50 YEARS WITH IMPACT Journal of Applied Ecology 1913 2013 British Ecological Society CELEBRATING 100 YEARS

Journal of Applied Ecology 2013, **50,** 1105–1115 doi: 10.1111/1365-2664.12125

A scenario for impacts of water availability loss due to climate change on riverine fish extinction rates

Pablo A. Tedesco[1]*, Thierry Oberdorff[1], Jean-François Cornu[1], Olivier Beauchard[2], Sébastien Brosse[3,4], Hans H. Dürr[5,6], Gaël Grenouillet[3,4], Fabien Leprieur[7], Clément Tisseuil[1], Rainer Zaiss[8] and Bernard Hugueny[1]

[1]Département Milieux et Peuplements Aquatiques, Muséum National d'Histoire Naturelle, UMR Biologie des ORganismes et des Ecosystèmes Aquatiques (UMR BOREA, IRD 207-CNRS 7208-UPMC-MNHN), 43 rue Cuvier, 75231 Paris cedex, France; [2]Netherlands Institute for Sea Research (NIOZ), Korringaweg 7, 4401 NT Yerseke, The Netherlands; [3]Université de Toulouse, UPS, ENFA, UMR5174 EDB (Laboratoire Évolution et Diversité Biologique), 118 route de Narbonne, F-31062 Toulouse, France; [4]CNRS, UMR5174 EDB, F-31062, Toulouse, France; [5]Faculty of Geosciences, Utrecht University, P.O. box 80115, 3508 TC Utrecht, The Netherlands; [6]Department of Earth and Environmental Sciences, Ecohydrology Group, University of Waterloo, Waterloo, ON, Canada N2L3G1; [7]UMR 5119 ECOSYM (CNRS-IFREMER-UM2-IRD), Université Montpellier 2, Place Eugène Bataillon, 34095 Montpellier Cedex 5, France; and [8]Institut de recherche pour le développement, Secteur Cartographie, 32, avenue Henri Varagnat, 93143 Bondy, France

Summary

1. Current models estimating impact of habitat loss on biodiversity in the face of global climate change usually project only percentages of species 'committed to extinction' on an uncertain timescale. Here, we show that this limitation can be overcome using an empirically derived 'background extinction rate–area' curve to estimate natural rates and project future rates of freshwater fish extinction following variations in river drainage area resulting from global climate change.

2. Based on future climatic projections, we quantify future active drainage basin area losses and combine them with the extinction rate–area curve to estimate the future change in extinction rate for each river basin. We then project the number of extinct species in each river basin using a global data base of freshwater fish species richness.

3. The median projected extinction rate owing to climate change conditions is *c.* 7% higher than the median background extinction rate. A closer look at the pattern reveals great geographical variations highlighting an amplification of aridity by 2090 and subsequent increase in extinction rates in presently semi-arid and Mediterranean regions. Among the 10% most-impacted drainage basins, water availability loss will increase background extinction rates by 18·2 times (median value).

4. Projected numbers of extinct species by 2090 show that only 20 river basins among the 1010 analysed would experience fish species extinctions attributable to water availability loss from climate change. Predicted numbers of extinct species for these rivers range from 1 to 5.

5. *Synthesis and applications*. Our results strongly contrast with previous alarming predictions of huge surface-dependent climate change–driven extinctions for riverine fishes and other taxonomic groups. Furthermore, based on well-documented fish extinctions from Central and North American drainages over the last century, we also show that recent extinction rates are, on average, 130 times greater than our projected extinction rates from climate change. This last result implies that current anthropogenic threats generate extinction rates in rivers far greater than the ones expected from future water availability loss. We thus argue that conservation actions should be preferentially focused on reducing the impacts of present-day anthropogenic drivers of riverine fish extinctions.

---

*Correspondence author. E-mail: pablo.tedesco@mnhn.fr

Key-words: aridity index, current anthropogenic threats, diversity loss, drainage area, freshwater fish diversity, habitat availability, time to extinction

Introduction

Current rates of species and population extinction due to human actions, considered to be higher than background extinction rates, are projected to increase substantially over the next few hundred years (Pereira *et al.* 2010). However, the degree to which extinctions presently occur or will occur in the future is still a subject of debate in the scientific literature (Heywood *et al.* 1994; Pimm & Raven 2000; Thomas *et al.* 2004; Duraiappah & Naeem 2005; Pereira *et al.* 2010; Stork 2010; He & Hubbell 2011). Indeed, knowing how rapidly Earth is losing and will lose species, and the responsible drivers of this loss, is crucial to anticipate biological, ethical, practical and economic consequences of this loss. Basically, anthropogenic perturbations may accelerate population or species extinction rates by two nonexclusive processes. First, anthropogenic perturbations can act directly on population demographic parameters (e.g. births and deaths) in such a way that the population size decreases until extinction (e.g. habitat destruction, overexploitation), a process known as deterministic extinction (Tilman, Lehman & Yin 1997). Second, anthropogenic perturbations can reduce the size of a population without affecting its demography (e.g. by reducing habitat availability for a species) and thus increase the probability of stochastic extinction, as the probability of a species to become extinct is inversely related to its initial population size (Leigh 1981). When populations are very small, more complex dynamics may occur where deterministic processes such as Allee effects (e.g. Berec, Angulo & Courchamp 2007) or critical habitat sizes (e.g. Pereira & Daily 2006) may induce an inevitable decline of populations.

Global climate change, thought to potentially represent the most pervasive threats to biodiversity (Thomas *et al.* 2004), may amplify future extinctions through both deterministic and stochastic processes. Several studies attempting to anticipate how extinction patterns will be affected by a changing climate rely on species–area relationships (SAR) (Bellard *et al.* 2012). These approaches, applied to predict species loss after climate-driven reductions in habitat availability, do not however distinguish between deterministic and stochastic extinction processes and, more importantly, only project species 'committed to extinction' on an uncertain time-scale (Heywood *et al.* 1994; Pereira *et al.* 2010) because the time required to reach the new equilibrium is unknown (Fig. 1a). Reducing this uncertainty is particularly important for conservationists as the lag time between becoming 'committed to extinction' and actually going extinct may range from decades to many millennia (Stork *et al.* 2009). Thus, complementing SAR approaches by dynamic approaches quantifying true extinction rates (i.e. number of extinctions per unit time), such as the one presented in Fig. 1b, is now critically needed to start organizing sound, science-based conservation actions (e.g. Wearn, Reuman & Ewers 2012). Indeed, the potential delays between being 'committed to extinction' and becoming extinct (i.e. the 'relaxation time'; Diamond 1972) constitute a window of opportunity to prevent these potential extinctions (Kuussaari *et al.* 2009; Wearn, Reuman & Ewers 2012).

