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Vulnerability of European freshwater catchments to climate change

DANIJELA MARKOVIC[1,2,3], SAVRINA F. CARRIZO[4], OSKAR KÄRCHER[1], ARIANE WALZ[5] and JONATHAN N. W. DAVID[6]

[1]*Faculty of Business Management and Social Sciences, Osnabrück University of Applied Sciences, Caprivistr. 30A, Osnabrück 49076, Germany,* [2]*Center of Applied Biology, Department of Phytomedicine, Hochschule Geisenheim University, Von-Lade-Str. 1, Geisenheim 65366, Germany,* [3]*Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, Berlin 12587, Germany,* [4]*Freshwater Biodiversity Unit IUCN Global Species Programme, 219c Huntingdon Road, Cambridge CB3 ODL, UK,* [5]*Institute of Earth and Environmental Science, University of Potsdam, Karl-Liebknecht-Str. 24-25, Potsdam 14476, Germany,* [6]*Oxford University Centre for the Environment, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK*

Abstract

Climate change is expected to exacerbate the current threats to freshwater ecosystems, yet multifaceted studies on the potential impacts of climate change on freshwater biodiversity at scales that inform management planning are lacking. The aim of this study was to fill this void through the development of a novel framework for assessing climate change vulnerability tailored to freshwater ecosystems. The three dimensions of climate change vulnerability are as follows: (i) *exposure* to climate change, (ii) *sensitivity* to altered environmental conditions and (iii) *resilience* potential. Our vulnerability framework includes 1685 freshwater species of plants, fishes, molluscs, odonates, amphibians, crayfish and turtles alongside key features within and between catchments, such as topography and connectivity. Several methodologies were used to combine these dimensions across a variety of future climate change models and scenarios. The resulting indices were overlaid to assess the vulnerability of European freshwater ecosystems at the catchment scale (18 783 catchments). The Balkan Lakes Ohrid and Prespa and Mediterranean islands emerge as most vulnerable to climate change. For the 2030s, we showed a consensus among the applied methods whereby up to 573 lake and river catchments are highly vulnerable to climate change. The anthropogenic disruption of hydrological habitat connectivity by dams is the major factor reducing climate change resilience. A gap analysis demonstrated that the current European protected area network covers <25% of the most vulnerable catchments. Practical steps need to be taken to ensure the persistence of freshwater biodiversity under climate change. Priority should be placed on enhancing stakeholder cooperation at the major basin scale towards preventing further degradation of freshwater ecosystems and maintaining connectivity among catchments. The catchments identified as most vulnerable to climate change provide preliminary targets for development of climate change conservation management and mitigation strategies.

Keywords: catchment connectivity, climate change, exposure, freshwater biodiversity, gap analysis, resilience, sensitivity, vulnerability

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Introduction

Freshwaters cover less than one per cent of the earth's surface, yet are home to approximately six per cent of all known animal species (Strayer & Dudgeon, 2010; Woodward *et al.*, 2010). Of those that have been assessed on the Red List of Threatened Species™ (n = 25 007), more than 29% are currently at risk of extinction (IUCN, 2013), primarily due to a combination of pollution, unsustainable land use, overutilization of freshwater resources, anthropogenic disruption of hydrological habitat connectivity and introduction of alien species (cf. Strayer & Dudgeon, 2010; Mantyka-Pringle *et al.*, 2014). These threats combined with the importance of freshwater for human development suggest that freshwater ecosystems and the biodiversity they support are, and will remain, among the most endangered globally (Palmer *et al.*, 2008).

Climate change is expected to exacerbate these current threats to freshwater ecosystems, leading to alterations in the magnitude, frequency, duration, timing and variability of thermal and hydrological freshwater attributes (Bates *et al.*, 2008; Heino *et al.*, 2009; Woodward *et al.*, 2010; Poff *et al.*, 2012).

Correspondence: Danijela Markovic, tel. +49 541 969 2033, fax +49 541 969 3036, e-mail: markovic@quant-works.de

However, predictions of the full scope of interactions, feedback loops and synergies among stressors are still clearly beyond the capacities of existing models. Furthermore, many freshwater species are already shifting their ranges and phenology in response to recent climate change (Hickling *et al.*, 2005; Parmesan, 2006; Comte *et al.*, 2013), with dispersal possibilities of obligate aquatic species strongly restricted by the dendritic hierarchical structure of river networks and numerous dispersal barriers present therein, such as dams and natural obstacles (Liermann *et al.*, 2012).

To date, assessments of the potential effects of climate change on freshwater biodiversity have been restricted to the application of the niche-based species distributions models (e.g. Comte *et al.*, 2013; Domisch *et al.*, 2013; Markovic *et al.*, 2014). Such models relate current conditions to existing species distributions and project these using climate change models, thus only considering exposure to climate change. However, as outlined by Dawson *et al.* (2011), one must consider all aspects of vulnerability to assess the biodiversity consequences of climate change, that is exposure, sensitivity and resilience. To date, in an ecological context, this vulnerability framework has predominantly been applied to marine and the terrestrial ecosystems (Chin *et al.*, 2010; Foden *et al.*, 2013). Most previous studies of vulnerability of freshwater ecosystems to climate change have been constrained to single taxonomic groups and to the effects of sensitivity and exposure (see Haidekker & Hering, 2008; Conti *et al.*, 2014; Hershkovitz *et al.*, 2015; Pyne & Poff, 2016). For example, Pyne & Poff (2016) used sensitivity and exposure to assess the insect vulnerability to projected thermal warming and hydrological change in the Western United States. Conversely, vulnerability assessments of freshwater ecosystems to climate change that integrate all aspects of vulnerability (exposure, sensitivity and resilience) are still lacking.

This study seeks to address this knowledge gap. It assesses the vulnerability of freshwater ecosystems to climate change at the catchment scale and identifies priority catchments for conservation measures to mitigate climate change impacts. We focus on European river and lake catchments, represented by 1685 freshwater species of plants, fishes, molluscs, odonates, amphibians, crayfish and turtles. Following the vulnerability terminology of Turner *et al.* (2003), as adopted for freshwater ecosystems by Poff *et al.* (2012), the three climate change vulnerability dimensions are as follows: (i) extrinsic *exposure* to climate change (i.e. the extent to which environmental conditions in each catchment will change), (ii) intrinsic *sensitivity* to altered environmental conditions (i.e. the lack of potential for freshwater species to persist in a catchment) and (iii) *resilience* (i.e. the aspects of a catchment that enable freshwater species to cope under climate change). The exposure, sensitivity and resilience estimates were combined to provide comprehensive assessments of the vulnerability of European river and lake catchments to a range of climate change scenarios. Finally, based on vulnerability category and coverage by the European protected areas network, we identified priority catchments that facilitate the development of broadscale climate change conservation management strategies.

Materials and methods

Species data

Distribution maps were obtained for 1685 European freshwater species including 323 plants, 508 fishes, 657 molluscs, 134 odonates, 54 amphibians, five crayfish and four turtles (see https://www.iucn.org/theme/species/our-work/freshwater-biodiversity/what-we-do/biofresh-0 for more details). This data set includes native portions of species ranges throughout Europe that were compiled by the IUCN Global Species Programme as part of the Red List assessment process. The IUCN Red List Categories and Criteria are a widely recognized system for classifying species' extinction risk at the global scale (IUCN, 2013, 2014). Following a range of quantitative criteria, species' extinction risk is mapped to one of eight categories of threat ('Extinct', 'Extinct in the wild', 'Critically Endangered', 'Endangered', 'Vulnerable', 'Near Threatened', 'Least Concern' and 'Data Deficient'). The categories 'Critically Endangered', 'Endangered' and 'Vulnerable' are described as 'Threatened', implying high extinction risk (IUCN, 2013).

