant variables, which were subsequently assessed for their relative importance to discriminate between the two groups (Figure 1 and Supplementary material S3). The BRT model with the selected set of explanatory variables was successfully modeled (Supplementary material S3) with a cross-validated AUC of 0.87 (standard error = 0.014). Of all explanatory variables, latitude of the species range centroid was selected as by far the most relevant variable (31% variable importance), followed by the IUCN Red List classification (8%), commercial relevance (6%) and vulnerability to fishing (6%). Climate susceptible species were characterized by more southwardly positioned distribution range centroids (41.6º vs. 47.8º N as a mean value in susceptible and non-susceptible species, respectively), smaller range sizes (175 x 10^3 km^2 vs. 1686 x 10^3 km^2), and lower elevations within their ranges (717.7 m vs. 892.2 m a.s.l.), with a higher proportion of exclusively freshwater species (93% vs. 66%; Figure 2). Susceptible species were also characterized by a smaller maximum body length (23.4 cm vs. 41.0 cm), higher proportion of threatened species (63% vs. 31%), lower proportion of commercially relevant species (25% vs. 74% of highly commercial, commercial and minor commercial species), and lower vulnerability to overfishing (32.6 vs. 38.5 vulnerability index; Figure 3), as well as by higher temperature-related values (Supplementary material S4). Bootstrapping indicated significant differences between the groups in each of the variables. Species that are susceptible to climate change are mainly distributed within the Mediterranean region, whereas the non-susceptible species distribution mainly covers central and northern European regions, as well as the Carpathian region (Figure 4).

Species ranking based on the association of their traits with climate change susceptibility characteristics is presented in Table 2 and Supplementary material S5. The five top-ranked climate susceptible species were Acheron spring goby (*Knipowitschia milleri*), Corfu valencia (*Valencia letourneuxi*), *Iberochondrostoma almacai,* Evia barbel (*Barbus euboicus*) and Malaga chub (*Squalius malacitanus*). Most of the species with the high climate-susceptibility ranks are also classified as highly threatened according to the IUCN classification (Table 2). Interestingly, the highest ranked species, *K. milleri*, was not classified within the IUCN Red List as threatened by climate change. Other high-ranking species that were not recognized as threatened by climate change were *S. malacitanus*, Almiri toothcarp (*Aphanius almiriensis*), and Trichonis dwarf goby (*Economidichthys trichonis*). Species with the lowest ranking scores, i.e. with low climate change susceptibility, were humpback whitefish (*Coregonus pidschian*), Arctic flounder (*Liopsetta glacialis*), northern pike (*Esox lucius*), burbot (*Lota lota*), and European perch (*Perca fluviatilis*). A complete list of all species' rankings is presented in Supplementary material S5.

Discussion

In the present study, significant differences in life-history and climatic niches were observed between the European freshwater species susceptible to climate change and those that are not, such as species body size, range size, distribution and thermal envelopes. The latitude of the species range centroid was by far the most influential trait. Overall, southern regions with the warmer, Mediterranean climate comprised a higher proportion of species susceptible to climate change (Figure 4). Out of the 20 highest-ranking climate susceptible species, 12 are endemic to Greece, one endemic to Greece and southern Albania, and the other seven to the Iberian Peninsula. These results support recent findings that the species from lower latitudes and tropical, warm-water habitats, are at greater risk from climate change and warming (Payne & Smith, 2016; Payne et al., 2016; Comte & Olden, 2017b). Freshwater basins in Southern Europe are characterized by recurrent flood and drought events (Bernardo et al., 2003). Whereas species in such habitats might be generally adapted to hydrological fluctuations, they are likely to be impacted by a further increase in frequency and strength of extreme hydrological conditions, induced by climate change and increased anthropogenic water demand (Filipe et al., 2013; Radinger et al., 2018). Moreover, among such species, adapted towards higher upper thermal tolerances, specialization to thermal extremes is accompanied by a reduced physiological flexibility and adaptation capacity to respond to changing environmental conditions (Payne & Smith, 2016; Payne et al., 2016; Comte & Olden, 2017b). Such heat-tolerant species are also adapted to temperatures near their physiological thermal limits, with a narrow safety margin for further temperature increases (Sinclair et al., 2016; Comte & Olden, 2017b). However, not all the species in this region are adapted to thermal fluctuations and extremes. For example, *V. letourneuxi* is associated with spring-fed habitats with stable thermal conditions, and its susceptibility to climate change is more likely to be driven by habitat fragmentation and low population densities (Kalogianni et al., 2010). Freshwater basins in Southern Europe are also of particular conservation concern due to an elevated pressure by a range of anthropogenic impacts that further exacerbate effects of climate change, such as pollution, water resource development and consumption, and biological invasions (Xenopoulos et al., 2005; Clavero & García-Berthou, 2005; Walther et al., 2009; Vörösmarty et al., 2010; Comte & Olden, 2017a). The Mediterranean region is characterized by a wide expansion of alien invasive species, which is expected to be further intensified under current climate change scenarios (Clavero et al., 2010; Filipe et al., 2013).