Freshwater ecosystems and particularly rivers are among the most intensively human-influenced habitats on Earth (Dudgeon *et al.* 2006), and there is no doubt that the recent documented regional and global extinctions of freshwater fauna are due to human activities (Ricciardi & Rasmussen 1999). For fish, a well-studied and high-interest

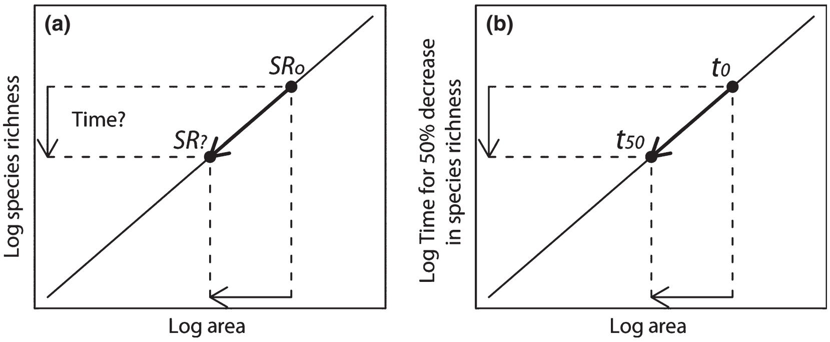

Fig. 1. Two methods for assessing the impact of habitat loss on species richness. (a) Based on the species–area relationship (SAR), a reduction in surface area leads to a new equilibrium with lower species richness in a drainage basin, but the time to reach this new equilibrium is unknown. (b) Assuming that the instantaneous extinction rate of populations decrease with the area occupied, a reduction in area should accelerate the speed at which species are lost through time and allows estimating the species richness of a drainage basin at time *t*. This is particularly true for closed systems such as river drainage basins as they actually receive new colonists so rarely that immigration processes can be neglected.

taxon, habitat degradation and fragmentation, overexploitation, eutrophication and introduction of non-native species are believed to be among the greatest actual diversity threats world-wide (Townsend & Crowl 1991; Fagan *et al.* 2002; Nilsson *et al.* 2005; Dudgeon *et al.* 2006; Giam *et al.* 2012). Among these factors, habitat loss through reductions in water availability, on which we exclusively focus here, has been predicted to greatly endanger fish species in the near future (Xenopoulos *et al.* 2005; Xenopoulos & Lodge 2006). For example, Xenopoulos *et al.* (2005) have applied climate change scenarios to 325 river drainage basins world-wide using relationships between fish species richness and river discharge (Oberdorff, Guegan & Hugueny 1995), that is, an equivalent of SAR for rivers. Results project 4–22% (quartile range) fish species 'committed to extinction' by 2070 in about 30% of the rivers analysed, due to reductions in river discharge from climate change (Xenopoulos *et al.* 2005). Although this approach may be useful for assessing fish vulnerability to climate change, it is, however, helpless to assess the time frame of the predicted species loss (Bellard *et al.* 2012).

Here, we tackle this question by combining an empirical extinction rates–drainage area relationship (Hugueny, Movellan & Belliard 2011) with expected freshwater habitat losses from climate change (i.e. a reduction in active surface area of river drainage basins, active area being the area having a perennial river flow) to evaluate the magnitude and geographical distribution of future regional fish extinctions from these habitat losses. Despite the availability of empirical relationships between extinction rates and area for some taxa in natural conditions (e.g. Quinn & Hastings 1987; Hugueny, Movellan & Belliard 2011), this is the first time to our knowledge that such a relationship is applied to predict how stochastic extinctions will be accelerated facing a climate-driven habitat shrinkage. We use a highly significant ($r = -0{\cdot}92$; $P < 0{\cdot}0001$) extinction rates–drainage area relationship recently obtained for natural fish populations (Hugueny, Movellan & Belliard 2011). The extinction rates–drainage area relationship was built by mixing estimates of population extinction rates following the fragmentation of rivers during the early Holocene (around 8000 years ago) with extinction rates estimated from fossil records ($>10^6$ years) and recent population surveys (<100 years) (Hugueny, Movellan & Belliard 2011). This relationship provides the expected extinction rate of populations as a function of area for drainage basins suffering no anthropogenic impact (i.e. the background extinction rate).

Based on a global geospatial framework (91 949 river drainage basins), and on future climate data from 18 Global Circulation Models (GCMs) from one of the most 'pessimistic' IPCC scenarios (A2) (Pachauri & Reisinger 2007), we used this relationship in a forecasting mode to project future surface-dependent extinction rates in river drainage basins world-wide. By doing this, we assume all other factors are held constant, similarly to previous approaches based on SAR (Thomas *et al.* 2004; Xenopoulos *et al.* 2005) (e.g. considering no other disturbance acting and no change in population growth rates). Finally, we compare our projected extinction rates to recent observed rates to evaluate the current vision that the decrease in species range size (or in habitat size) expected under climate change scenarios could lead to species extinction rates exceeding rates from recent human-driven extinctions (Pereira *et al.* 2010).

Materials and methods

BACKGROUND AND PROJECTED EXTINCTION RATES

We considered two kinds of population extinctions rates: (i) background extinction rates (BER), representing extinction rates expected under natural conditions and current climate; and (ii) projected extinction rates (PER), representing extinction rates estimated from water availability loss due to future climate change and discarding other potential impacts.

In a recent study, Hugueny, Movellan & Belliard (2011) applied a faunal relaxation approach, along with data provided by fossil records and population surveys to estimate natural extinction rates of freshwater fish populations from the northern hemisphere. Based on the likely assumption that area, through population size, is a major determinant of extinction rate, they provide an empirical and general extinction–area relationship that we use here to predict extinction rates related to change in habitat area from climate change.

This relationship (extracted from Fig. 5 in Hugueny, Movellan & Belliard 2011) allows calculation of the expected extinction probability per species per year, e, as a function of river drainage area, A (in km²):

$$e = f(A) = 1 - \left[1/\exp(cA^b)\right] \qquad \text{eqn 1}$$

where $c = 0{\cdot}0073$ and $b = -0{\cdot}6724$. Because in our case $e<<1$, e is a very accurate estimation of the instantaneous rate of extinction per species, and for this reason, the term 'rate' will be used henceforth. Background extinction rates, BER, were computed by applying equation (1) to the active drainage areas available under current climate conditions, A_{cc}, such that BER = $f(A_{\mathrm{cc}})$. Projected extinction rates, PER, were computed by applying equation (1) to the active drainage areas expected under future (year 2090) climate conditions, A_{fc}. The basic idea is that a change in climate will directly result in a change in surface water supply, A, which will modify in turn the stochastic extinction rate of freshwater fish species, e. We then assess in what proportion the background extinction rate should increase (or decrease) by 2090 due to water availability loss or gain using ratios of PER/BER for each drainage basin. This ratio evaluates the impact of climate change through water availability changes, without accounting for other potential stressors.

ACTIVE DRAINAGE AREA AND FUTURE CHANGES

The geo-referenced global river network HydroSHEDS (Lehner, Verdin & Jarvis 2008), complemented with river networks and watershed polygons that we constructed based on Jenson & Domingue's methodology (1988) for rivers above 60°N and below

60°S, provided drainage boundaries for *c.* 1 700 000 river drainage basins world-wide. Basins smaller than 12 km² (i.e. the smallest river drainage basin with a nonzero freshwater fish species richness, based on our global data base) were further excluded from the analysis as these basins presumably correspond to virtual coastal drainages. This leads us to finally retain 91 949 river drainage basins covering 98·6% of the terrestrial surface.

We took the conservative assumption that only perennial (or active) drainage area is available to freshwater fish populations. Parameter A from equation (1) (i.e. drainage area) was thus computed using only the active portion of river drainage basins. We estimated active drainage areas using a model linking perennial river density and climatic aridity, only available for the African continent (Paugy, Zaiss & Troubat 2008) (Fig. 2). River drainage density results from a complex balance between climate, geomorphology and hydrology. However, within intermediate ranges of climatic conditions (i.e. precipitation or aridity), a change in climate would directly result in a change in surface water supply (e.g. Wit & Stankiewicz 2006). Below and above this intermediate range of climatic conditions, no or stable perennial drainage density is observed, respectively (Wit & Stankiewicz 2006). We further validated this framework using climatic aridity data (Fig. 2) and compute active drainage areas as follows.

