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Opinion Paper: how vulnerable are Amazonian freshwater fishes to ongoing climate change?

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Summary

With around 15% of all described freshwater fish species in the world, the Amazon Basin is by far the most fish species-rich freshwater ecosystem on the planet. In this opinion paper, a rough evaluation is given on just how vulnerable Amazonian freshwater fishes are to ongoing climate change. And to argue that current anthropogenic threats through rapid expansion of human infrastructure and economic activities in the basin could be a far greater threat to fish communities than those anticipated by any future climate change. Conservation actions in the Amazon Basin should focus preferentially on reducing the impacts of present-day anthropogenic threats.

Introduction

The Amazon Basin concentrates the highest freshwater biodiversity on earth. This is especially true for fishes, with around 2300 species already recognized (Brosse et al., 2013; also see Reis et al., 2003 for an estimate of 3000 described species), representing around 15% of all freshwater fishes described worldwide (Fig. 1). Based on rates of new Amazonian fish species descriptions the actual number inhabiting the Amazon Basin is probably greatly underestimated (Winemiller and Willis, 2011). The processes having generated this highly diverse fish fauna are incomplete (Hubert and Renno, 2006; Albert et al., 2011). However, high speciation rates (formation of new species) and low rates of species extinction over several millions of years through the diversity in aquatic habitats and the stability in favorable climatic conditions are most probably involved (Junk et al., 2007; Albert et al., 2011).

The great majority of Amazonian fishes belong to five dominant groups: Characins, catfishes, cichlids, killifishes and electric fishes (Lowe-McConnell, 1987). It is estimated that about half of the Amazonian species occur in large rivers and their floodplains, with the remainder in small lowland tributaries and mountain streams, where endemism seems highly probably due to isolation processes (Junk et al., 2007).

Compared to most other riverine ecosystems on Earth, the Amazon Basin and its fish fauna are still overall in a relatively good state of conservation despite a substantial increase in potential threats such as habitat fragmentation and flow modification caused by dams, deforestation, fisheries overexploitation and industrial pollution (Castello et al., 2013). Global climate change may further amplify these threats regionally and in the near future eventually endanger the Amazonian fish fauna. The question is: How vulnerable are Amazonian freshwater fishes to ongoing climate change?

Climate change could act through (i) direct species extinction and/or (ii) progressive shifts in the structure and composition of current assemblages due to changes in species distributional ranges following an increase in water temperature. Concerning point (i), climate change is expected to cause shifts in precipitation patterns leading to the predominance of longer dry periods and an overall decrease in water availability for this riverine system. Such a reduction in water availability (or its correlate drainage area) is expected to exacerbate extinctions of freshwater organisms such as fishes (Oberdorff et al., 1995; Hugueny et al., 2011). Regarding point (ii), climate change is expected to increase water temperature over the Amazon Basin, whereby fish species will have to move throughout the riverine system, expanding and contracting their natural ranges in order to maintain their optimal temperature conditions. For instance,

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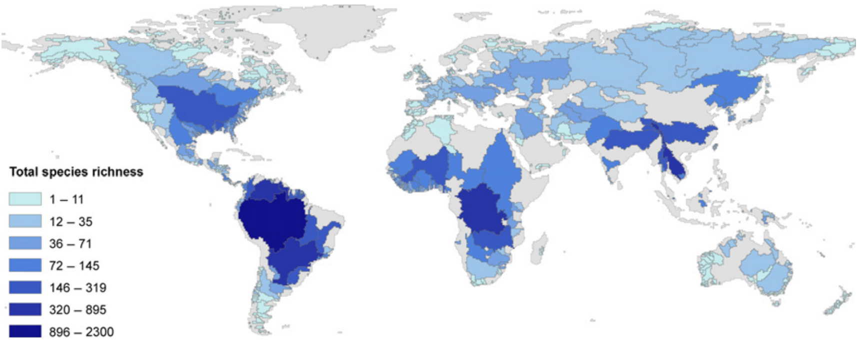

Fig. 1. Global freshwater fish species richness patterns at the drainage basin grain (after Oberdorff et al., 2011)

temperature-tolerant species would most probably expand their ranges over the river basin.