The non-native portions of species ranges were excluded due to missing information on their impact on resident communities. The data were mapped to the HydroBasins level eight resolution catchments (Lehner & Grill, 2013), which delineates European river and lake systems into 18 783 catchments (average area of 536.3 km^2, hereafter called 'catchments'; see Fig. S1). The HydroBasins dataset is based on high-resolution elevation data obtained from the NASA's Shuttle Radar Topography Mission (SRTM), except for regions above 60 degrees northern latitude, where coarser scale elevation data were used (HYDRO1k, developed by the U.S. Geological Survey). Given the dendritic, hierarchical structure of river and stream networks, the catchment resolution is more appropriate for mapping freshwater species occurrences than grid cell mapping and ensures compatibility between the analysis and management scales (Luck *et al.*, 2009). Also, freshwater conservation planning requires consideration of river networks, their connectivity and the surrounding land. As such, an alternative to a species-based approach in determining appropriate conservation areas is a catchment-based approach. The latter is a more general concept in conservation planning, as one looks at the entire catchment, rather than on individual species (see Mattson & Angermeier, 2007; Linke *et al.*, 2008).

Climate and hydrological data

The climatic and hydrological data describing the thermal and hydrological regimes across Europe for the 20th and 21st century were derived from the global gridded 0.5° × 0.5° WATCH (Water and Global Change) data set (https://gateway.ceh.ac.uk/, accessed on 5 September 2013). For more details on the data set, see http://www.eu-watch.org/data_availability, Hagemann *et al.* (2011) and Weedon *et al.* (2011). Specifically, we used the bias-corrected (see Piani *et al.*, 2010) daily data on air temperature and naturalized flows generated by WaterGAP (Döll *et al.*, 2003), GWAVA (Meigh *et al.*, 1999) and LPJmL (Bondeau *et al.*, 2007) hydrological models (HMs) for three time periods: 1971–2000 (hereafter called 'baseline'), 2021–2050 (hereafter called '2030s') and 2071–2100 (hereafter called '2080s'). We focussed on naturalized flows obtained from running the hydrological component of the HMs only (i.e. without the water usage component) due to the substantial differences between how each HM represented the anthropogenic and social impacts on river flow (Haddeland *et al.*, 2011). The Worldclim 30 arc-second (approximately 1 km×1 km) data set (Hijmans *et al.* (2005); www.worldclim.org, accessed on 14 April 2014) was used to derive the catchment specific altitudinal range, in addition to the average and maximum temperatures over the period 1960–2000 (hereafter called 'extended baseline'). Altitude is based on the SRTM digital elevation data.

All future projections were based on three general circulation models (GCMs), ECHAM5, CNRM and IPSL, with each following the A2 and B1 emission scenarios. A2 and B1 storylines describe a world with continuously increasing global population and regionally oriented economic growth (A2), and a world where global population peaks mid-century and declines thereafter and introduces clean and resource-efficient technologies (B1) (Nakicenovic *et al.*, 2000). The use of different emission scenarios provides an incorporation of the anthropogenic and social impacts in the vulnerability analyses and thus extends consideration of the hydrological model projections beyond 'climate-only' related changes in hydrological regimes. Finally, the climatic data combined with the hydrological data results in 54 distinct sets (3 HMs × 3 GCMs × 2 scenarios × 3 time periods; Fig. S2).

Protected areas

The protected areas used in this analysis include data obtained from the World Database on Protected Areas (WDPA, https://www.protectedplanet.net/, accessed on 20 August 2013) and the Natura 2000 database (www.eea.europa.eu, accessed on 22 March 2013) (Fig. S3). From the WDPA data set, we only considered protected areas with IUCN categories I-IV, corresponding to strict nature reserves, wilderness areas, ecosystem conservation and protection areas, conservation areas for natural features and areas with conservation through active management. All Natura 2000 sites were used in our study, as they comprise Special Protected Areas (SPA) and adopted Sites of Community Importance (SCI), designated by EU Member States under the Birds Directive (79/409/EEC) and the Habitats Directive (92/43/EEC) with the aim of long-term protection of Europe's most valuable and threatened species and habitats. The total area protected (PA) within each individual catchment was calculated by overlaying the union of the WDPA and Natura 2000 layers with the catchments layer using ESRI ArcGIS analysis tools (Fig. S3).

Exposure assessment

The conceptual framework for calculation of the exposure indicators is based on the indicators introduced by Richter *et al.* (1996) and Poff *et al.* (1997). Further elaboration of the concept for the thermal regimes is provided by Olden & Naiman (2010) and for the flow regimes by Laizé *et al.* (2014). Underlying these approaches is the assumption that ecologically relevant hydrological and thermal regime alterations are best described by changes to the (i) magnitude, (ii) frequency, (iii) duration, (iv) timing and (v) variability of regime attributes.

Magnitude. The magnitude of hydrological and thermal events represents the availability of the freshwater habitat for both in-stream and riparian species. In addition, the magnitude of thermal events plays a fundamental role in determining the water quality and distribution of aquatic species (Caissie, 2006; Comte *et al.*, 2013).

Frequency. The frequency of events, in particular extreme events such as floods and droughts or heat and cold waves (i.e. extraordinary high or low air temperatures), affects population dynamics through impacts on reproduction or increases in species mortality (Richter *et al.*, 1996).

Duration. The duration of events, in particular increases in the duration of droughts and summer heat stress (in terms of prolonged periods with no rain or with significantly higher than average summer air temperature), may lead to significant distortions in community structure and composition, and poses elevated, potentially lethal risks, for cold-water species (Markovic *et al.*, 2013).

Timing. The timing of events, in particular the timing of annual extremes, may impair ecological success of particular life stages. Thus, changes in event timing may result in weakening of or breaks in the trophic interactions (Woodward *et al.*, 2010).

Variability. The variability of hydrological and thermal regimes strongly affects food-web synchrony. Changes in regime variability may affect habitat availability and lead to disruption of established patterns in food-web synchrony (Kishi *et al.*, 2005).

To address the climate change-related alterations of hydrological and thermal regimes, we used a set of indicators specified in Table S1. For each hydrological and thermal regime indicator, Table S1 provides the information on the type of change described by the indicator (magnitude, frequency, duration, timing or variability) and the methodology used to calculate the indicator. Firstly, for each indicator, the change between baseline and future conditions was determined (2030s vs. baseline and 2080s vs. baseline). Secondly, the results for each GCM were merged for each of the emission scenarios by averaging the corresponding indicator values per grid cell and across all HMs for discharge related indicators. The use of the multimodel average for predicted climate is based on earlier findings that multimodel averages of present-day climate generally outperform any individual model (Pierce *et al.*, 2009; Knutti *et al.*, 2010). Thirdly, the grid cell-related hydrological and thermal alterations were calculated by counting the number of indicators exceeding the respective thresholds (see Table S1), selected following Laizé *et al.* (2014) and Van Vliet *et al.* (2013). Fourthly, the catchment-related hydrological and thermal alterations were calculated from the corresponding gridded layers using the ESRI ArcGIS zonal statistics tool. Finally, the exposure to climate change was determined by merging the catchment-related hydrological and thermal alterations and then normalizing to a 0–1 scale.