Climatic aridity was measured using the De Martonne's aridity index DM = $P/(T + 10)$, where P is the total annual precipitation (in mm) and T the mean annual temperature (in °C) (De Martonne 1926). This aridity index has been widely used for climatic classification (e.g. UNESCO 1979) and aridity quantification, being inversely related to aridity conditions (e.g. Wang & Takahashi 1999). For instance, a DM value of 10 (without unit value) is considered as the upper limit categorizing arid climates (Meigs 1952), and a value over 30 usually characterizes forested landscapes (Wang & Takahashi 1999). We computed DM values for every 2·5 arc-minute grid cell, as present and future climate data were available at that scale. We then averaged the DM index for every 120 arc-minute grid cell covering the African continent and related it to the current perennial river density (Fig. 2). This 'zoom out' ensures getting a large river density gradient and prevents cases of topographically related river absence (e.g. mountainous areas) or rivers flowing through arid regions sustained by upstream inputs. We then fitted a regression model with segmented relationships using '*segmented*' library (Muggeo 2008) from R package (R Development Core Team 2011) to obtain break-point estimates as shown in Fig. 2. Using smaller or larger grid cells (from 30 to 150 arc-minute) did not change the shape of the relationship nor the break points.

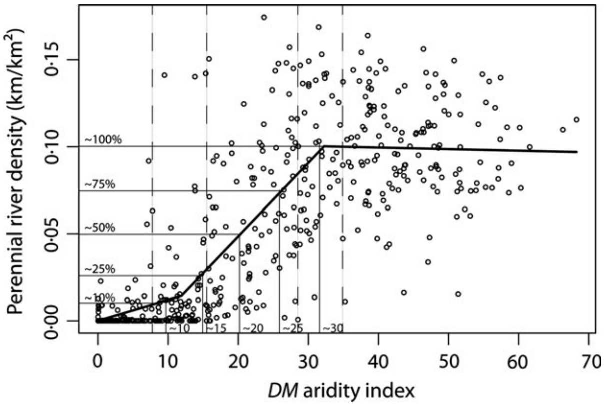

Fig. 2. Relationship between perennial river density and De Martonne's aridity index (DM) for African rivers. Dashed lines show the confidence limits of the break points from the segmented relationship. We define the active drainage area of a basin (see Fig. 3 for an example) using this segmented relationship as a framework: we included 100% of grid-cell area if DM ≥ 30; 75% if 25 ≤ DM < 30; 50% if 20 ≤ DM < 25; 25% if 15 ≤ DM < 20; 10% if 10 ≤ DM < 15; and 0% if DM < 10. Approximate percentages and DM values were used for simplicity.

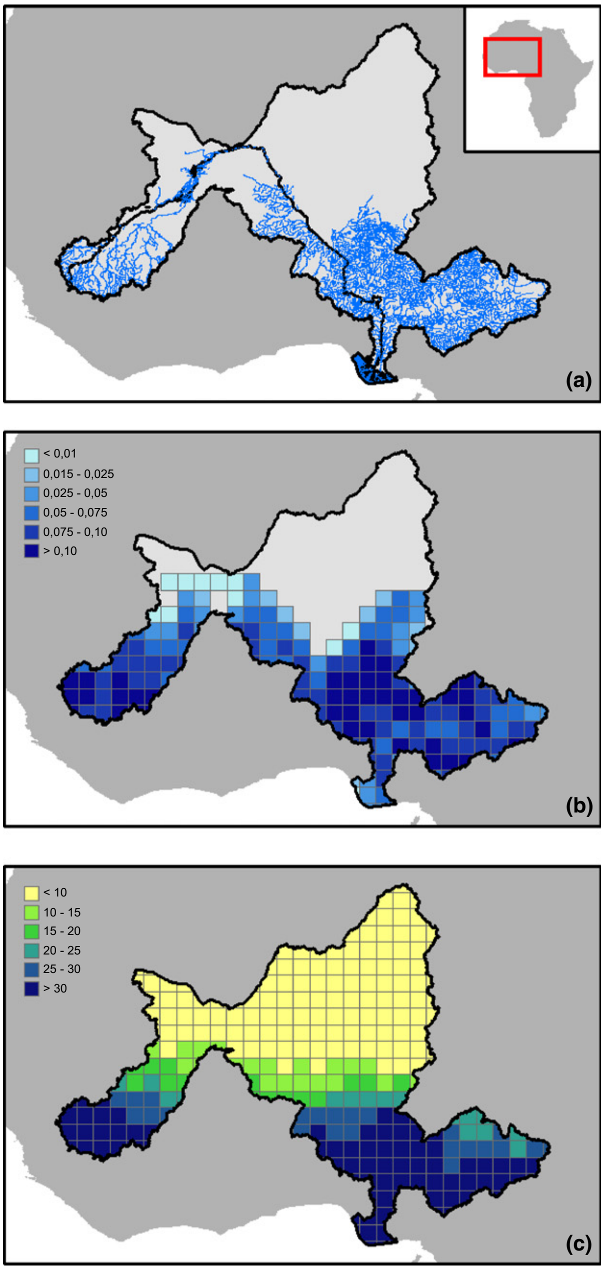

Fig. 3. Relationship between the perennial drainage network of an African river drainage basin (a), its perennial drainage density by grid cell (b) and the corresponding DeMartonne aridity index by grid cell (c).

To compute current and projected active drainage areas worldwide, we applied the following rule based on the obtained segmented relationship (Figs 2 and 3) on every 2·5 arc-minute grid cell within each river drainage basin: we included 100% of grid-cell area if $DM \geq 30$; 75% if $25 \leq DM < 30$; 50% if $20 \leq DM < 25$; 25% if $15 \leq DM < 20$; 10% if $10 \leq DM < 15$; and 0% if $DM < 10$. We applied this framework to current climate conditions to calculate 'present-day' BER (i.e. background extinction rates) and to each GCM temperature and precipitation outputs to calculate 'climate change' PER (i.e. projected extinction rates). In cases where active drainage area (present or future) dropped to zero because all grid cells have a DM below 10, we replaced this value by the smallest percentage of active drainage area found in our data set (0·00031%). This approach has no consequence on the resulting patterns since, in most cases (98%), zero values of active drainage area are found under both present and future climate conditions in a given river drainage basin, resulting in no change in extinction rate.

PRESENT AND FUTURE CLIMATE DATA

Temperature and precipitation data for current and future conditions were drawn from WorldClim (Hijmans *et al.* 2005; describing present conditions based on data sets generally ending by 1990) and Conservation International (Downscaled Future Climate Scenarios 2·5-min resolution, 2009; http://futureclimates.conservation.org), respectively. Projected climate conditions under the A2 scenario were considered from the Special Report on Emission Scenarios (SRES; Pachauri & Reisinger 2007). The A2 scenario is based on a very heterogeneous world with continuously increasing global population and regionally oriented economic growth and is among the most 'pessimistic' potential scenarios available (note that recent studies do not recommend using the more optimistic 'B-family' SRES scenarios because of underestimations in greenhouse gas emissions for the actual period; Beaumont, Hughes & Pitman 2008). Future climate projections under this scenario for year 2090 were derived from 18 GCMs (see Appendix S1 in Supporting information for models list and details on the downscaling method).