Here we will try to provide rough elements of these two aspects by (i) determining how many species could become extinct in the Amazon basin by 2080 due to a reduction in the drainage area caused by climate change, and (ii) for one temperature tolerant species (i.e. the emblematic Amazonian species, *Arapaima gigas*), analyzing the anticipated changes in its distribution range following a progressive increase in water temperatures.

Materials and methods

Climate change and Amazonian fish extinctions

To determine how many species would become extinct in the Amazon Basin due to climate change through a reduction in water availability, we used an empirically derived 'fish natural extinction rates-river basin area' curve previously established for riverine fishes worldwide (Hugueny et al., 2011). This relationship allows a calculation of the anticipated natural extinction rate per species per year, e, as a function of the river drainage area, A (in km²):

$$e = f(A) = 1 - [1/\exp(cA^b)], \qquad (1)$$

where $c = 0.0073$ and $b = 0.6724$. Based on this relationship and following the methodological approach detailed in Tedesco et al. (2013), we first estimated the reduction in drainage area of the Amazon River basin expected from climate change according to the most 'pessimistic' climatic scenario available A2 scenario from the Special Report on Emission Scenarios (SRES; Pachauri and Reisinger, 2007) and averaging results of 18 Global Circulation Models (GCMs) (see Tedesco et al., 2013 for details). Further calculated was the new population extinction rate under the reduction in drainage area anticipated from climate change. Then, using the number of strictly freshwater fish species known to occur in the Amazon basin (i.e. 1773 species in our data base) and the new population extinction rate expected under drainage area loss, we predicted how many species would be threatened by extinction in the Amazon Basin by the year 2080. 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:

$$\mathrm{E} = \mathrm{SR0} - \mathrm{SR0}[1 - f(A)^t], \qquad (2)$$

with $f(A)$ given by equation (1) and SR0 being the initial species richness.

Over a period of t years, the drainage area may change from A0 to At (i.e. in our case, the area reconstructed for 1990 and the one projected for 2080). Here, we compute E applying equation (2) using exclusively the surface of the drainage area of the Amazon Basin projected for 2080. By doing so, we took the conservative assumption of an instantaneous change in extinction rates between 1990 and 2080. The major interest of using the methodology described above, compared to those previously that only projected species 'committed to extinction' on an uncertain time-scale [i.e. species-area relationship (SAR) models], is that it allows the prediction of a number of extinct species in a given time frame (Tedesco et al., 2013).

Climate change and shifts in species range distribution: Adaptation and vulnerability

To illustrate the topic we focused here on an emblematic Amazonian species: *Arapaima gigas*, the largest fish species in the Amazon (> 3 m and > 200 kg) and naturally distributed in most Amazon Basin rivers with the notable exception of the upstream section of the Madeira River (Bolivian Amazon) where a series of rapids probably acts as barriers to colonization (Fig. 2).

Throughout its natural distribution, decades of overexploitation have seriously depleted natural populations, justifying its inclusion in the CITES II list. The interesting (paradoxical) part of the story is that *Arapaima gigas*, originally absent from the Bolivian Amazon (Fig. 2), colonized these waters following an involuntary introduction at the beginning of the 1970s via the Peruvian side of the Madre de Dios River Basin (Miranda-Chumacero et al., 2012). Now considered an invasive in Bolivian waters, this well illustrates the ability of a species to colonize habitats with new suitable environmental conditions. This giant fish is more and more exploited as a food source in Bolivia and its market value is

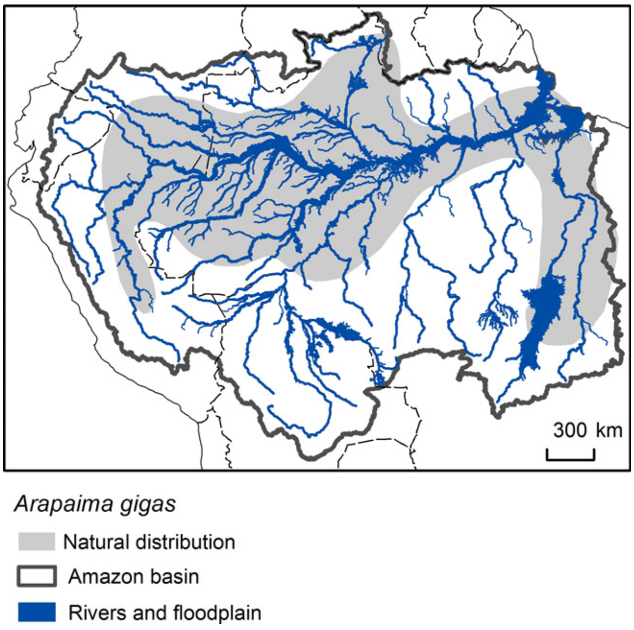

Fig. 2. Natural distribution of *Arapaima gigas* in the Amazon Basin as defined by Hrbek et al. (2005)

constantly increasing. However, this non-native predatory species could also cause changes in the abundance and distribution of native species (Carvajal-Vallejos et al., 2014).