Sensitivity assessment

Freshwater ecosystems dominated by threatened, restricted-range species (i.e. species with a geographically restricted area of distribution) and those with narrow environmental tolerances are likely to suffer greater impacts from climate change than ecosystems containing only more common and/or widespread species (Markovic *et al.*, 2014). For example, temperature, flow regime and presence of other species are known to affect spatial patterns of trout species (see Wenger *et al.*, 2011). The sensitivity assessment applied here combines various concepts including the threat, range-restricted and ecoregion-restricted criteria of freshwater Key Biodiversity Areas (KBA) (Holland *et al.*, 2012), the Alliance for Zero Extinction concept (Ricketts *et al.*, 2005) and the species traits approach (Foden *et al.*, 2013). Specifically, the following attributes of sensitivity were considered:

Presence of threatened species. This criterion reflects species' risk of extinction following the IUCN Red List of Threatened Species™, which classifies threatened species into categories 'Critically Endangered' (CR), 'Endangered' (EN) or 'Vulnerable' (VU) based on a globally accepted set of quantitative criteria (IUCN, 2014). Given that CR, EN and VU species are at extremely high risk or very high risk of extinction in the wild (IUCN, 2014), we consider climate change as an additional threat increasing their extinction risk. We assigned a score based on the total number of species classified in any of the three categories (i.e. 0 for a catchment with no threatened species and 1 for a catchment with the maximum number of threatened species; 'standard scoring'). An alternative 'conservative scoring' assigns the score 1 to a catchment if at least one threatened species was present, otherwise, 0. Two estimates of this sensitivity component were calculated, with one using the European and the other using the global species' Red List Categories. The use of the two Red List Categories (European and global) is justified by differences in determining species' extinction risk: the European Red List (IUCN 2010 European Red List, downloaded on 3 February 2014) identifies European species threatened with extinction at the European level (Pan-Europe and the European Union) according to IUCN regional Red Listing guidelines; the IUCN Red List of Threatened Species™ (i.e. the global species' Red List) identifies species threatened with extinction at the global scale, following a set of specific criteria that are relevant to all species and all regions of the world (IUCN, 2013).

Presence of species with restricted ranges. Species with small (restricted) ranges generally have higher extinction risk than widespread species (Purvis *et al.*, 2000). As such, the inherent vulnerability of restricted-range species to external pressures is compounded by climate change-related effects. Following Holland *et al.* (2012), a threshold value for the extent of occurrence (EOO) of 50 000 km^2 for odonates and 20 000 km^2 for other taxa groups was used to identify species with restricted ranges. Here, the total range size was used as a proxy for the species' EOO. We calculated a score based on the total number of species with restricted ranges per catchment (i.e. 0 for a catchment with no such species and 1 for a catchment with the maximum number of such species; 'standard scoring'). Alternatively, for 'conservative scoring', a catchment was assigned the score 1 if at least one restricted-range species was present, otherwise, 0.

Presence of species confined to a single biogeographic unit. We used freshwater ecoregions of the world (Abell *et al.*, 2008) as the biogeographic units. For each catchment and each taxa group, we identified the proportion of species that occur in a single freshwater ecoregion. Critical proportions of ecoregion-restricted species were set to 5% for all taxa groups, except for fish with a threshold of 25% based on Holland *et al.* (2012). If the proportion of ecoregion-restricted species is higher than the given thresholds for any of the taxa groups (i.e. higher than 25% for fish or higher than 5% for any of the other taxa groups), a catchment was assigned the score 1 for this sensitivity attribute, otherwise, 0.

Unique catchments. If a catchment represents the entire known range of any species, then it was considered unique (Linke *et al.*, 2008), and thus, the catchment's biodiversity is highly sensitive to climate change effects. We calculated the uniqueness value of all catchments for each species ('Uval_s') as the ratio between the catchment area occupied by a species (0 if the species is currently not present, otherwise, the catchment area size) and the total species' range area. The final catchment specific uniqueness score ('Uscore') is then calculated following $\mathrm{Uscore}(c) = \max(\mathrm{Uval}_s), s = 1, \ldots, s_c$, where s_c denotes the species inhabiting catchment c.

Species with narrow environmental tolerance. Tolerance to a wide range of climatic conditions is tightly linked to the ability of a species to resist and recover from environmental change (Poff *et al.*, 2012). We used the air temperature range (maximum–minimum) over the extended baseline period (1960–2000) across a species current range as a proxy for species environmental tolerance breadths (see Angilletta, 2009). Species' tolerance breadths ('TB_s') vary from 'TB_{min}' (i.e. the tolerance range for a species with the lowest tolerance) to 'TB_{max}' (i.e. the tolerance range for a species with the highest tolerance). Each species was assigned a normalized score such that TBn_s=1-(TB_s-TB_{min})/(TB_{max}-TB_{min}), (i.e. TBn_s is 0 for species with the highest tolerance and 1 for species with the lowest). The catchment specific score for this sensitivity attribute ('TB_{score}') was then the maximum normalized score across species inhabiting the particular catchment (i.e. $\mathrm{TB_{score}}(c) = \max(\mathrm{TBn}_s), s = 1, \ldots, s_c$, where s_c denotes the total number of species inhabiting the catchment *c*). Here, the argument for using the species' tolerance breadths is that it enables a rough estimate on whether or not a species is a 'narrow specialist' or a 'generalist', given that species with narrow habitat requirements (specialist) are more sensitive to environmental change than generalists (Angilletta, 2009). We note that the use of the species' tolerance breadths approach using the temperature range is not applicable for the discharge range. Because of the nested hierarchy of drainage basins and associated downstream flow accumulation, the discharge range varies with the characteristics of the area drained by a river reach.

Catchment specific sensitivity was calculated as an average across the individual scores of the five sensitivity attributes described above – presence of threatened species, presence of species with restricted ranges, presence of species confined to a single biogeographic unit, irreplaceability of catchments and presence of species with narrow environmental tolerance. The sensitivity assessments based on the standard and conservative catchment scoring are hereafter referred to as 'standard' and 'conservative' approach, respectively.

Resilience assessment

Habitat connectivity and availability of diverse freshwater environments (e.g. from mountainous streams to lowland rivers) are one of the key factors influencing recolonization ability of species and thus species resilience to climate change. We adopted the resilience concept of Poff *et al.* (2012), which considers resilience more broadly as a structural feature of the landscape, that is catchments, and not solely as a species' trait. To account for the hydrological catchment connectivity, we considered both natural dispersal barriers (drainage divides of the major basins were estimated using the Pfafstetter coding feature of HydroBasins, see Lehner & Grill, 2013) and the anthropogenic barriers (dams and obstacles). The geographic location of about 5500 dams and obstacles (referred to hereafter as 'dams') across the European catchments was extracted from the ECRINS (European Catchments and Rivers Network System) database (http://www.eea.europa.eu/data-and-maps/data/european-catchments-and-rivers-network, accessed on 14 February 2014). We considered two dispersal situations: (i) under consideration of dams as dispersal barriers and (ii) without consideration of dams, that is the situation before connectivity disruption by the barriers. The following resilience attributes were considered.

Altitudinal range. Altitudinal range (the maximum elevational gradient, i.e., the positive difference between the highest and lowest points in a given catchment) provides an indirect measure of the basin-specific differences in the opportunities available to freshwater species to escape thermal stress, where basins with a small altitudinal range provide less opportunity than those with alpine streams (e.g. Comte *et al.*, 2013). For each catchment, the maximum altitudinal range across the connected catchments was used.

Latitudinal gradient. Many freshwater species are already expanding their ranges to higher latitudes in response to climate change (Hickling *et al.*, 2005; Domisch *et al.*, 2013). Consequently, the basins' latitudinal range can be used as a proxy for resilience to adverse effects of climate change. To assess the opportunity for species to move northwards in response to climate change (Hickling *et al.*, 2005; Domisch *et al.*, 2013), we calculated the maximum latitudinal range for each catchment as the difference between latitudes of the northernmost border of the northernmost connected catchment and southernmost border of the southernmost connected catchment.

Network density. The network density represents a natural source of resilience for freshwater species within a catchment (Campbell Grant *et al.*, 2007) and was quantified as the ratio between the total length of river network in a catchment and the catchment area.