PROJECTED NUMBERS OF SPECIES EXTINCTIONS

Besides ratios of PER/BER (see above), we further assessed the impact of water availability loss from climate change by computing the expected number of extinct species per drainage basin by 2090. For a given drainage basin area A and assuming species to be identical with regard to extinction risk and no colonization process, the expected number of extinct species over t years is given by:

$$E = SR_0 - SR_0[1 - f(A)]^t \qquad \text{eqn 2}$$

with $f(A)$ given by equation (1) and SR_0 being the initial species richness. Over a period of t years, the drainage area may change from A_0 to A_t (i.e. in our case, the area reconstructed for 1990 and the one projected for 2090). The exact value of E depends on how area changes with time. However, here, we compute E applying equation (2) using exclusively the 2090 projected drainage area over a period of 100 years (from 1990 to 2090), therefore $f(A) = \text{PER}$. By doing so, we take the conservative assumption of an instantaneous change in extinction rates between present and 2090. Our approach also assumes no colonization and no speciation processes to occur. These assumptions are realistic as within this very restricted temporal window (100 years), no speciation is expected and geological events, such as river captures that can favour inter-drainage exchanges, are unlikely to occur.

We used a global data base of the total number of native freshwater fish species present by river drainage basin (Brosse *et al.* 2013) to estimate SR_0. Since each river drainage basin is regarded as a biogeographic island (Hugueny, Oberdorff & Tedesco 2010), only strictly freshwater native species were considered (secondary or migratory euryhaline fishes were systemically withdrawn on the basis of species descriptions provided in Fishbase (Froese & Pauly 2010).

DEALING WITH UNCERTAINTIES

Uncertainty from future climate models

Climate models are currently the best tools we have for simulating future climate scenarios. There is, however, no single 'best' climate model as models vary spatially and temporally in their ability to simulate current climate (Beaumont, Hughes & Pitman 2008). To evaluate the potential uncertainties induced by our multi-model average-based scenario of future climate conditions, we computed extinction rates from each GCM separately (see Appendix S1, Supporting information).

Uncertainty from the extinction rate–area relationship

The extinction rate vs. drainage area relationship that we use here to compute BER and PER was built by Hugueny, Movellan & Belliard (2011) incorporating data from three different approaches: faunal relaxation, fossil records and population surveys. Each approach may have been affected by different sources of bias. For instance, species present in fossil records may be only the most abundant and thus less prone to extinction species. To evaluate the uncertainty in the fit of Hugueny, Movellan & Belliard (2011) relationship potentially caused by the use of three different approaches, we rebuilt this relationship using alternatively only two of the approaches. This leads to three possible relationships that provide confidence bounds for equation (1). Minimum and maximum slope and intercept values of equation (1) were then used to compute extinction rates.

Measuring the uncertainty in future projections

We used the average forecast of all possible combinations of GCMs and extinction rate–area relationships as the final output analysed, that is, as an estimate of the area-dependent projected extinction rates. The variability of extinction rates between projections was measured by calculating the standard deviation across the 54 possible projections (i.e. the combinations of 18 GCMs and three extinction rate–area relationships).

Uncertainty from our conservative assumptions

As already mentioned, to perform our projections, we applied a series of conservative assumptions: (i) we only consider perennial drainage area, (ii) we use one of the most pessimistic climate change scenarios, and (iii) we project richness losses assuming an instantaneous change in extinction rates between present and 2090. These assumptions are likely to inflate our estimates of PER and extinction numbers.

RECENT EXTINCTION RATES

We defined recent extinction rates as extinction rates based on observed extinctions that have occurred during the last hundred years (Miller, Williams & Williams 1989). It is supposed to be inflated with respect to BER due to recent and ongoing anthropogenic perturbations (e.g. pollution, habitat degradation, overexploitation, introduction of exotic species) but not by water availability shrinkage due to climate change. RER were calculated using data available on freshwater fish species presently considered extinct from several bibliographic and Web sources (see Table S1, Supporting information). We restricted data to drainage basins from North and Central America, where fish species extinctions are well established (e.g. Jelks *et al.* 2008). RER per drainage basin were computed using

$$\mathrm{RER} = 1 - (1 - E/SR_0)^{1/t} \qquad \text{eqn 3}$$

with SR_o being the historical native species richness of the drainage basin, E being the number of species recently extinct and $t = 100$ years.

Results

As predicted by our extinction rates–area curve, background extinction rates of river drainage basins worldwide are generally low (median BER = 0·000796 sp^{-1} year^{-1}, $n = 91\,949$; interquartile range: 0·000375–0·001258; minimum and maximum values: 0·0000002–0·999), although high BER values (e.g. > 0·01) are found for drainage basins located in arid and semi-arid regions with narrow or no perennial river networks. Projections under climate change conditions lead to an overall increase in extinction rates (median PER = 0·000853 sp^{-1} year^{-1}, $n = 91\,949$; interquartile range: 0·000404–0·00134; minimum and maximum values: 0·0000002–0·999). Even if this overall increase in extinction rates is rather small (*c.* 7%), a closer look at the pattern reveals important geographical variations (Fig. 4). Following Fig. 4, the projected changes range from negative values (i.e. a decrease in extinction rates) up to extremely high