Assuming that the genus *Arapaima* is monospecific (but see Stewart, 2013a,b), we used the MaxEnt modelling algorithm (Phillips et al., 2006; Elith et al., 2011) to identify potential future favorable areas for the species. MaxEnt gives an estimate of the probability of presence of the species (ranging between 0 and 1) as a function of environmental factors and has been extensively used by scientists, and governmental and non-governmental organizations for modeling future species distributions under ongoing climate change.

We used the area of natural distribution of the species as defined by Hrbek et al. (2005) and further selected average monthly minimum temperature as the main candidate predictor constraining this natural distribution (Oberdorff et al., 2011 unpub. results). The future environment was represented by changes predicted under the A2 scenario (the most pessimistic scenario, see above) for 2020, 2050 and 2080 and estimated via three global climate models (i.e. Canadian Centre for Climate Modelling and Analysis, CGCM3.1 Model, T47 resolution – CCCMA; Atmospheric Research, Australia, Mk3.5 Model – CSIRO; Hadley Centre for Climate Prediction, Met Office, UK, HadCM3 Model – HADCM3). MaxEnt models were then fitted and projected using both current and future climate.

Results

Climate change and Amazonian fish extinctions

According to the models, and considering the most 'pessimistic' climatic scenario [A2 scenario from the Special Report on Emission Scenarios (SRES; Pachauri and Reisinger, 2007)], the reduction in the Amazon Basin surface area should be < 1% (i.e. surface area loss of 46 005 km^2 over a total perennial surface area of 5 852 526 km^2) (Fig. 3). According to equation (1) the actual rate of extinction in the basin is 0.0000002067 species per year and will increase to 0.0000002078 species per year in 2080, following the reduction in surface area of the basin. According to the model, the consequential number of extinct fish species in 2080 should be zero (i.e. 0.034 species).

We did not estimate future climate projection uncertainty in our extinction rate-area relationship model. However, results of a previous study performed on a global scale and including the Amazon Basin show that these uncertainties are quite low for this basin (standard deviation of projected change in extinction rate between 0 and 5%) (Tedesco et al., 2013).

Climate change and shifts in species range distribution: Adaptation and vulnerability

As shown in Fig. 4 the MaxEnt model reproduces the natural species range well but also interestingly predicts perfectly the presence of *Arapaima gigas* in the lowlands of northern