Climate-susceptible species were also characterized by a smaller body and range size (Figures 2, 3). These traits, which are also related to a lower dispersal ability (Radinger & Wolter, 2014), are well recognized as predictors of climate change susceptibility in fish (e.g. Ficke et al., 2007; Isaak & Rieman, 2013; Chessman, 2013; Pearson et al., 2014; Radinger et al., 2017). A characteristic example of small-bodied and range-restricted species are the three endemic species from the Evrotas River in Greece: Evrotas chub (*S. keadicus*), Evrotas minnow (*Pelasgus laconicus*) and Spartian minnowroach (*Tropidophoxinellus spartiaticus*). These species, ranked among the 20 most susceptible species to climate change in the present study (Table 2), are found either exclusively in the Evrotas River basin, or in that and few neighboring systems (Barbieri et al., 2015). Smaller-bodied fish are facing elevated overall extinction risk in freshwater habitat due to multiple threats, such as habitat loss and fragmentation (Olden et al., 2007; Kalinkat et al., 2017; Kopf et al., 2017), which explains higher threat level observed in climate-susceptible species in the present study. Observed lower commercial relevance and lower vulnerability to fishing of climate-susceptible species both stem from a smaller body size and related faster life history of such species.

It is important to acknowledge certain limitations of the data sources used in this study, such as species and trait coverage, reliability of methods applied for threat and extinction risk classification, and potential assessors' biases (Clavero & García-Berthou, 2005; Keith et al., 2014; Trull et al., 2018). Taxonomic bias in conservation science (Clark & May, 2002) could potentially affect our results through uneven data coverage and quality. However, there is a lack of research specific to fish regarding this problem, and thus, this represents an area for future research. Furthermore, species that are not classified within IUCN Red List as threatened by climate change can comprise those that are not yet assessed for their major threats, or those where experts deem the threat from climate change negligible relative to other threats. Nevertheless, the focus of our study on a well-studied group such as European species ensured that the basic life history data and IUCN Red List assessments were mostly available (Kopf et al., 2017). IUCN Red List is sometimes considered to understate or improperly account for climate change as a threat, mostly due to ambiguous definitions and criteria (Trull et al., 2018). However, recent studies have indicated that the IUCN classification is more efficient in detecting species vulnerable to climate change than anticipated (Keith et al., 2014; Pearson et al., 2014). IUCN Red List assessment process was designed to overcome possible individual-level, assessor biases, and all threat assignments should be made based on objective criteria established by the organization (IUCN 2017). Consequently, any potential biases can be expected to be generally consistent across species, and therefore should not affect relative comparisons among species. Notwithstanding all the caveats, the databases used in the present study still represent the most comprehensive sources of data and the best available knowledge (Olden et al., 2007; Vega et al., 2017).