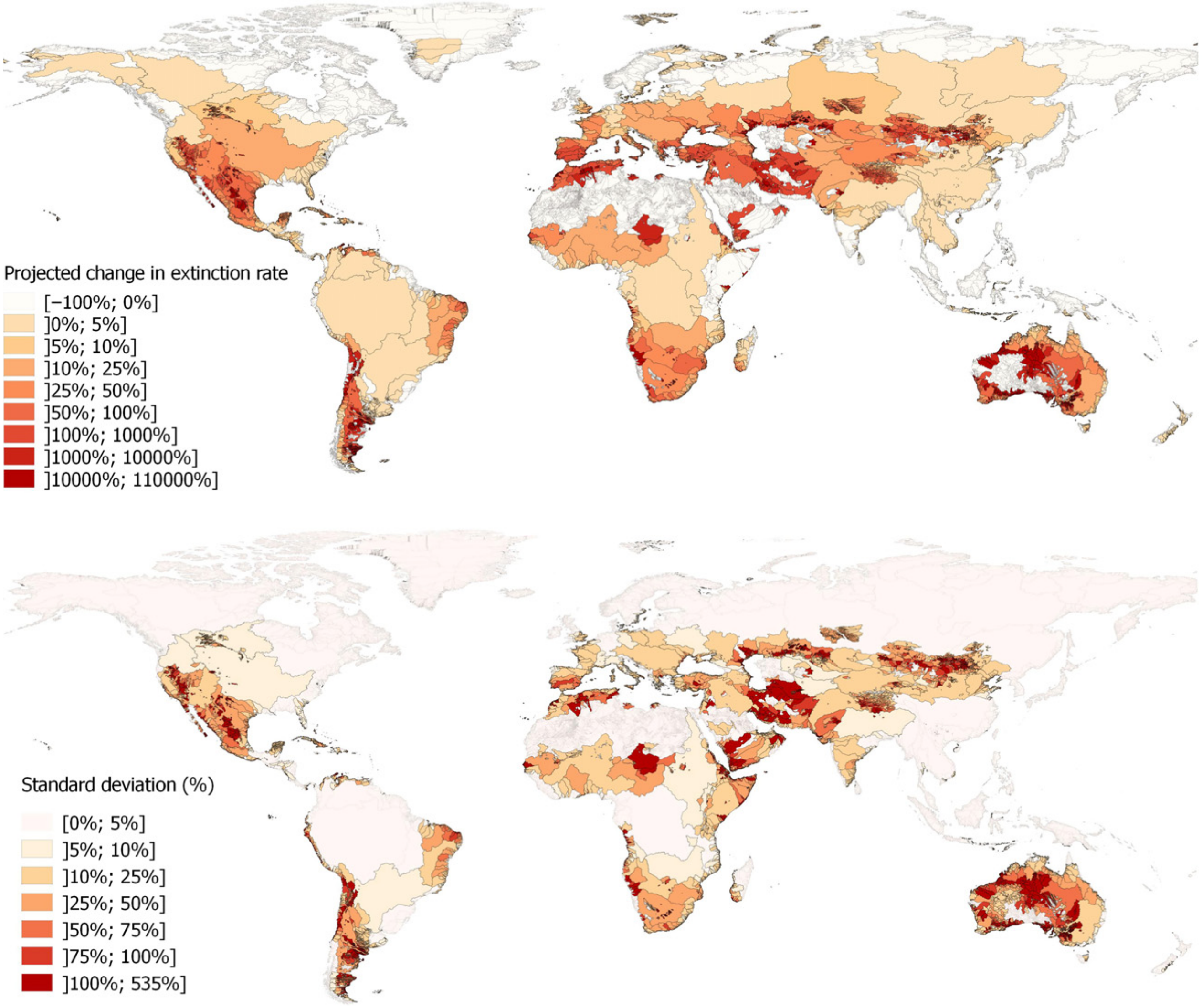

Fig. 4. Global patterns of proportional increase or decrease in extinction rates between future and current climatic conditions (i.e. PER/BER ratio) and their relative standard deviations. Negative values of projected change in extinction rate depict drainage basins where extinction rates may decrease, while positive values depict drainage basins where extinction rates may increase.

values, over a thousand times their current levels of extinction rate. However, 73% of drainage basins should remain unchanged or should gain habitat by 2090, generating no change or a concomitant decrease in their extinction rates, while 27% should suffer an increase in extinction rates. Drainage basins projected to experience an increase in extinction rates are located in regions where semi-arid and Mediterranean climates currently occur (i.e. south-west USA, Mexico, southern America, north-east Brazil, northern and southern Africa, southern Europe, western and middle Asia, and Australia). Area loss in these drainage basins will hasten natural extinction rates by 1·24 times (median value). However, among the 10% most-impacted drainage basins, water availability loss will hasten background extinction rates by 18·2 times (median value) by 2090. These multi-model average-based results are confirmed given the generally low levels of uncertainty combining variability from both climate change models and the extinction rate–area relationship (median relative standard deviation in PER/BER ratios = 0%; interquartile range: 0–5·7%; Fig. 4). Furthermore, the overall nature of our results remains essentially unchanged when applying our framework to each GCM separately (Appendix S1, Supporting information).

We then translated our surface-dependent projected extinction rates into numbers of extinct species in drainage basins by 2090. Under the expected changes in water availability due to climate change and setting $t = 100$ years, equation (2) gives us the number of species that may go regionally extinct in our 1010 river drainage basins due to habitat loss by the end of the century (Fig. 5). Only 35 river drainage basins among the 1010 analysed should experience fish species extinctions ≥ 1 by 2090. These extinctions can be attributed to water availability loss in only 20 of these river drainage basins (i.e. river basins with PER/BER ratios >1; see Table 1). Predicted numbers of extinct species for these rivers range from 1 to 5 (mean value = 1·97 ± 1·82 SD), affecting drainage basins located in arid, semi-arid or Mediterranean regions, for example small drainage basins from western Mexico, western Australia, northern Africa and Middle East (Fig. 5; Table 1).

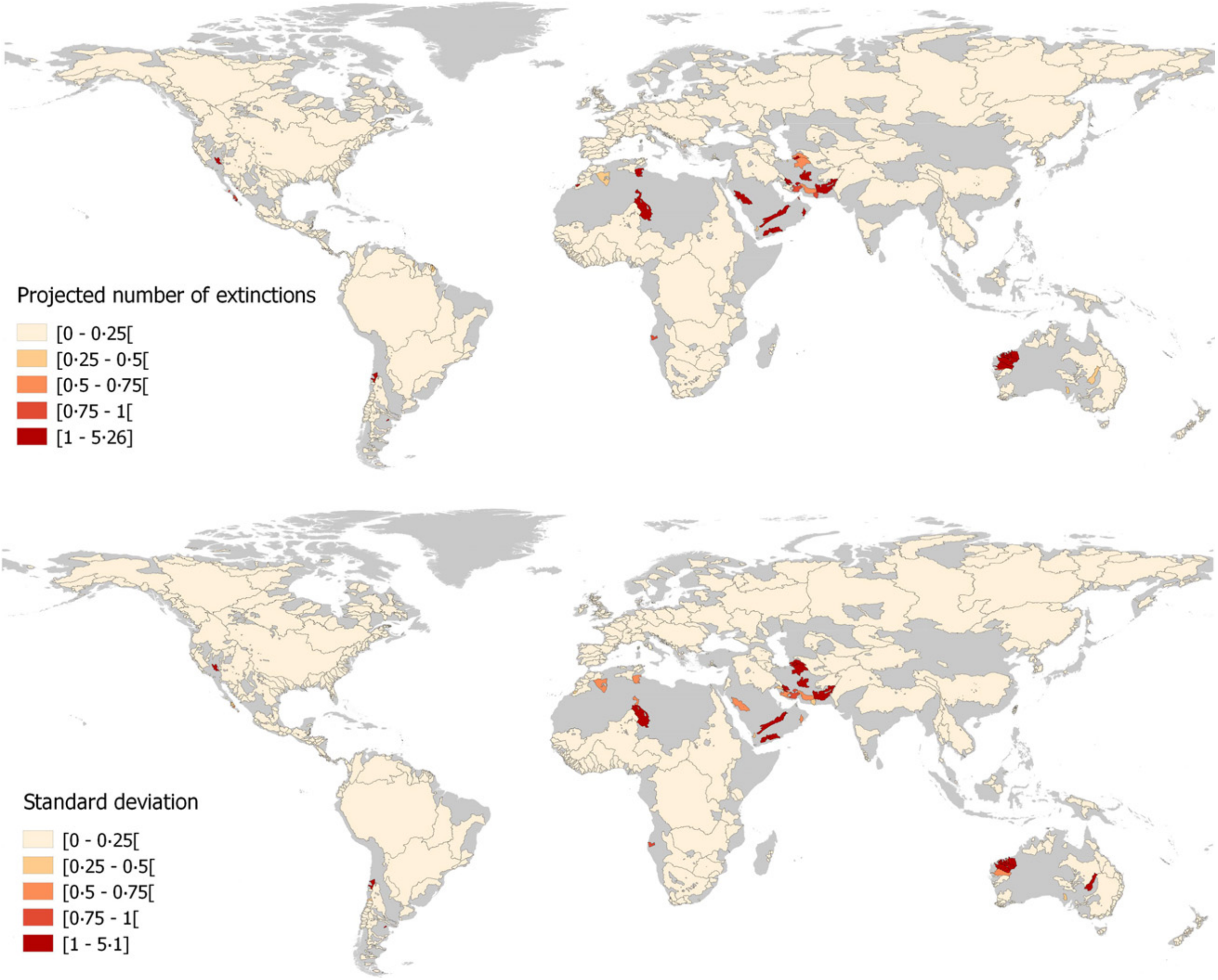

Fig. 5. Mean projected species richness loss by 2090 and their associated absolute standard deviations for 1010 river drainage basins under year 2090 climate conditions.