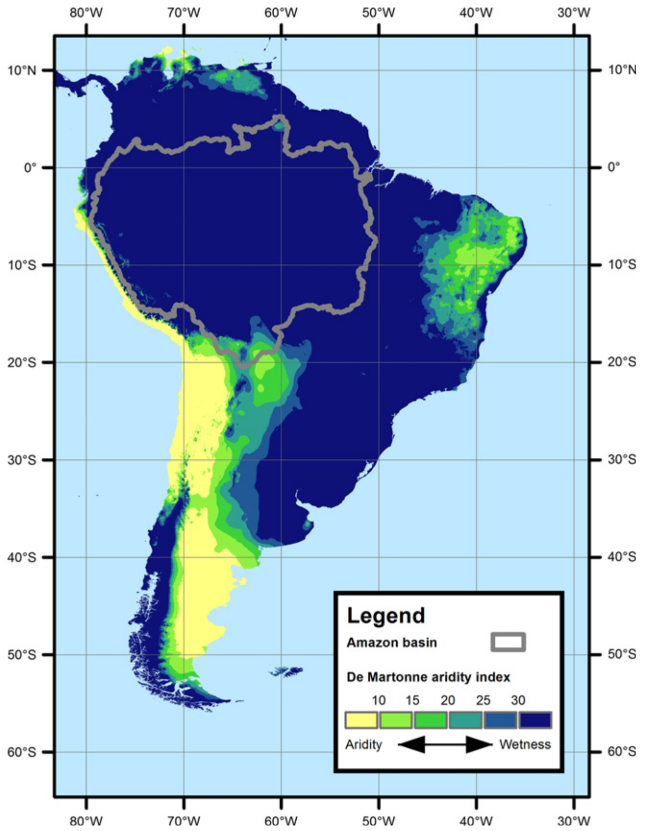

Fig. 3. Projection of De Martonne aridity index (DM) values for year 2080 under the A2 scenario and based on future climate data from 19 Global Circulation Models (GCMs). According to this projection the Amazon Basin should be relatively preserved from aridity with the exception of its most southern part

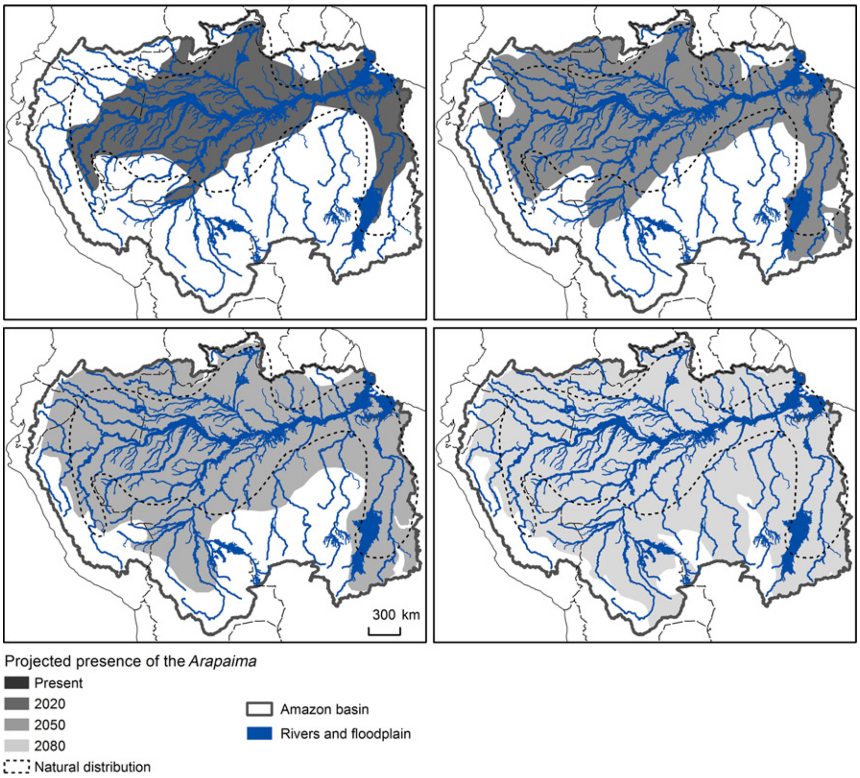

Fig. 4. Potential expansion of geographic distribution, *Arapaima gigas* (A.g) (years 2020, 2050, 2080) according to MaxEnt model, using as main predictor average monthly minimum temperature (calculated from WorldClim; Hijmans et al., 2005). Selected were 2500 random points in natural *A. gigas* distribution to simulate presence-only records for MaxEnt model. Projections from averages of three global climate models

Bolivia from where it was originally absent and to where it has now adapted. This last result strongly suggests that (i) the average monthly minimum temperature is a relevant predictor of *A. gigas* natural distribution, (ii) the artificial presence of *A. gigas* (introduced) in Bolivian waters is limited at present by its temperature optimum (i.e. its presence in Bolivian waters is strictly controlled by its natural minimum temperature range), and (iii) the presence of rapids in the upstream part of the Madeira River probably acted as barriers to colonization for this species, explaining its original absence in Bolivian waters (Goulding, 1979). The model also predicts an *A. gigas* progressive extension of its range over almost the entire Amazon Basin and a future distribution only limited by altitude, through changes in rivers morphology (an increase in the river slope and consequent absence of floodplain environments) (Fig. 4). This prediction does not take into account the dispersal restriction that could result from current and planned hydroelectric development throughout the Amazon Basin, more specifically in the Bolivian part of the basin (Finer and Jenkins, 2012; Castello et al., 2013).