Network complexity. The network complexity represents a natural source of resilience for freshwater species (Poff *et al.*, 2012) and was quantified as the total number of connected catchments to each catchment within the study area.

For each resilience attribute, all catchments were sorted by score and then normalized to the 0–1 scale (i.e. 0 for a catchment with the smallest and 1 for a catchment with the largest value for the particular resilience attribute). Finally, catchment specific resilience was calculated as an average of the corresponding values for the resilience attributes.

Climate change vulnerability assessment

Within each catchment, each of the three dimensions that make up the vulnerability of freshwater ecosystems to climate change, namely exposure, sensitivity and resilience, was assigned a category of 'low' (≤0.25), 'medium' (>0.25 and ≤0.50), 'high' (>0.5 and ≤0.75) or 'very high' (>0.75). Furthermore, to align all three vulnerability dimensions to the same 'low' to 'very high' scale, we used 1-resilience, as counterpart of the resilience. As such, the highest vulnerability is expected for catchments with 'very high' exposure, 'very high' sensitivity and 'very high' 1-resilience. Given that vulnerability is considered here as a combination of all three dimensions, each having four categories, the threedimensional logical matrix has $4^3 = 64$ possible combinations (Table S2). For example, the combination 'high', 'very high' and 'very high' is possible three times (i.e., (i) 'high' exposure and 'very high' sensitivity and 1-resilience; (ii) 'high' sensitivity and 'very high' exposure and 1-resilience; (iii) 'high' 1-resilience and 'very high' sensitivity and exposure). The possible combinations of the exposure, sensitivity and 1-resilience categories can be mapped to 'low', 'medium', 'high' or 'very high' climate change vulnerability in a variety of ways (e.g. Chin *et al.*, 2010; Comer *et al.*, 2012; Foden *et al.*, 2013). Here, we used four different vulnerability assessment methods for classifying the vulnerability of a catchment. This allows us to explore the sensitivity of the vulnerability mapping to assumptions about how the three vulnerability dimensions interact (see Table S2 for details): Vulnerability Assessment Method 1 (VAM_1) is the most conservative, with the climate change vulnerability calculated as the average of the three vulnerability components (i.e. depending on the mean value of the sensitivity, 1-resilience and the exposure score) and classified as 'low' ($\leq$0.25), 'medium' (>0.25 and $\leq$0.50), 'high' (>0.5 and $\leq$0.75) or 'very high' (>0.75). As such, VAM_1 has 7 score sets in the category 'low', 22 in 'medium', 25 in 'high' and 10 in 'very high'. VAM_2 is based on the symmetric distribution of scores, with 10 score combinations in the category 'low', 22 in 'medium', 22 in 'high' and 10 in 'very high'. VAM_3 is based on a positively skewed distribution of scores, with 19 score combinations in the category 'low', 19 in 'medium', 16 in 'high' and 10 in 'very high'. VAM_4 employs the rule that categories are assigned to score combinations based on the lowest dimension score; for example, 'low' score in any vulnerability dimension must lead to a 'low' vulnerability to climate change and so forth, with the 'very high' vulnerability category only assigned if all three vulnerability dimensions scored 'very high'. This results in 37 score combinations in the category 'low', 7 in 'medium', 19 in 'high' and 1 in 'very high'.

To help inform and facilitate the development of climate change conservation management strategies, we assessed the number of catchments in each vulnerability category within the European protected areas network (Natura 2000 and WDPA). The latter was carried out for each of the assessment methods (VAM_1 to VAM_4), for the combination of the first three methods (VAM_1 to VAM_3) and for the combination of all assessment methods (VAM_1 to VAM_4). When combining the vulnerability results of the multiple assessment methods, a catchment was assigned a particular vulnerability category (e.g. 'very high' vulnerability) only if the same category was assigned for all considered vulnerability assessment methods, otherwise it was categorized as 'no consensus'. Finally, we conduct a gap analysis and search for the catchments with <25% of surface area being protected by the European protected area networks and 'high' to 'very high' vulnerability to climate change.

In our analysis, each indicator for the corresponding vulnerability dimension was treated equally; that is, there was no weighted estimation of certain indicators. In addition, all species are treated equally within our vulnerability assessment.

Results

To explore the vulnerability of European freshwater to climate change at the catchment scale, each vulnerability dimension (exposure, sensitivity and 1-resilience) was analysed separately and in combination with all others. The absolute Pearson correlations between the three vulnerability dimensions are below 0.1 for all combinations of scenarios (A2, B1), time periods and dispersal situations, indicating very little statistical dependence.

Exposure

Catchments characterized by a combination of large predicted changes in both thermal and hydrological regimes are mainly located in Spain, the Balkan countries and Baltic Sea countries (Fig. 1a, b). For example, changes to hydrological regimes will mainly affect southern Europe by the 2030s, but are predicted to increase by the 2080s and affect the Pechora, Northern Dvina and Mezen River basins in Russia and northern Scandinavian catchments. Whilst there is little variability between the scenarios for the 2030s (Fig. 1a, b, Fig. S4), variability increases with time so that the percentage area of categories 'high' and 'very high' exposure increases from 33.6% for 2030s to 84.8% for 2080s B1 scenario and from 25.2% to 92.6% for 2080s A2 scenario (Fig. S4).

Sensitivity

The sensitivity patterns based on the European Red List are almost identical to those based on the Global Red List (Fig. 1c, d, Fig. S5), and thus, only the latter is considered in further analyses. The highest numbers of threatened, restricted range or ecoregion-restricted species were found in catchments along the Croatian Adriatic Sea coastline, for the Balkan Lakes Ohrid and Prespa and the Duero, Tajo and Guadiana River basins in Spain (Fig. S5). Lake Ladoga the only home of the fish species *Coregonus ladogae* and the West Highlands of Scotland were found to be highly unique with respect to species' composition. Additionally, warm-adapted species in the southernmost parts of Europe appear to be less sensitive to climate warming than species in central and northern Europe (Fig. S5f).

The number of globally threatened species per catchment is generally below 5 (84% of the study area). However, for 21 catchments, it is between 15 and 60. As a result, when using the relative species numbers to calculate the individual sensitivity attributes, the majority of catchments were assigned 'low' sensitivity (Fig. S6a, b). In contrast, when applying the conservative