Table 1. Predicted numbers of extinct species with their uncertainty levels for 20 (over 1010) drainage basins expected to suffer the greatest diversity losses due to water availability shrinkage from climate change

Drainage basin	Country	PER/BER ratio	Richness loss by 2090 (± SD)
Robe	Australia	341·82	1·95 (± 1·72)
Huasco	Chile	297·20	1·34 (± 1·86)
Sherlock	Australia	228·62	2·74 (± 1·69)
Fortescue	Australia	205·90	1·77 (± 2·12)
Copiapo	Chile	153·29	1·61 (± 1·62)
Yule	Australia	130·00	2·64 (± 1·68)
Ashburton	Australia	119·09	1·34 (± 1·62)
Maharlu	Iran	119·07	1·34 (± 2·7)
Kor	Iran	104·70	3·21 (± 5·9)
El Abid	Tunisia	78·44	1·5 (± 0·70)
Gorgan	Iran	67·72	1·19 (± 3·51)
De Grey	Australia	47·12	2·14 (± 1·65)
Las Pocitas	Mexico	44·01	1·76 (± 0·55)
Noun	Morocco	39·14	3·70 (± 0·43)
Sirjan	Iran	39·01	1·5 (± 0·94)
Pichin Lora	Afghanistan	37·24	1·8 (± 1·60)
Valcheta	Argentina	20·39	1·41 (± 1·42)
Adana	Saudi Arabia	13·80	1·42 (± 1·26)
Death Valley	USA	9·40	1·29 (± 1·71)
Mashkel	Iran	3·98	5·26 (± 3·18)

Finally, RER/PER ratios between recent (i.e. real) and projected extinction rates computed for North and Central American drainage basins indicate that human-induced extinctions rates from the last 100 years are between *c.* 2 to 821 times greater than our projected surface-dependent extinction rates (Table 2).

Discussion

Our study asks how and where freshwater fish extinction rates should vary with climate change projections in habitat loss (i.e. active drainage area loss) and is not intended to capture all other possible drivers of future extinctions. Despite a significant increase in extinction rates projected for semi-arid and Mediterranean regions, our predictions show that very few river drainage basins (20 over 1010) should actually suffer species extinctions by 2090 due to habitat (i.e. water availability) loss from climate change. Moreover, the number of predicted species extinctions is rather low, even under the conservative assumptions applied, which inflate our estimates rather than the reverse (see methods section). Alternative, less conservative, assumptions could have been made (e.g. using the total drainage area, applying optimistic climate change scenarios or applying a progressive change in extinction rate through time until 2090), inevitably reducing our projected estimates of extinction rate and richness loss. As a consequence, our results represent inflated estimates ensuring that our predictions are defensible when compared with previously reported extinction projections.

The most-impacted drainage basin in terms of richness loss, the Mashkel basin from Iran, is predicted to lose up to five species by the end of the century, and the remaining drainage basins where shrinking area-related extinctions are projected should lose from one to four species (see Table 1). Confidence bounds for richness losses show small levels of uncertainty related to climate models and extinction rate–area relationships (e.g. the maximum loss projected for the Mashkel basin is eight species). These uncertainty levels are even smaller when looking at the global picture, as confidence limits confirm that no extinction is projected for most drainage basins (Fig. 5). The number of drainage basins with projected extinctions by the end of the century could increase if information on species richness becomes available for the regions not evaluated here (i.e. grey zones in Fig. 5). However, our global data set of freshwater fish species distribution covers nearly 80% of the continental surfaces (Brosse *et al.* 2013) and should thus be representative of the magnitude of extinctions related to drainage area loss. Furthermore, many of these nonevaluated zones are deserts (dry or glaciated) with only few or no fish species.

While this finding gives us good reasons to be optimistic for the near future of freshwater fishes regarding water availability loss driven by climate change, we should keep in mind that desert, semi-arid and Mediterranean river drainage basins usually host many narrow endemic species (i.e. species inhabiting a single river drainage basin; Oberdorff, Lek & Guegan 1999; Tedesco *et al.* 2012) and that regional extinction of these species may lead to a global net biodiversity loss, as they are, unlike more widespread species, not replaceable from elsewhere. Furthermore, our projections show substantial increases in extinction rates for some drainage basins. Even if this increase in extinction rates should not cause numerous extinctions by 2090, it may nevertheless represent an important issue for the longer term and for local conservation strategies.

Table 2. Comparison between background (BER), projected (PER) and recent (RER) extinction rates for North and Central American drainage basins

Drainage basin	Country	Freshwater fish species considered extinct	BER	PER	RER	Ratio RER/BER	Ratio RER/PER
Alabama	USA	1	0·000003	0·000003	0·000060	17·36	17·35
Ameca	Mexico	2	0·000015	0·000020	0·001053	69·95	52·56
Armeria	Mexico	1	0·000019	0·000027	0·000606	32·17	22·20
Colorado (Texas)	USA	3	0·000006	0·000010	0·000541	90·61	55·72
Colorado	USA	2	0·000002	0·000003	0·000606	252·41	180·65
Death Valley	USA	4	0·000325	0·003656	0·006908	21·23	1·89
Rio Grande	USA	10	0·000004	0·000006	0·001206	331·12	204·07
Guadalupe	USA	1	0·000011	0·000015	0·000174	16·23	11·25
Housatonic	USA	1	0·000026	0·000026	0·000488	18·94	18·94
Hudson	USA	1	0·000007	0·000007	0·000171	23·61	23·61
Mississippi	USA	2	0·000000	0·000001	0·000091	182·51	166·72
Nelson	Canada	1	0·000001	0·000001	0·000142	156·85	146·97
Panuco	Mexico	3	0·000005	0·000007	0·000571	110·18	86·51
Papaloapan	Mexico	1	0·000007	0·000008	0·000308	43·14	40·76
Potomac	USA	1	0·000008	0·000008	0·000168	21·25	21·09
Sabine	USA	1	0·000005	0·000006	0·000124	22·71	22·02
Sacramento	USA	2	0·000004	0·000005	0·002229	536·16	491·55
Saint Laurent	Canada	8	0·000001	0·000001	0·000708	823·33	821·13
San Joaquin	USA	1	0·000004	0·000005	0·000953	229·15	210·09
Susquehanna	USA	1	0·000005	0·000005	0·000190	41·48	41·45
Mean values						152·02	131·83