Discussion

Climate change and Amazonian fish extinctions

While our finding of no fish extinctions expected in 2080 gives us good reasons to be optimistic for the near future of Amazonian freshwater fishes regarding los of water availability driven by climate change, we should, however, keep in mind that habitat loss, even if usually identified as the most severe threat to biodiversity, represents only one aspect of future climate change. Other components, for example heat stress and associated oxygen limitation could also lead to an increase in extinction rates of the most vulnerable fish species of the Amazon Basin. Furthermore, several modeling studies suggest that the combination of global climate change and deforestation could increase regional drying, and beyond certain thresholds that a basin-wide shift to a dry alternative is possible (see Leadley et al., 2014 for a review). However, whether this might occur and the limits beyond which it might occur are subject to high uncertainty (Davidson et al., 2012).

Another potential source of extinction rate underestimation could come from the Hugueny et al. (2011) model assumption that all species are identical with regard to risk of extinction. Obviously species with restricted ranges within a drainage basin should display higher extinction rates than more widely distributed species (Saupe et al., 2015). However there is no way to include this parameter in the model at this time. Improving the model sensitivity in this regard will certainly refine our predictions and may increase the projected extinction rate found in our study. In the same way climate change could also affect frequency, duration and magnitude of hydrological events, potentially damaging species adapted to the present flow regimes (e.g. Freitas et al., 2013). Our approach does not account for seasonal hydrological variability and could thus underestimate future extinction rates for the Amazon Basin if the latter experiences stronger annual variability in flow regimes in the future.

Climate change and shifts in species range distribution: Adaptation and vulnerability

By using *Arapaima gigas* as an example, we focused on a species tolerant of warmer conditions and noticed an obvious expansion of its range following climate warming. However, cold-water species are also present, albeit in small numbers, in the upper areas of the Amazon Basin. For these species living mainly in altitudinal regions, a reduction in the distribution range is obviously expected. However, this negative effect should be limited. Indeed, the rich fauna of the Amazonian fish genera was essentially modern 13 million years ago (Hoorn et al., 2010) and the species found today are the descendants of this earlier fauna when temperatures were higher (Knorr et al., 2011). If niche conservatism (i.e. the tendency of species and clades to retain their niches and related ecological traits over time) applies here (Comte et al., 2014) we thus expect most of the species currently inhabiting the Amazon Basin to be tolerant of warmer conditions.

Other potential threats could originate with climate change. For example, both range expansion and contraction of species due to global warming may also change the structure and composition of fish assemblages within the Amazon Basin, creating new interactions (e.g. competition, predation), and pathogen exchanges between species that could lead to potential extinctions. Moreover, most of the predictions concerning range expansion rely on the hypothesis that Amazonian fishes are effective dispersers. Although migratory species abound throughout the Amazon Basin, most of the fish fauna is composed of small-bodied species for which dispersal and/or migratory capacities are largely unknown but are most probably limited (Albert et al., 2011). Therefore, the ability of Amazonian fish species to track future thermal shifts remains to be evaluated.

To conclude in this opinion paper, we have given a rough and quite positive picture of what might be the effects of climate change on the fish fauna of the Amazon Basin, solely focusing on changes that a reduction in surface area or an increase in temperature might produce. However, there is rising evidence that the structure and function of Amazonian freshwater ecosystems are increasingly impacted by rapid expansions in infrastructure and economic activities (Castello et al., 2013). Four main drivers of freshwater ecosystem degradation are recognized: deforestation, construction of dams and navigable waterways, pollution, and overfishing. These disturbances have generated negative effects on fish communities not only in the Amazon (Petrere et al., 2004; Castello et al., 2013; Pelicice et al., 2014) but also worldwide (Vörösmarty et al., 2010). For instance, a recent study considering twenty well-sampled Central and North American river basins with riverine fish extinctions caused by human perturbations, shows that the present extinction rates for these basins are some 150 times greater than natural extinction rates (Tedesco et al., 2013).

Thus our general message here is that these latest disturbances should be much more stressful for Amazonian fishes, and therefore of much more immediate concern than will be climate change. We believe that conservation actions should focus preliminarily on reducing the effects of these ongoing anthropogenic threats. Furthermore, given the multiplicity of disturbances, there is also an urgent need to develop a better understanding of the combined and interactive effects of these stressors (including climate change) on Amazonian fish biodiversity.

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