Trait-based risk assessments are increasingly used for species profiling (Pacifici et al., 2015; Liu et al., 2017; MacLean & Beissinger, 2017). The approach presented in this study might be considered a valid and promising approach to be used as a screening tool, i.e. to quickly assess large groups of species regarding their susceptibility to climate change and other threats based on species traits, and to identify research and management priorities. Our results indicate that the European environmental policy related to climate change mitigation and adaptation (EEA, 2012, 2017) should be mainly focused on the Mediterranean region. This is especially important since this region is also predicted to have the highest frequency of droughts and extreme high temperatures, strongest reduction in precipitation and river discharges, the highest aggregate climate change impact and the lowest adaptation capacity (Milly et al., 2005; Dankers & Feyen, 2008; Fischer & Schär, 2010; ESPON Climate, 2011; Stagge et al., 2011; Rojas et al., 2012; Filipe et al., 2013; Jacob et al., 2014; Russo et al., 2014). Our results are further supported by findings by Markovic and colleagues (2014), who estimated that the greatest reduction in European freshwater fish diversity due to climate change is likely to occur in the southern regions of Europe. Moreover, the Mediterranean region was also identified as a European priority area regarding climate change impacts for other species groups. A similar distributional pattern of species susceptible to climate change was previously also reported for aquatic insects such as Plecoptera, Ephemeroptera and Trichoptera (Hering et al., 2009; Conti et al., 2014), mammals (Levinsky et al., 2007), as well as for terrestrial species in general (Pacifici et al., 2015).

Species ranking conducted here indicated priority species for further research and monitoring regarding climate change (e.g. *V. letourneuxi*, *I. almacai* and *B. euboicus*; Table 2). Moreover, it also identified species whose IUCN Red List status potentially needs to be reconsidered or updated, such as highly ranked but apparently non-susceptible species (e.g. *K. milleri*), or highly ranked species without a proper threat category (e.g. *K. goerneri*, classified as Data Deficient species). As such, it has a potential to be used as a "Robin Hood Approach" (Punt et al., 2011), where assessments based on information-rich species are used to evaluate and categorize those that are information-poor. There is a need for climate change vulnerability assessments that would be based on quantitative approaches and consistent set of criteria, such as trait-based approaches advocated by IUCN (Foden et al., 2013; Trull et al., 2018). The approach presented here should be a good step in that direction.

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Table 1. Variables used in the analysis, with their data sources, general descriptive statistics and coverage (proportion of species with available data). See Supplementary material S1 for more information.

	Variable name	Data source	Median; mean ± SD (range); proportions (%) for categorical data	Coverage (%)
1	Game fish	FishBase	Yes: 14, No: 86	100
2	IUCN Red List status	FishBase/IUCN	EX: 3, CR: 12, EN: 11, VU: 16, NT: 4, LC: 48, DD: 6	100
3	Climate zone (Köppen climate classification)	FishBase	Subtropical: 26, temperate 73, polar: 1	100
4	Preferred habitat	FishBase	Pelagic: 3, pelagic-neritic: 3, benthopelagic: 64, demersal: 30	100
5	Minimum value of the water depth range (m)	FishBase	2; 11.2 ± 17.9 (0 - 100)	18
6	Maximum value of the water depth range (m)	FishBase	80; 106.7 ± 138.8 (1 - 700)	14
7	Freshwater preference	FishBase	Exclusively freshwater: 75, enters saltwater: 25	100
8	Maximum recorded body length (cm)	FishBase	21.7; 35.2 ± 60.5 (2.2 - 800)	98
9	Lateral body shape type	FishBase	Eel-like: 1, elongated: 38, fusiform/normal: 59, short and/or deep: 1	77
10	Aspect ratio of the caudal fin	FishBase	1.6; 1.6 ± 0.6 (0.4 - 3.4)	34
11	Trophic level	FishBase	3.3; 3.4 ± 0.6 (2.1 - 4.5)	13
12	Batch spawner	FishBase	Yes: 12, no: 88	55
13	Reproductive guild (first classification)	FishBase	Bearers: 1, guarders: 18, nonguarders: 81	53
14	Reproductive guild (second classification)	FishBase	Brood hiders: 10, clutch tenders: 5, external brooders: 10, internal live bearers: 2, nesters: 18, open water/substratum egg scatterers: 57	28
15	Maximum recorded longevity (years)	FishBase	9; 13.8 ± 17.4 (1 - 118)	30
16	Commercial importance	FishBase	Of no interest: 41, subsistence fisheries: 4,	40

