













How likely are adaptive responses to mitigate the threats of climate change for amphibians globally?

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Abstract. Whether species are capable of adapting to rapid shifts in climate raises considerable interest. Analyses based on niche models often assume niche conservatism and equilibrium with climate, implying that species will persist only in regions where future climatic conditions match their current conditions and that they will colonize these regions promptly. However, species may adapt to changing climate and persist where future climates differ from their current optimum. Here, we provide a first macroecological generalization to the approach of evolutionary rescue, by comparing the expected shift in mean temperature within the geographic range of 7193 species of amphibians worldwide, under alternative warming scenarios. Expected evolutionary change is expressed in units of standard deviations of mean temperature, per generation (Haldanes) and compared with theoretical models defining the maximum sustainable evolutionary rates (MSER) for each species. For the pessimistic emission scenario RCP8.5, shifts in mean temperature vary between near-zero and 6°C within the geographic ranges for most species, with a median equal to 3.75°C. The probability of evolutionary rescue in temperature peaks is higher than 0.05 for about 55% of the species and higher than 0.95 for only 12% of the species. Therefore, the predicted shift in mean temperature would be too extreme to deal with for almost half of the species. When evolutionary plasticity is incorporated, this scenario becomes more optimistic, with about 44% of the species being likely to shift their thermal peaks tracking future warming. These figures are not random in geographical space: evolutionary rescue would be unlikely in the tropics, especially in South America (Amazonia), parts of Africa, Indonesia, and in the Mediterranean region. Given the uncertainty in demographic and genetic parameters for species' responses to climate change, we caution that it remains difficult to assess the realism of the macroecological generalization. In any case, it may be precautionary to assume that our results are not liberal, showing low probability of adaptation for most of the species and thus that the persistence of populations by evolutionary rescue may, in general, be unlikely in the long term.

Highlights:

1. When predicting the impacts of future climate change in short time scales, it is usually assumed that populations will persist by niche conservatism and dispersal towards suitable environments.
2. We use a macroecological approach to evaluate potential evolution rescue of worldwide amphibians threatened by climate changes, allowing persistence to adaptation to changing temperatures within species' ranges.
3. We estimated the expected evolutionary rates, in Haldanes, for mean temperature from present to 2080-2100 within the species ranges of 7193 amphibians worldwide and evaluated if they are lower than Maximum Sustainable Evolutionary Rates (MSER), so genetic adaptation and phenotypic plasticity would be plausible.
4. Our analyses revealed that probability of evolutionary rescue is lower than 5% for about 45% of the species, and that only 12% of species would potentially adapt to climate change. These figures vary geographically, with lower adaptive potential in the tropics and Mediterranean region.
5. Although more detailed and realistic models for evolutionary responses to climate change are necessary, our macroecological approach suggest that adaptation is not an easy route for species persistence in the short run

Keywords. Adaptation, Amphibians, Climate Change, Ecological Niche Models, Eco-Evolutionary Models, Geographical Ranges, Grinnelian niche, Trailing Edges

Introduction

There is now a considerable interest in evaluating how species will cope with global changes, particularly in terms of their adaptive potential in relation to rapid shifts in climate (particularly temperature) and habitat conversion. New eco-evolutionary models (see Hendry 2017 for a recent account) allow estimation of the possibility of rapid adaptation to climate change, enhancing complexity and realism in relation to more empirical and correlative niche models (Kearney and Porter 2009, Diamond 2018, Diniz-Filho et al. 2019). In general, niche models predict species distribution under future climates by assuming niche conservatism and equilibrium with current climate, thus implying that species will only persist in regions where future climates match their preferred current conditions and that may be promptly colonized (see Franklin 2009, Peterson et al. 2011, Araújo et al. 2011, Guisan et al. 2017). However, in theory, species could adapt to changing climates, even in relatively short times, and persist in regions where future conditions will differ from their current tolerance (Lavergne et al. 2010, Hoffmann and Sgrò 2011, Franks and Hoffmann 2012, Norberg et al. 2012, Thuiller et al. 2015).