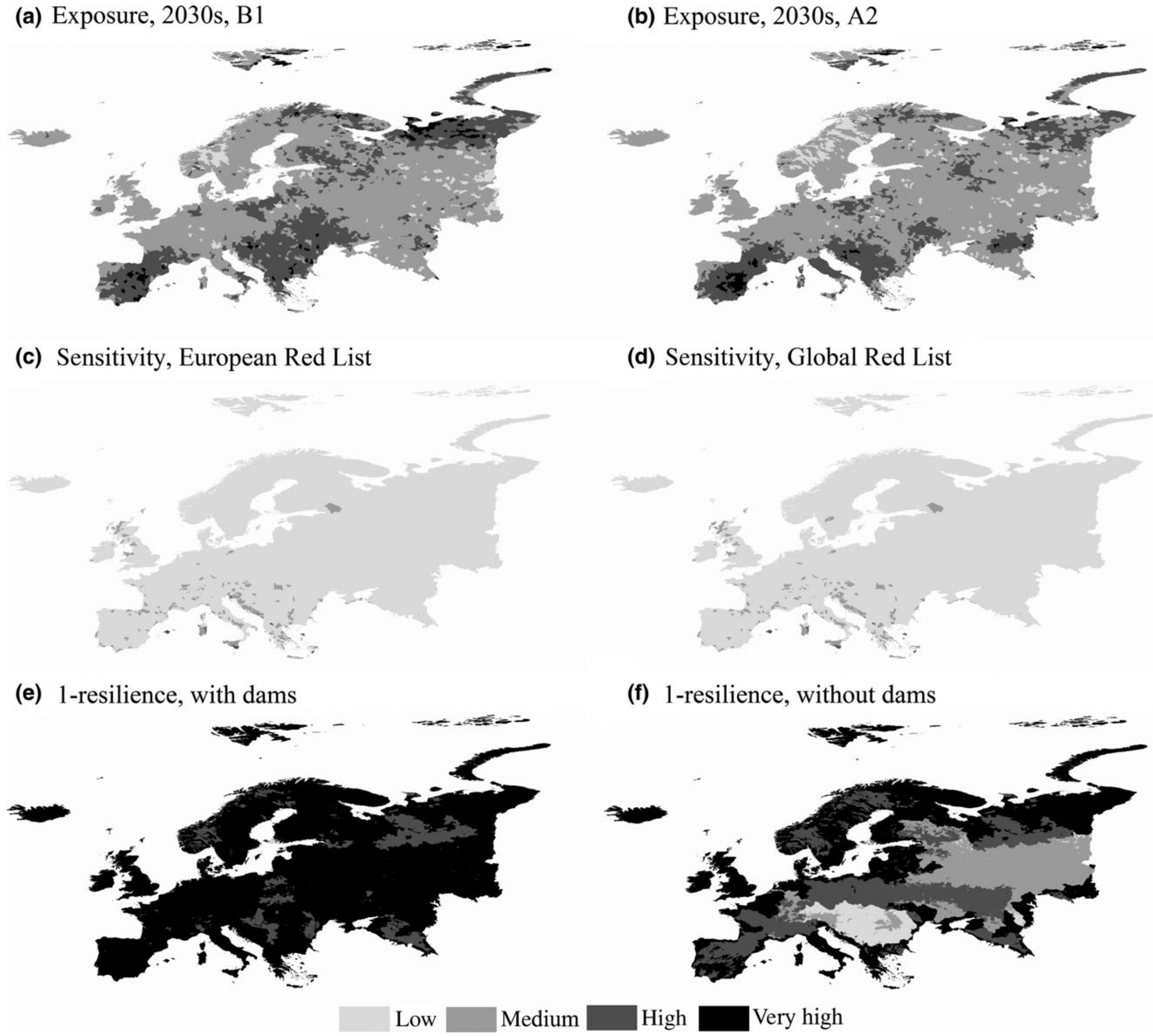

Fig. 1 The final scores for the three vulnerability dimensions (exposure, sensitivity and resilience): (a) the exposure for 2030s following B1 scenario; (b) the exposure for 2030s following A2 scenario; (c) the sensitivity based on all five sensitivity dimensions with the 'presence of threatened species' using the European Red List and (d) using species' global Red List Category; (e, f) show 1-resilience score with (e) and without (f) consideration of the influence of dams.

approach, the majority of catchments (>90%) are in the sensitivity categories 'medium' to 'high' (Fig. S6c, d).

Resilience

The degree of a catchment's connectivity appears to have a prevailing influence on all resilience components. Owing to numerous dispersal barriers, resilience is low for the majority of catchments (Fig. 1e, f). Consequently, the natural potential of the basins' altitudinal range, latitudinal gradient or river network complexity to provide species the opportunity to cope with climate change is considerably low, except for the Northern Caucasus region in Russia and the Piedmont region in Italy (Fig. S7). Without dams, the Danube, Neva, Dnieper and the Volga basins could provide 'high' to 'very high' resilience potential due to their high altitudinal range and latitudinal gradient (Fig. S7).

Climate change vulnerability

Tables 1 and S3–S6 provide summary statistics for the number of catchments, percentage surface area and percentage protected area for each climate change vulnerability category and each vulnerability method, whilst Tables S7 and S8 provide summary statistics for

Table 1 Summary statistics for the climate change vulnerability categories following the Vulnerability Assessment Method 1 (VAM_1). Within VAM_1, the vulnerability categories are based on the mean value of the exposure, sensitivity and 1-resilience scores

	Scenario/category	2030s B1 dams	2030s A2 dams	2080s B1 dams	2080s A2 dams	2030s B1 no dams	2030s A2 no dams	2080s B1 no dams	2080s A2 no dams
No. of catchments	Low	0	0	0	0	1087	1080	9	12
	Medium	13161	14243	6333	4166	14501	15098	11342	9531
	High	5600	4515	12411	14536	3174	2581	7397	9176
	Very high	9	12	26	68	8	11	22	51
Surface area (%)	Low	0.0	0.0	0.0	0.0	6.0	5.9	0.0	0.0
	Medium	71.9	76.9	38.9	25.8	77.2	80.2	63.6	54.2
	High	28.0	22.9	60.8	73.3	16.7	13.8	36.1	45.2
	Very high	0.1	0.1	0.3	0.9	0.1	0.1	0.3	0.5
Protected area (%)	Low	0.0	0.0	0.0	0.0	7.8	12.5	0.0	64.0
	Medium	10.1	10.1	9.4	8.4	11.0	10.5	10.4	10.2
	High	16.1	17.2	13.6	13.2	17.4	18.8	15.2	14.4
	Very high	58.2	32.8	36.4	26.0	53.7	35.0	34.5	32.0

No. of catchments is the number of catchments in each vulnerability category ('low', 'medium', 'high' and 'very high'). Surface area denotes the percentage of the total study area (10 073 990 km^2), and protected area denotes the percentage of the surface area found within the European protected area networks (Natura 2000 and WDPA for IUCN categories I–IV). Note that for 13 catchments, the climate change vulnerability could not be estimated due to missing data on the resilience components.

the combinations of the methods. A comparison between the vulnerability estimates based on the 'standard' and the 'conservative' sensitivity approaches is provided for VAM_1 (Table 1 vs. Table S3 and Fig. 2 vs. Fig. S8). We remind the reader that 'standard' and 'conservative' approach refers to assessments based on the standard and conservative catchment scoring, respectively (see Section Materials and methods).

The 'conservative' sensitivity approach predicted 'medium' to 'high' sensitivity to climate change for the majority of catchments (Fig. S6), because the presence of a single threatened or restricted-range species was sufficient to register sensitivity. As such, the 'conservative' sensitivity approach generally predicted higher vulnerability than the 'standard' approach (e.g. for 2030s B1 scenario with dams, 66.5% of area with 'high' vulnerability for the 'conservative' approach vs. 71.9% of area with 'medium' vulnerability for the 'standard' approach). Consequently, within all further analyses, the 'standard' sensitivity approach was used, as it provides a relative sensitivity for a given species composition and is thus more appropriate to characterize vulnerability of the freshwater ecosystems at the catchment scale than the 'conservative' approach, which considers individual species.

Overall, there are considerable variations in the spatial distribution of vulnerability categories and the corresponding summary statistics across different vulnerability methods (Table 1 and Tables S4–S6; Fig. 2 and Figs S9–S11). As the most conservative method, the main classifications of VAM_1 are 'medium' and 'high' vulnerability throughout all scenarios and timelines (Table 1, Fig. 2). These results are nearly consistent with those of VAM_2, still having the main classifications 'medium' and 'high', but having a slight shift regarding the 'no dams' situation towards the categorization 'low' (Table S4, Fig. S9). For VAM_3 (Table S5, Fig. S10), there is a stronger tendency towards the classifications 'low' and 'medium', mainly explained by the positively skewed distribution of scores. As in VAM_2, the scenarios with no dams have a remarkably higher number concerning the 'low' vulnerability classification. When considering connectivity disruption by dams, the VAM_3 suggests 'medium' vulnerability for about 85% of the total studied catchment's area (Table S5, Fig. S10). For VAM_4, irrespective of the scenario and timeline, more than 95% of European river and lake catchments are predicted to be in the 'low' vulnerability category (Table S6, Fig. S11). Such vulnerability predictions are highly unrealistic given predicted shifts in climate and widespread impoundment of rivers. Therefore, following the precautionary principle (Myers, 1993), we focus on VAM_1, VAM_2 and VAM_3 in further analyses but provide results for VAM_1 to VAM_4 in the Supporting Information (Table S8, Fig. S12).