			minor commercial: 15, commercial: 35, highly commercial: 5	
17	Average global landings/production	FishBase	828.4; 10461.4 ± 23020.9 (0 - 104902.8)	12
18	Resilience to fishing pressure[1]	FishBase	1: 3, 2: 12, 3: 58, 4: 27	100
19	Vulnerability to fishing[1]	FishBase	32.9; 36.5 ± 16.6 (10 - 88.7)	100
20	Temperature tolerance (max - min reported T, °C)	FishBase	15; 14.4 ± 5.2 (1 - 32)	21
21	Number of inhabited freshwater basins	WRI (2006)/IUCN(range)	2; 8.5 ± 14.6 (0 - 82)	96
22	Global Human Footprint	WCS & CIESIN (2005)/IUCN(range)	6; 7.8 ± 7.8 (0 - 46)	96
23	Longitude of the centroid of species range	IUCN(range)	18.6; 17.2 ± 17.4 (-81.1 - 117.2)	96
24	Latitude of the centroid of species range	IUCN(range)	44.6; 45.8 ± 6.3 (34.4 - 70.1)	96
25	Range size (km^2)	IUCN(range)	32499; 1180481 ± 3799809 (13 - 35987250)	96
26	Mean elevation within the species range (m)	USGS (2010)/IUCN(range)	590.4; 833.8 ± 652.5 (3.9 - 2373.6)	96
27	Annual mean temperature (°C)	MERRAclim/IUCN(range)	13.5; 13.4 ± 4.1 (-3.7 - 22.7)	96
28	Mean diurnal temperature range (°C)	MERRAclim/IUCN(range)	19.9; 19.5 ± 2.9 (7.2 - 27.0)	96
29	Temperature isothermality (°C)	MERRAclim/IUCN(range)	44.9; 45.3 ± 3.9 (34.5 - 55.0)	96
30	Temperature seasonality (st. dev. x 100) (°C)	MERRAclim/IUCN(range)	780.6; 800.0 ± 180.6 (312.6 - 1515.3)	96
31	Maximum temperature of the warmest month (°C)	MERRAclim/IUCN(range)	35.7; 35.0 ± 4.6 (20.3 - 43.2)	96
32	Minimum temperature of the	MERRAclim/IU	-8.6; -8.5 ± 7.6 (-36.4 - 8.8)	96

	coldest month (°C)	CN(range)		
33	Temperature annual range (°C)	MERRAclim/IU CN(range)	43.3; 43.5 ± 7.5 (17.1 - 65.9)	96
34	Mean temperature of the most humid quarter (°C)	MERRAclim/IU CN(range)	22.9; 22.7 ± 3.5 (10.8 - 30.5)	96
35	Mean temperature of the least humid quarter (°C)	MERRAclim/IU CN(range)	4.2; 3.9 ± 5.8 (-19.8 - 16.5)	96
36	Mean temperature of the warmest quarter (°C)	MERRAclim/IU CN(range)	23.2; 23.1 ± 3.7 (11.0 - 31.0)	96
37	Mean temperature of the coldest quarter (°C)	MERRAclim/IU CN(range)	3.9; 3.6 ± 5.7 (-19.9 - 15.6)	96
38	Annual mean specific humidity (g of water / kg of air)	MERRAclim/IU CN(range)	7.2; 7.2 ± 0.9 (3.5 - 10.1)	96
39	Specific humidity of the most humid month (g of water / kg of air)	MERRAclim/IU CN(range)	11.2; 11.1 ± 1.0 (6.7 - 14.3)	96
40	Specific humidity of the least humid month (g water / kg air)	MERRAclim/IU CN(range)	4.0; 4.0 ± 1.1 (0.8 - 7.1)	96
41	Specific humidity seasonality (g water / kg air)	MERRAclim/IU CN(range)	255.4; 249.7 ± 52.3 (123.0 - 395.5)	96
42	Specific humidity of the most humid quarter (g water / kg air)	MERRAclim/IU CN(range)	10.4; 10.4 ± 1.0 (6.2 - 13.6)	96
43	Specific humidity of the least humid quarter (g water / kg air)	MERRAclim/IU CN(range)	4.5; 4.4 ± 1.1 (1.0 - 7.5)	96
44	Specific humidity of the warmest quarter (g water / kg air)	MERRAclim/IU CN(range)	10.3; 10.3 ± 1.0 (6.2 - 13.3)	96
45	Specific humidity of the	MERRAclim/IU	4.5; 4.4 ± 1.2 (1.0 - 7.6)	96

coldest quarter (g water / kg air)	CN(range)

[1] intrinsic traits of each species, estimated based on its biology and key life history traits.