Diniz-Filho et al. (2019) recently proposed a macroecological approach to applying eco-evolutionary models, such as the one developed by Burger and Lynch (1995), to calculate the probability of evolutionary rescue under changing environments (see also Carlson et al. 2014, Bell 2013, 2017, Diniz-Filho and Bini 2019). In short, the idea is to select a target climatic variable (e.g., temperature) and calculate the predicted evolutionary rate to the future, expressed in units of standard deviations of mean temperature, per generation, measured in Haldanes (H), within the species' range (either for species' centroid or throughout the trailing edge of the geographic range obtained by niche models). The predicted evolutionary rate is then compared with theoretical expectations built under distinct theoretical evolutionary models for Maximum Sustainable Evolutionary Rates (MSER). If $H < \text{MSER}$, then the rate of change in the target variable is relatively low in comparison to the theoretical maximum rate; hence, in this case the change falls within the species' adaptive potential. Evolutionary rescue would thus allow persistence of populations by adaptation to the novel climate conditions occurring within the current geographic range of the species. On the other hand, if $H > \text{MSER}$, then evolutionary change in climate is too fast for the species to cope with, and extinction is more likely in the long run, depending on how well populations are able to persist in suboptimum environments.

Given the high rate of population declines in amphibians worldwide and the well-known sensitivity of this group to environmental changes at local scales (Nori et al. 2018), it is not surprising that many previous macroecological studies have focused on evaluating potential amphibian species losses under different threats, including climate changes (e.g., Hof et al. 2011, Munguia et al. 2012, Thuiller et al. 2019). In general,

these studies predict high rates of species losses due to climate change and interaction with other factors, mainly habitat loss (although the effects of the pathogenic fungal disease chytridiomycosis is, in principle, independent of these two other threats; see Hof et al. 2011). However, as already pointed out, it is possible that evolutionary rescue may buffer extinctions and geographic range loss, so understanding potential adaptations to increasing temperatures is one of the frontlines in amphibian ecophysiological research (Angilletta 2009, Urban et al. 2014, Ficetola and Maiorano 2016, Bovo et al. 2018).

Despite many advances in amphibian ecophysiology, using this current knowledge to predict species loss or persistence under climate changes is quite challenging. This is because detailed physiological, demographic, and genetic parameters are available for just a few species, and the relatively low phylogenetic signal in such traits make it difficult to adopt imputation strategies (see Swenson 2014) to generalize the values for the entire group. It is also important to highlight that 24% of the amphibians are classified as "data deficient" by IUCN, revealing that even basic ecological and biological data are lacking for the group (Nori et al. 2018). Finally, there are many different aspects to consider in addition to potential adaptation to climate change when modeling range dynamics. In particular, the balance between adaptation and dispersal (which in turn is constrained by habitat loss along dispersal pathways) is quite hard to evaluate for large groups of species in heterogeneous landscapes and distinct biogeographic regions.

Despite all the knowledge gaps described above, we consider that a macroecological approach, in which a wide range of demographic and genetic parameters are used to evaluate the probability of evolutionary rescue for each species, may be a first step towards a more integrative evaluation of the potential generalized responses of species to climate change and other threats. Here, we evaluate the potential of evolutionary rescue at interspecific level for global amphibians under alternative warming scenarios. As most amphibian species have very restricted ranges, as a first approach we simply compare current and future (predicted by CCSM under alternative emission scenarios) mean temperatures within species ranges, without considering more complex population models within these geographic ranges (e.g., Skelly et al. 2007, Diniz-Filho et al. 2019). We compared Haldanes for temperature shifts with MSER to evaluate if a given species has a low or high probability of adaptation to climate changes. With this approach we show that, except where phenotypic plasticity is moderate to high, most species will be unable to adapt to expected levels of climate change, at least for the most pessimistic emission scenarios. Moreover, as previously suggested by Sunday et al. (2011), the failure in adaptation is more common for richer, tropical regions, which is expected considering the lower range of physiological tolerances of ectotherms in these regions.