Under consideration of connectivity disruption by dams, vulnerability is generally one category higher than without consideration of dams (Table 1 and Tables S4 and S5). The differences between dispersal options are particularly pronounced in the Danube, Neva, Dnieper and the Volga basins (Fig. 2 and Figs S9 and S10). For the 2030s, there is a consensus among the applied methods that the majority of catchments have 'low' to 'medium' vulnerability to climate change (>60% of the study area, Table S7, Figs 3 and

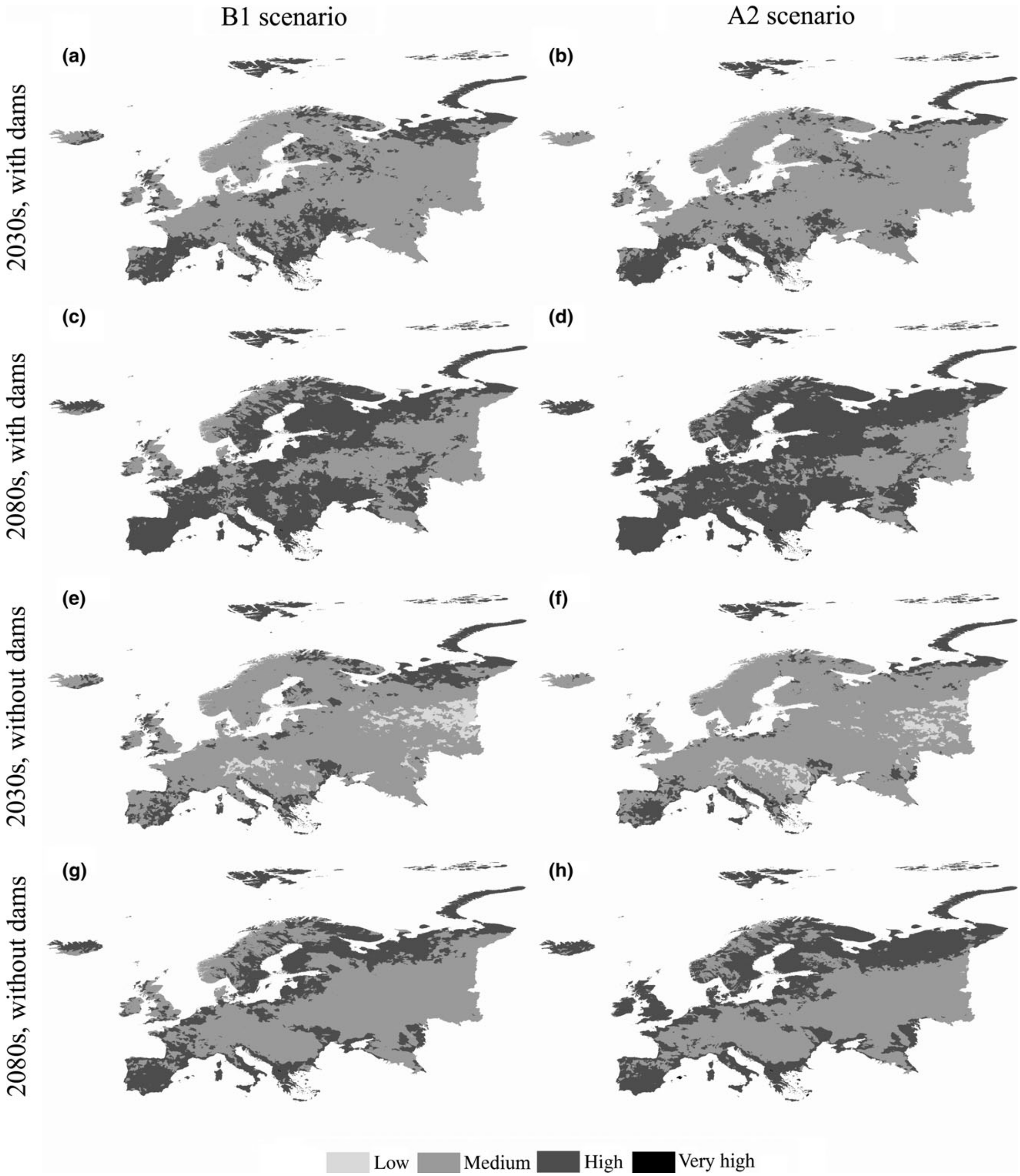

Fig. 2 Vulnerability to climate change for European freshwater ecosystems at the catchment scale using the method VAM_1: (a) 2030s exposure, B1 scenario, with dams; (b) 2030s exposure, A2 scenario, with dams; (c) 2080s exposure, B1 scenario, with dams; (d) 2080s exposure, A2 scenario, with dams; (e) 2030s exposure, B1 scenario, without dams; (f) 2030s exposure, A2 scenario, without dams; (g) 2080s exposure, B1 scenario, without dams; (h) 2080s exposure, A2 scenario, without dams. The sensitivity dimension is based on the species Global Red List Category and adopts the standard approach. Summary statistics are provided in Table 1.

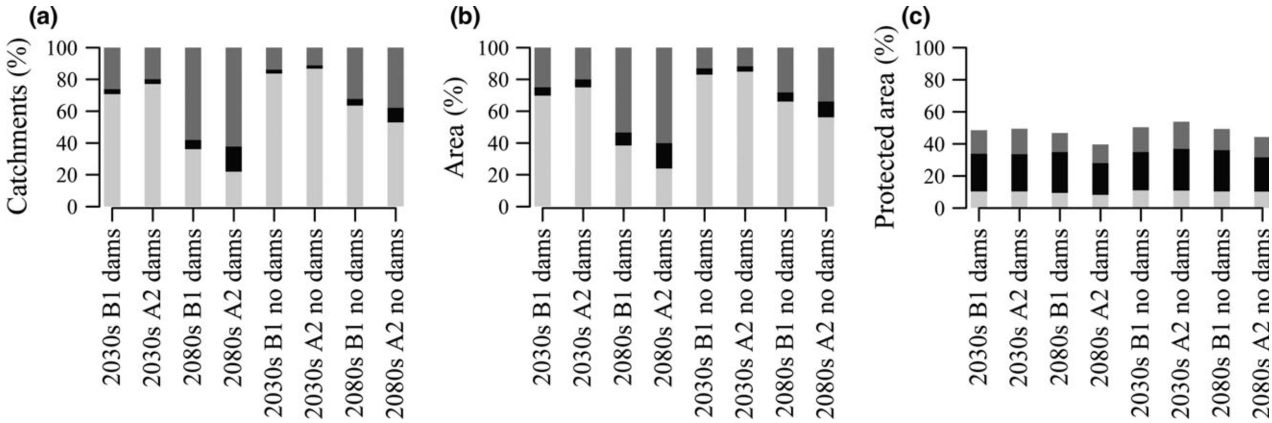

Fig. 3 Summary statistics for the VAM_1 to VAM_3 based vulnerability categories 'low to medium' (light grey) and 'high to very high' (black), with 'no consensus' (dark grey) denoting catchments where the three vulnerability estimation methods did not agree on the vulnerability category (see Table S7 for details): (a) the percentage of studied catchments (the total number of the studied catchments is 18 783); (b) the percentage of the total study area (10 073 990 km^2), and (c) the percentage of the corresponding surface area that is within the European protected area networks (Natura 2000 and WDPA for IUCN categories I-IV). Note that for 13 catchments the climate change vulnerability could not be estimated due to missing data on the resilience components.