Table 2. European freshwater fish species with the highest ranking scores, estimated based on the association of their traits with the climate change susceptibility characteristics, as indicated by the BRT model. Complete ranking list of all species is presented in Supplementary material S5.

Rank	Species	Climate change susceptibility according to IUCN	IUCN Red List category	Ranking score
1	*Knipowitschia milleri*	non-susceptible	CR	82.5
2	*Valencia letourneuxi*	susceptible	CR	82.1
3	*Iberochondrostoma almacai*	susceptible	CR	81.6
4	*Barbus euboicus*	susceptible	CR	81.4
5	*Squalius malacitanus*	non-susceptible	EN	80.9
6	*Aphanius baeticus*	susceptible	EN	80.7
7	*Knipowitschia goerneri*	susceptible	DD	80.5
8	*Squalius keadicus*	susceptible	EN	80.5
9	*Pelasgus laconicus*	susceptible	CR	80.4
10	*Tropidophoxinellus spartiaticus*	susceptible	VU	80.3
11	*Iberocypris palaciosi*	susceptible	CR	80.1
12	*Pelasgus epiroticus*	susceptible	CR	80.0
13	*Aphanius almiriensis*	non-susceptible	CR	79.8
14	*Anaecypris hispanica*	susceptible	EN	79.5
15	*Salaria economidisi*	susceptible	CR	79.5
16	*Squalius torgalensis*	susceptible	EN	79.4
17	*Cobitis trichonica*	susceptible	EN	78.9
18	*Valencia hispanica*	susceptible	CR	78.6
19	*Economidichthys trichonis*	non-susceptible	EN	78.6
20	*Knipowitschia thessala*	susceptible	EN	78.5

Figure captions

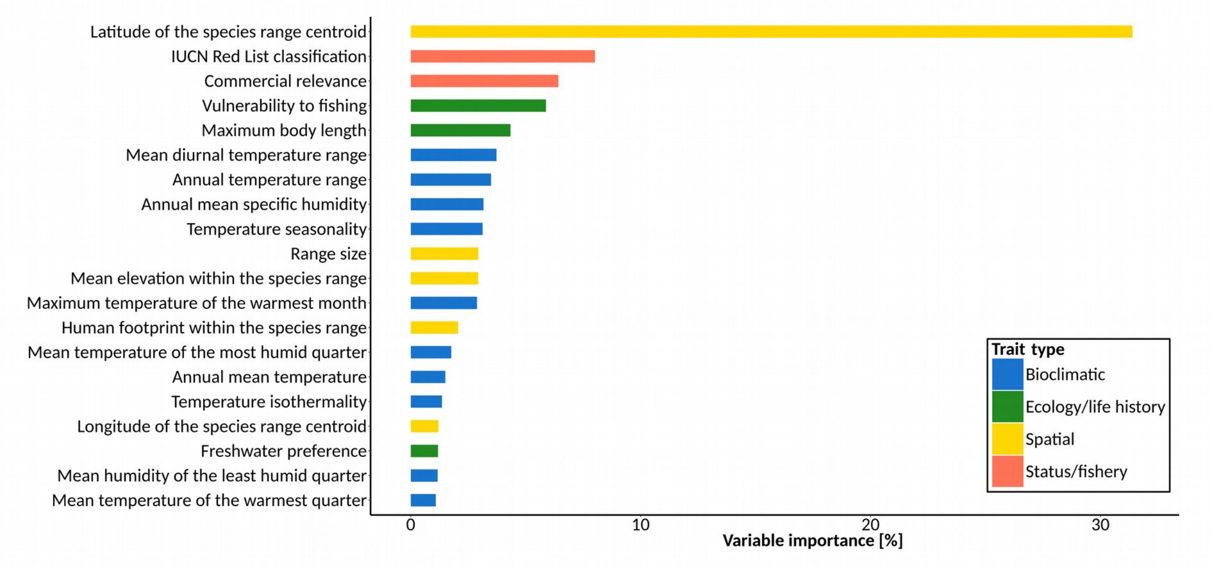

Figure 1. Variables selected by the boosted regression tree (BRT) model as the most relevant descriptors of climate change susceptibility in European freshwater fish species; 20 most relevant variables are presented, which together account for 90% of the total relative variable influence.