However, our projected species extinction numbers are, in any case, not of the order of magnitude of the ones predicted for freshwater fishes (Xenopoulos *et al.* 2005; about 15% of the rivers studied would lose more than 20% of their fish fauna) or for other taxonomic groups (Thomas *et al.* 2004; 15–37% of a sample of 1103 land plants and animals predicted to become extinct as a result of climate change expected by 2050) based on SAR or related approaches. Contrary to these previous approaches that fail to provide a time frame in which species extinctions are likely to occur, our approach gives the time necessary to reach those extinction levels. For example, given our computed range of time lags for reaching extinction levels projected by Xenopoulos *et al.* (2005) (i.e. *c.* 1500 to 234 000 years, see Table S2 (Supporting information) for further details and standard deviation intervals), we can conclude that for freshwater fish, habitat loss (i.e. water availability loss) due to climate change is unlikely to represent a relevant extinction threat (note that the differences observed between our results and those of Xenopoulos *et al.* (2005) are due to the time frame we provide and are not related to differences in climate model projections). Indeed, other important and immediate threats, already listed above (i.e. habitat degradation and fragmentation, overexploitation, eutrophication and introduction of non-native species) and not considered here, are likely to be more detrimental for freshwater biodiversity than climate change through river drainage area variations. These threats seem to have already played a substantial role in regional extinctions of freshwater fish species world-wide. For instance, concerning Central and North America where riverine fish extinctions are well established (Jelks *et al.* 2008), twenty river basins have already lost a total of 47 freshwater fish species due to human perturbations (see Table S1, Supporting information). If we consider that these perturbations started 100 years ago (as suggested by Miller, Williams & Williams 1989), we obtain a mean river basin extinction rate value over 150 times greater than our background extinction rates (Table 2), a value tightly comparable to estimations from other vertebrate groups (Duraiappah & Naeem 2005) and over 130 times greater than our projected extinction rates (Table 2). Furthermore, among these 47 fish species, 30 were endemic to a single river basin (see Table S1, Supporting information), leading to a global net biodiversity loss. This result clearly shows that drainage surface contraction due to climate change will play a minor role in driving extinctions compared with currently acting anthropogenic drivers. A limit to this last comparison is that we did not consider explicitly the possible additive effect of changing climate during the last century in generating these recent extinctions. However, this effect is likely to be marginal as most recorded extinctions occurred before the 1980s and as evidence points a significant change in global average temperatures and precipitations only since the late 20th century (e.g. Crowley 2000) with much larger hydroclimatic changes expected in the 21st century (Milly, Dunne & Vecchia 2005). We feel thus that the major priorities for conservationists should be to focus first on reducing the impacts of these other important and present-day drivers of riverine fish extinctions (habitat degradation and fragmentation, overexploitation, eutrophication and introduction of non-native species; Townsend & Crowl 1991; Fagan *et al.* 2002; Nilsson *et al.* 2005; Dudgeon *et al.* 2006; Giam *et al.* 2011, 2012).

Here, we considered the loss of perennial rivers as the only cause of habitat loss. However, the amount of habitat available for freshwater fish species may also be reduced if increasing temperatures shrinks their thermal distributional limits, or if species are unable to adjust their distribution range to the new conditions (e.g. insurmountable barriers to dispersal). For instance, recent projections predict strong reductions in the range size of some cold-water species (e.g. Ruesch *et al.* 2012). Climate change could also affect frequency, duration and magnitude of hydrological events, potentially damaging species adapted to present flow regimes (e.g. Döll & Zhang 2010). For instance, Döll & Zhang (2010) analysing seasonal regimes and four other ecologically relevant indicators of river flow have shown geographically differential impacts of climate change at the global scale. Our approach being based on the persistence of annual perennial flow, and consequently not accounting for seasonal hydrological variability, could thus underestimate future extinction rates for river basins that will experience stronger annual variability in flow regimes. Another potential source of underestimation in our extinction rates is that our approach does not account for species with restricted ranges within drainage basins. For instance, species endemic to a specific river tributary that dries up under future climate conditions may go extinct within the timescale of habitat change, assuming no possible dispersal (He & Hubbell 2011). However, it should be acknowledged that most of the above methodological limits are shared with previous approaches based on SAR (e.g. Thomas *et al.* 2004; Xenopoulos *et al.* 2005), making our predictions, even if only partial, fully comparable with their results (i.e. projected extinction rates due to habitat loss). Thus, the particular interest and importance of our study is the general conclusion that previous studies based on SAR overestimated future extinctions if we consider time-delimited extinctions instead of percentage of species 'committed to extinction'.

To our knowledge, this study is the first to quantify background (natural) and project future extinction rates for a full species-rich group (i.e. freshwater fishes) at this spatial scale. We conclude that climate change, through direct habitat loss (i.e. loss in active river drainage area), will not severely affect freshwater fish species richness in the near future. This result implies that there still is a chance to counteract current and future fish species loss by preferentially focusing conservation actions on the other important anthropogenic threats generating ongoing extinctions in rivers (habitat degradation and fragmentation, overexploitation, eutrophication and introduction of non-native species; Townsend & Crowl 1991; Fagan *et al.* 2002; Nilsson *et al.* 2005; Dudgeon *et al.* 2006; Giam *et al.* 2011, 2012).

Acknowledgements

This manuscript greatly benefited from previous comments made by Paul Leadley, Georgina Mace, Michael Bode and two anonymous referees. We are very grateful to Didier Paugy who leads the Faunafri project (http://www.poissons-afrique.ird.fr/faunafri/) for providing data on perennial and intermittent rivers of Africa. We thank the French National Agency for Research (ANR-06-BDIV-010 and ANR-09-PEXT-008) and the European Commission (*BioFresh* project: FP7-ENV-2008-Contract no. 226874) for support. H. H. Dürr also acknowledges the Utrecht University through the High Potential Project G-NUX.

References

Beaumont, L.J., Hughes, L. & Pitman, A. (2008) Why is the choice of future climate scenarios for species distribution modelling important? *Ecology Letters*, **11**, 1135–1146.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.

Berec, L., Angulo, E. & Courchamp, F. (2007) Multiple Allee effects and population management. *Trends in Ecology & Evolution*, **22**, 185–191.

Brosse, S., Beauchard, O., Blanchet, S., Dürr, H.H., Grenouillet, G., Hugueny, B. *et al.* (2013) Fish-SPRICH: a database of freshwater fish species richness across the World. *Hydrobiologia*, **700**, 343–349.

Crowley, T.J. (2000) Causes of climate change over the past 1000 years. *Science*, **289**, 270–277.

De Martonne, E. (1926) Une nouvelle fonction climatologique: L'indice d'aridité. *La Meteorologie*, **2**, 449–458.

Diamond, J.M. (1972) Biogeographic kinetics - estimation of relaxation-times for avifaunas of southwest pacific islands. *Proceedings of the National Academy of Sciences of the United States of America*, **69**, 3199–3203.

Döll, P. & Zhang, J. (2010) Impact of climate change on freshwater ecosystems: a global-scale analysis of ecologically relevant river flow alterations. *Hydrology and Earth System Sciences*, **14**, 783–799.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Leveque, C. *et al.* (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, **81**, 163–182.

Duraiappah, A.K. & Naeem, S. (2005) *Ecosystems and Human Well-being: Current State and Trends: Findings of the Condition and Trends Working Group of the Millennium Ecosystem Assessment*. Island Pr, Washington, DC.

Fagan, W.F., Unmack, P.J., Burgess, C. & Minckley, W.L. (2002) Rarity, fragmentation, and extinction risk in desert fishes. *Ecology*, **83**, 3250–3256.