4), with up to 573 lake and river catchments predicted to have 'high' to 'very high' vulnerability for VAM_1 to VAM_3 (Table S7, Figs 3 and 4). For the 2080s, the consensus between the vulnerability methods is lower than for 2030s, suggesting considerable uncertainty. However, most methods indicate vulnerability increases for the 2080s compared to 2030s across southern Europe (Spain, Italy, Balkan countries) and northern Europe (Scandinavia and northernmost parts of Russia).

Lake Ohrid (shared by the Republic of Macedonia and Albania) and Lake Prespa (shared by Albania, Greece and the Republic of Macedonia) are predicted to have 'very high' vulnerability to climate change for VAM_1 to VAM_3 and all scenarios and timelines. Specifically, 'very high' overall vulnerability for the Lake Ohrid and Lake Prespa results from the combination of 'low' resilience, 'very high' sensitivity and 'very high' exposure. Similarly, 'high' to 'very high' vulnerability to climate change is predicted in Lake Skadar (shared between Albania and Montenegro), Lake Ladoga (Russia), the Greek islands of Rhodes and Lesbos, the Spanish island of Mallorca, the Italian islands of Sardinia and Sicily and for catchments along the Adriatic Sea coast, eastern Spain, southern Greece, western Italy, northern Russia and Finland, Crimea and in the northwest of England and highlands of Scotland (Fig. 4). For example, for catchments along the Adriatic Sea coast, 'high' overall vulnerability results from the combination of 'low', resilience, 'high' exposure and 'high' sensitivity. Furthermore, catchments with 'high' to 'very high' vulnerability to climate change for VAM_1 to VAM_3 (Figs 3 and 4 and Table S7) have, on average, <25% of their area covered by the European protected areas network. A gap analysis for the 2030s (the most pessimistic scenario (B1) with dams) identified priority catchments for future management actions (Fig. 5).

Discussion

We found high exposure in terms of thermal and hydrological regime alterations across the Ebro basin in Spain, Garonne in France, Pechora in Russia and catchments along the Adriatic coast and northern Scandinavia, confirming and refining the findings of Van Vliet *et al.* (2013) and Laizé *et al.* (2014). The biodiversity-rich ancient lakes of Ohrid and Prespa, situated in the central Balkans, are shown to be particularly sensitive to climate change. Lake Ohrid has probably the highest endemic species density (212 species/358 km^2) in the world (Albrecht & Wilke, 2008). The resilience of freshwater ecosystems to climate change was shown to be strongly impaired by the anthropogenic disruption of hydrological habitat connectivity by dams. The effect of dams was highest in the basins of the Danube, Neva, Dnieper and Volga Rivers, significantly reducing species' dispersal potential. Specifically, strictly aquatic species such as diadromous fishes (those that migrate between sea and freshwaters to complete their life cycle) are among the most impacted by this connectivity loss (Liermann *et al.*, 2012). Most of the European diadromous fish species are now endangered, signifying that climate change paired with connectivity loss needs to be considered within current conservation plans (Lassalle *et al.* (2008). We underline here that our intention was not to predict individual freshwater

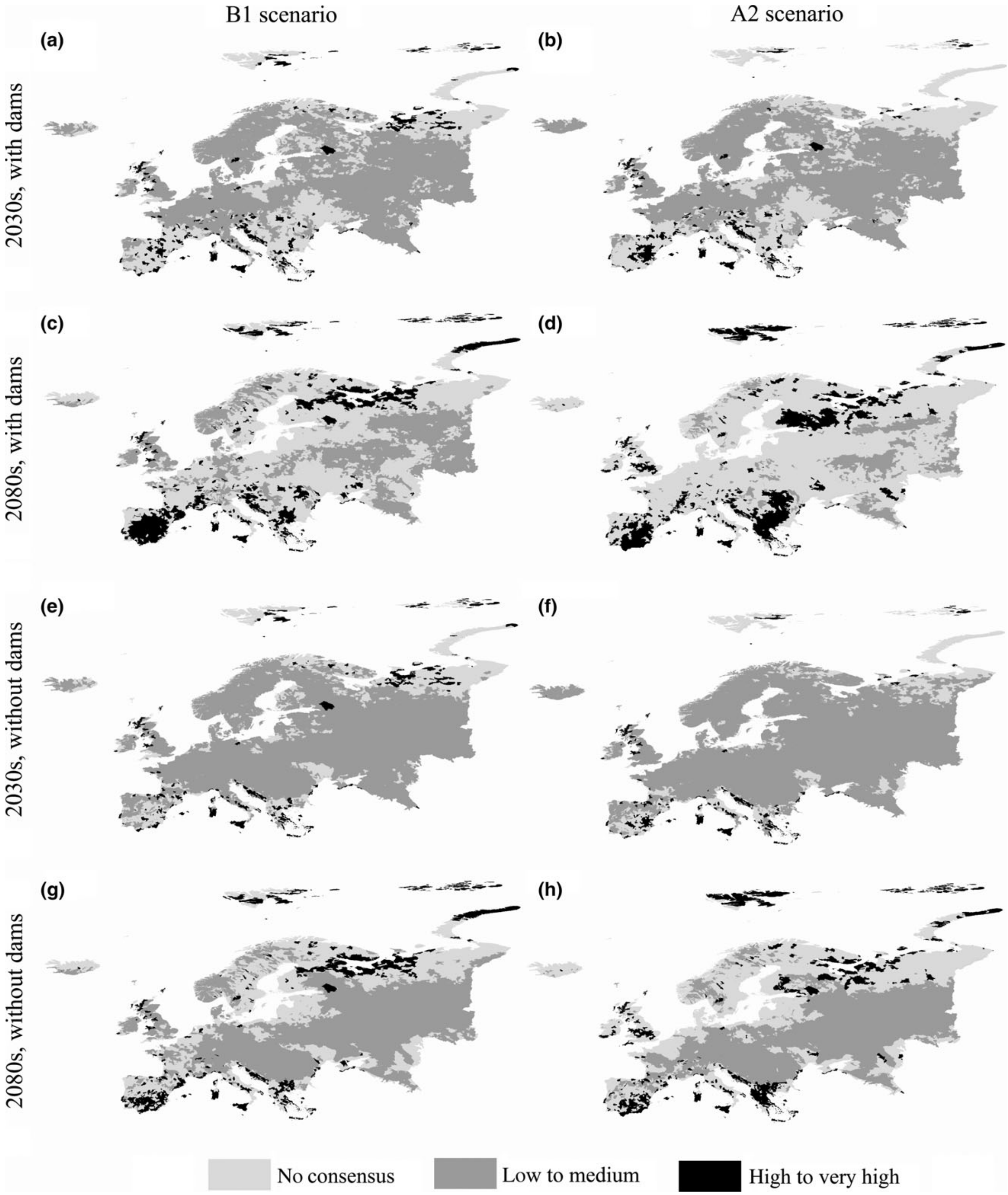

Fig. 4 Vulnerability to climate change for European freshwater ecosystems at the catchment scale based on combining the results of the methods VAM_1 to VAM_3: (a) 2030s exposure, B1 scenario, with dams; (b) 2030s exposure, A2 scenario, with dams; (c) 2080s exposure, B1 scenario, with dams; (d) 2080s exposure, A2 scenario, with dams; (e) 2030s exposure, B1 scenario, without dams; (f) 2030s exposure, A2 scenario, without dams; (g) 2080s exposure, B1 scenario, without dams; (h) 2080s exposure, A2 scenario, without dams. When combining the vulnerability results of the three assessment methods, a catchment was assigned the category 'low to medium' or 'high to very high' only if the same category was assigned for each of the three methods, otherwise it was assigned 'no consensus'. Summary statistics are provided in Table S7.