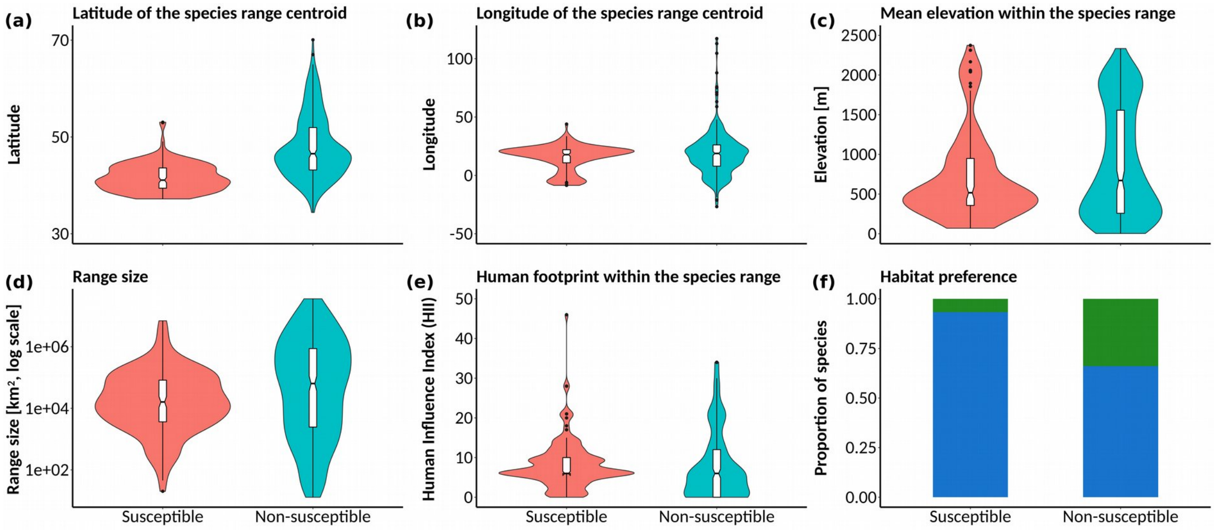

Figure 2. Violin-boxplots and barplots of the most relevant spatial variables in European freshwater fish species indicated as either susceptible (n = 148) or non-susceptible (n = 295) to climate change. Habitat preference: blue - exclusively freshwater species, green - species that also enter saltwater.