Froese, R. & Pauly, D. (2010) Fishbase. World Wide Web electronic publication. www.fishbase.org

Giam, X., Ng, T.H., Lok, A.F.S.L. & Ng, H.H. (2011) Local geographic range predicts freshwater fish extinctions in Singapore. *Journal of Applied Ecology*, **48**, 356–363.

Giam, X., Koh, L.P., Tan, H.H., Miettinen, J., Tan, H.T. & Ng, P.K. (2012) Global extinctions of freshwater fishes follow peatland conversion in Sundaland. *Frontiers in Ecology and the Environment*, **10**, 465–470.

He, F. & Hubbell, S.P. (2011) Species-area relationships always overestimate extinction rates from habitat loss. *Nature*, **473**, 368–371.

Heywood, V.H., Mace, G.M., May, R.M. & Stuart, S.N. (1994) Uncertainties in extinction rates. *Nature*, **368**, 105.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hugueny, B., Movellan, A. & Belliard, J. (2011) Habitat fragmentation and extinction rates within freshwater fish communities: a faunal relaxation approach. *Global Ecology and Biogeography*, **20**, 449–463.

Hugueny, B., Oberdorff, T. & Tedesco, P.A. (2010) Community ecology of river fishes: a large-scale perspective. *Community Ecology of Stream Fishes: Concepts, Approaches and Techniques* (eds K. Gido & D. Jackson), pp. 29–62. American Fisheries Society, Bethesda, MD, USA.

Jelks, H.L., Walsh, S.J., Burkhead, N.M., Contreras-Balderas, S., Diaz-Pardo, E., Hendrickson, D.A. *et al.* (2008) Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries*, **33**, 372–407.

Jenson, S.K. & Domingue, J.O. (1988) Extracting topographic structure from digital elevation data for geographic information-system analysis. *Photogrammetric Engineering and Remote Sensing*, **54**, 1593–1600.

Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R. *et al.* (2009) Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology & Evolution*, **24**, 564–571.

Lehner, B., Verdin, K. & Jarvis, A. (2008) New global hydrography derived from spaceborne elevation data. *EOS, Transactions, American Geophysical Union*, **89**, 93–94.

Leigh, E. (1981) The average lifetime of a population in a varying environment. *Journal of Theoretical Biology*, **90**, 213–239.

Meigs, P. (1952) *World Distribution of Arid and Semi-arid Homoclimates*. UNESCO Document, Paris.

Miller, R.R., Williams, J.D. & Williams, J.E. (1989) Extinctions of the North American fishes during the past century. *Fisheries*, **14**, 22–38.

Milly, P.C.D., Dunne, K.A. & Vecchia, A.V. (2005) Global pattern of trends in streamflow and water availability in a changing climate. *Nature*, **438**, 347–350.

Muggeo, V.M.R. (2008) Segmented: an R package to fit regression models with broken-line relationships. *R News*, **8**, 20–25 http://cran.r-project.org/doc/Rnews/.

Nilsson, C., Reidy, C.A., Dynesius, M. & Revenga, C. (2005) Fragmentation and flow regulation of the world's large river systems. *Science*, **308**, 405–408.

Oberdorff, T., Guegan, J.-F. & Hugueny, B. (1995) Global scale patterns of fish species richness in rivers. *Ecography*, **18**, 345–352.

Oberdorff, T., Lek, S. & Guegan, J.-F. (1999) Patterns of endemism in riverine fish of the Northern Hemisphere. *Ecology Letters*, **2**, 75–81.

Pachauri, R.K. & Reisinger, A. (2007) *Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva.

Paugy, D., Zaiss, R. & Troubat, J.J. (2008) Faunafri. World Wide Web electronic publication, www.ird.fr/poissons-afrique/faunafri

Pereira, H.M. & Daily, G.C. (2006) Modeling biodiversity dynamics in countryside landscapes. *Ecology*, **87**, 1877–1885.

Pereira, H.M., Leadley, P.W., Proenca, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarres, J.F. *et al.* (2010) Scenarios for global biodiversity in the 21st century. *Science*, **330**, 1496–1501.

Pimm, S. & Raven, P. (2000) Biodiversity - extinction by numbers. *Nature*, **403**, 843–845.

Quinn, J.F. & Hastings, A. (1987) Extinction in subdivided habitats. *Conservation Biology*, **1**, 198–208.

R Development Core Team. (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ricciardi, A. & Rasmussen, J.B. (1999) Extinction rates of North American freshwater fauna. *Conservation Biology*, **13**, 1220–1222.

Ruesch, A.S., Torgersen, C.E., Lawler, J.J., Olden, J.D., Peterson, E.E., Volk, C.J. *et al.* (2012) Projected climate-induced habitat loss for salmonids in the John Day River Network, Oregon, U.S.A. *Conservation Biology: The Journal of the Society for Conservation Biology*, **26**, 873–882.

Stork, N.E. (2010) Re-assessing current extinction rates. *Biodiversity and Conservation*, **19**, 357–371.

Stork, N.E., Coddington, J.A., Colwell, R.K., Chazdon, R.L., Dick, C.W., Peres, C.A. *et al.* (2009) Vulnerability and resilience of tropical forest species to land-use change. *Conservation Biology*, **23**, 1438–1447.

Tedesco, P.A., Leprieur, F., Hugueny, B., Brosse, S., Dürr, H.H., Beauchard, O. *et al.* (2012) Patterns and processes of global riverine fish endemism. *Global Ecology and Biogeography*, **21**, 977–987.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C. *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.

Tilman, D., Lehman, C.L. & Yin, C. (1997) Habitat destruction, dispersal, and deterministic extinction in competitive communities. *The American Naturalist*, **149**, 407–435.

Townsend, C.R. & Crowl, T.A. (1991) Fragmented population-structure in a native New-Zealand fish - an effect of introduced brown trout. *Oikos*, **61**, 347–354.

UNESCO. (1979) *Map of the World Distribution of Arid Regions*. UNESCO Document, Paris.

Wang, Q. & Takahashi, H. (1999) A land surface water deficit model for an arid and semiarid region: impact of desertification on the water deficit status in the loess plateau, China. *Journal of Climate*, **12**, 244–257.

Wearn, O.R., Reuman, D.C. & Ewers, R.M. (2012) Extinction debt and windows of conservation opportunity in the Brazilian Amazon. *Science*, **337**, 228–232.

de Wit, M. & Stankiewicz, J. (2006) Changes in surface water supply across Africa with predicted climate change. *Science*, **311**, 1917–1921.

Xenopoulos, M.A. & Lodge, D.M. (2006) Going with the flow: using species-discharge relationships to forecast losses in fish biodiversity. *Ecology*, **87**, 1907–1914.

Xenopoulos, M.A., Lodge, D.M., Alcamo, J., Marker, M., Schulze, K. & Van Vuuren, D.P. (2005) Scenarios of freshwater fish extinctions from climate change and water withdrawal. *Global Change Biology*, **11**, 1557–1564.

Received 29 March 2013; accepted 23 May 2013
Handling Editor: Michael Bode

Supporting Information

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

Appendix S1. General information on GCMs and downscaling method used in this study and metrics evaluating uncertainty levels related to GCMs.

Table S1. Central and North American extinct freshwater fish species from twenty drainage basins and their endemic status (i.e. species occurring in a single drainage basin).

Table S2. Estimated time necessary to attain extinction levels projected by Xenopoulos *et al.* (2005).