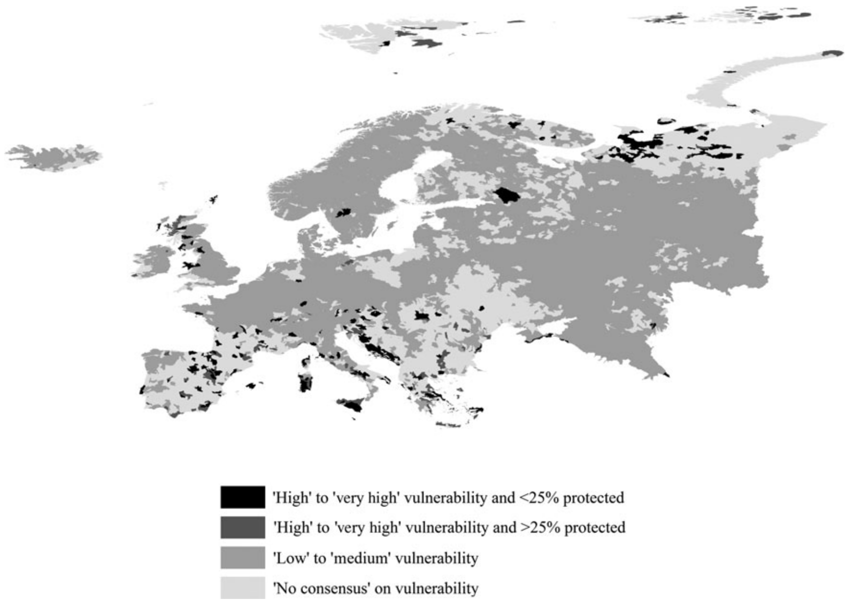

Fig. 5 The catchments requiring urgent management actions with <25% of surface area protected by the European protected area networks and predicted 'high' to 'very high' vulnerability to climate change based on the combination of VAM_1 to VAM_3 methods for 2030s exposure and the most pessimistic scenario (B1 scenario with consideration of dams).

species extinction risk due to climate change, as our framework does not allow us to do so with any acceptable degree of accuracy.

Our results highlight the Balkan Lakes and Mediterranean islands as most vulnerable, along with up to 573 lake and river catchments predicted to have 'high' to 'very high' vulnerability by 2030s according to the majority of our vulnerability assessment methods. Of these, <25% (by area) are situated within current protected areas, which generally have been designated for terrestrial conservation and therefore do not protect freshwater biodiversity (Nel *et al*., 2009, 2011). This, coupled with pollution due to poor land use practices and unsustainable water abstraction (Woodward *et al*., 2010), present a strong argument for review of the current protected area network to ensure persistence of freshwater ecosystems and the services they provide. The most vulnerable catchments identified in this study and the catchments identified in the gap analysis provide a practical starting point for future planning and mitigation strategies.

The variety of taxa groups studied (plants, fishes, molluscs, odonates, amphibians, crayfish and turtles) alongside the high spatial resolution of our study (>18 000 European lake and river catchments), consideration of upstream and downstream connectivity and multiple aspects of exposure, sensitivity and resilience, enabled us to decrease uncertainty in our climate change vulnerability estimates. By incorporating criteria of the Key Biodiversity Areas approach (KBA, Holland *et al*., 2012) into the climate change vulnerability framework, we provide a further basis for prioritizing catchments for management. Finally, our strategy of combining different vulnerability assessment methods surmounts the shortcomings of applying individual vulnerability assessment methods.

Despite our comprehensive framework, estimates of the vulnerability of European river and lake catchments to climate change are affected by several limitations. For example, our approach does not account for the variability in the dispersal capacity among the species studied. Also, the capacity for lake-dwelling species to seek refugia within lake ecosystems has not been included (Angilletta, 2009). More importantly, in addition to climatic factors, a complex interplay of other issues, including shifts in phenology, evolutionary adaptation, pollution, overabstraction of water and biotic interactions, determines species success in dealing with climate change. Also, the effects of climate change could be amplified by synergies with other stressors. For example, elevated temperatures during summer droughts could intensify the impacts of eutrophication and toxins by increasing pollutant concentrations (Woodward *et al*., 2010). Consequently, additional studies are required to further improve the vulnerability estimates presented here. Specifically, we need to further understand the role that hydrological catchment connectivity plays in species-specific ability to cope with climate change, how species evolutionary history confers adaptive potential and the effectiveness of current protected area networks in ensuring persistence of freshwater biodiversity. Furthermore, protected area planning will also need to facilitate species dispersal to more suitable habitats (Linke *et al*., 2011; Nel *et al*., 2011; Bagchi *et al*., 2013), including options that enable species' movement across dispersal barriers, or ultimately, options for assisted colonization (Hoegh-Guldberg *et al*., 2008; Olden *et al*., 2011).

In summary, climate change is expected to amplify existing threats within catchments, alongside causing novel shifts in the hydrological, thermal and biotic components of freshwater ecosystems. The ability of species and communities to adapt to climate change, together with the availability of in-stream refugia and options for species to move across natural and artificial barriers, will become increasingly important as time progresses. Additionally, an important instrument in dealing with climate change is management actions and mitigation strategies (Stein *et al*., 2013). Specifically, strong cross-sector cooperation among government and industry stakeholders to implement Integrated River Basin Management (IRBM) is required. This should be supported by systematic conservation planning and long-term monitoring schemes that rely on a synergetic use of *in situ* measurements and earth observation data (cf. Dörnhöfer & Oppelt, 2016). A shift in thinking from terrestrial management approaches to one of focal areas, critical management zones and catchment management zones (Abell *et al*., 2007) will provide the framework for freshwater management. Within this framework, immediate action should include a review of management plans to ensure that freshwater systems are targets for conservation and identification of opportunities to increase catchment resilience. Therefore, to sustain freshwater biodiversity in the future, a proactive, strategic and holistic management approach is needed to reconcile the needs of all ecosystem actors.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. A comparison of different HydroBasins data set resolutions.
Figure S2. Flow chart for the derivation of climatic and hydrological change indicators.
Figure S3. European protected area network and percentage protected area per catchment.
Figure S4. Individual components of exposure to climate change.
Figure S5. Individual attributes of sensitivity to climate change.
Figure S6. Sensitivity to climate change for freshwater ecosystems.
Figure S7. Individual attributes of resilience to climate change.
Figure S8. Vulnerability to climate change based on the method VAM_1, conservative sensitivity estimates.
Figure S9. Vulnerability to climate change based on the method VAM_2.
Figure S10. Vulnerability to climate change based on the method VAM_3.
Figure S11. Vulnerability to climate change vulnerability based on the method VAM_4.
Figure S12. Vulnerability to climate change based on the combination of the VAM_1 to VAM_4.
Table S1. Exposure indicator methodologies and thresholds.
Table S2. Different methods for the estimation of the vulnerability to climate change.
Table S3. Summary statistics for the VAM_1 based vulnerability categories and the conservative sensitivity assessment.
Table S4. Summary statistics for the VAM_2 based vulnerability categories.
Table S5. Summary statistics for the VAM_3 based vulnerability categories.
Table S6. Summary statistics for the VAM_4 based vulnerability categories.
Table S7. Summary statistics for the combination of VAM_1 to VAM_3 based climate change vulnerability categories.
Table S8. Summary statistics for the combination of VAM_1 to VAM_4 based climate change vulnerability categories.