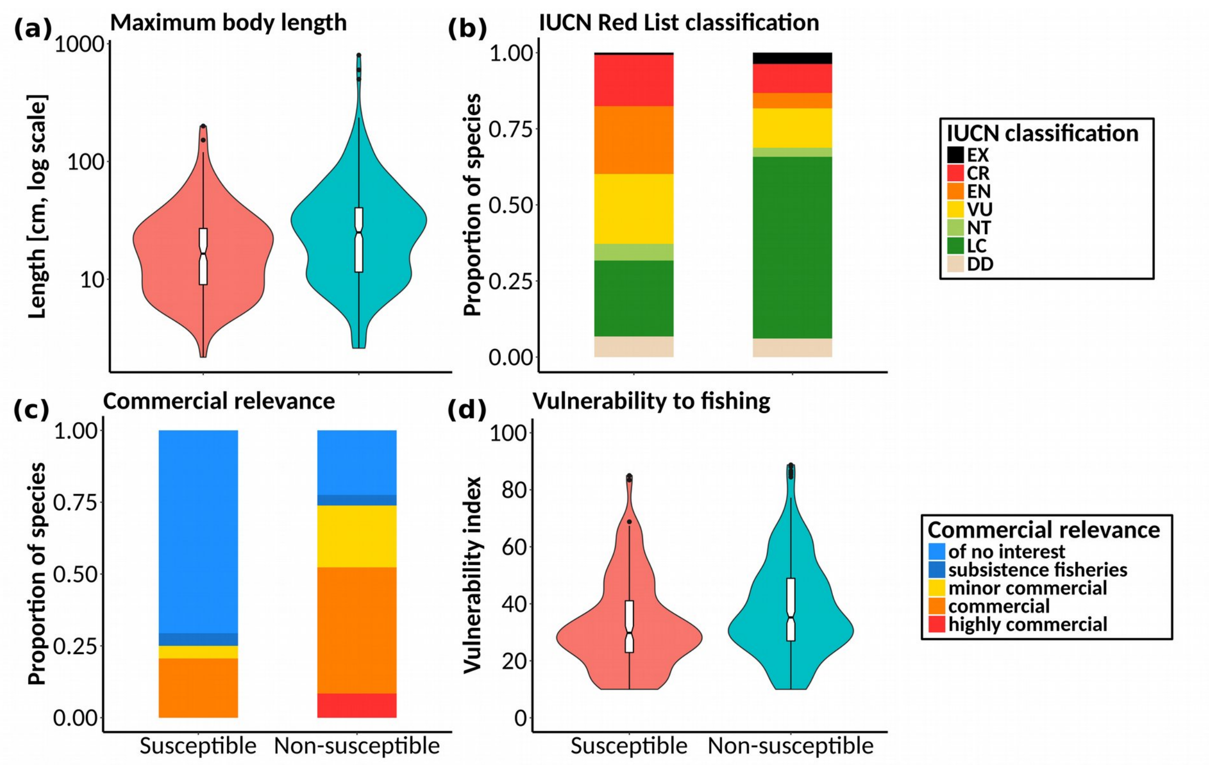

Figure 3. Violin-boxplots and barplots of the most relevant life history traits and variables related to threat and commercial status in European freshwater fish species indicated as either susceptible (n = 148) or non-susceptible (n = 295) to climate change.

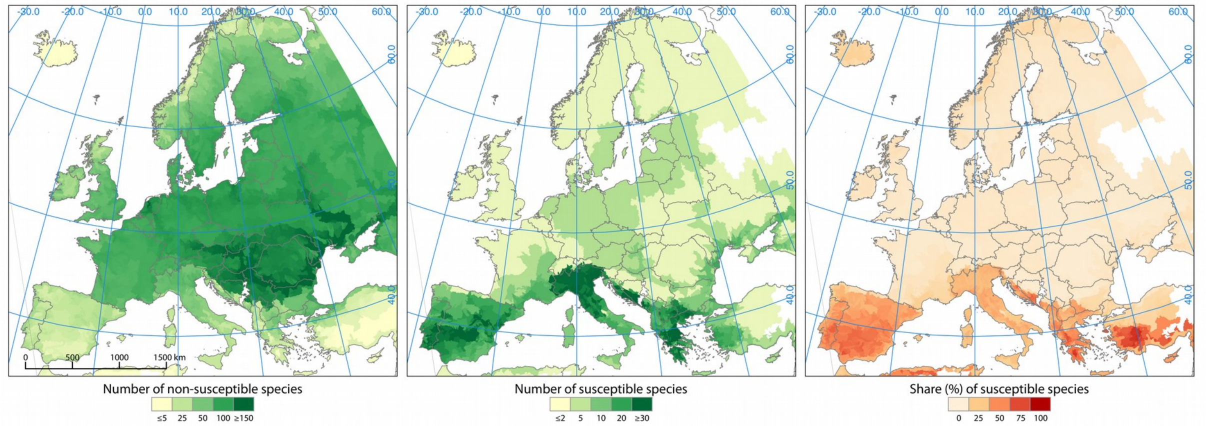

Figure 4. Richness of freshwater fish species across Europe indicated as either susceptible (middle panel) or non-susceptible (left panel) to climate change, and the relative share of susceptible species in the local total species richness (right panel).