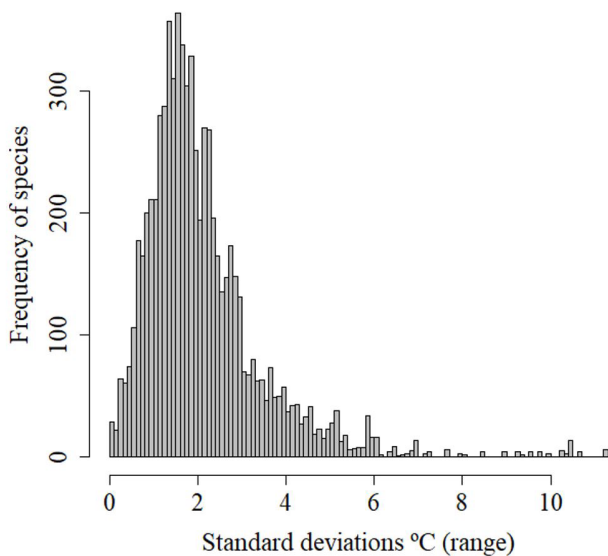


Figure 1. Statistical distribution of standard deviation for mean annual temperature (°C) within the geographic range of 7193 species of amphibians worldwide. This distribution is based on a bootstrap across the distribution of standard deviations for the 2028 species with ranges larger than 10 cells (see text for details).

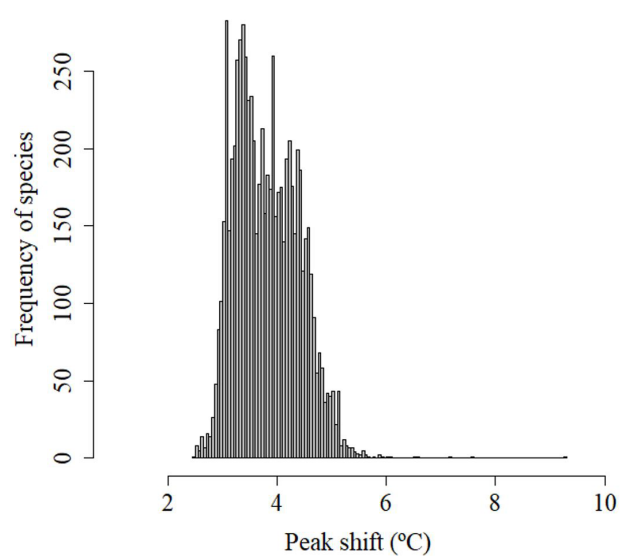


Figure 2. Peak shifts in the mean annual temperature ($Y_0 - Y_T$) as projected from climate models across the species' geographic range (1° spatial resolution) for 7193 amphibian species, between 1950–1999 (Y_0) and 2080–2100 (Y_T) using the emission scenario CCSM RCP8.5.

Methods

We used the geographic ranges of 7193 species of amphibians worldwide, matching the recent review and phylogeny by Jetz and Pyron (2018). The species distributions were obtained from the IUCN¹ (see also Batista et al. 2013), complemented with many other sources, and overlaid on a world grid with 1° of resolution (latitude and longitude) to obtain the presence and absence matrix of species (the matrix is available from the main authors upon request).

Mean annual temperature for the present (1950–1999) and for 2080–2100 under four alternative emission scenarios (RCP2.6, RCP4.5, RCP6.0, and RCP8.5) were obtained from EcoClimate (Lima-Ribeiro et al. 2015) for the global circulation model CCSM4 and rasterized to the 1° resolution grid. These RCPs represent alternative greenhouse gas concentration trajectories along the 21st century, with increasing global energy imbalances, so warming, from RCP2.6 to RCP8.5 by the year 2100. For each of the 7193 species, the mean temperature throughout its geographical range, as well as the temperature for each cell, were compared between current and future conditions to estimate the mean temperature shift within the species distribution (see Skelly et al. 2007, Angilletta 2009). We did not perform niche modeling with the aim of comparing current and future distributions, as often done. Rather, we analyzed temperature shifts within the current species ranges (so we are actually assuming limited dispersal; see Thuiller 2004). As we are only analyzing shifts in mean temperatures within ranges, we are assuming model “c” in Huey and Kingsolver (1993; see their Fig. 2), in

which the entire tolerance curve shifts through time and independent evolution of maximum and minimum temperatures is not permitted.

The shift in the mean temperature in the species range can be expressed in Haldanes (H) predicted for the near future. This was done by standardizing the shift in temperature by the standard deviation of temperature in species range and by the number of generations (Gingerich 2001), so that

$$H = \frac{Y_0 - Y_T}{\sigma g} \quad (1)$$

where Y_0 and Y_T are the mean temperatures within the geographic range in the present and in the future (assumed to be adaptive peaks for the species), σ is the standard deviation of Y_0 (the variation in temperature across the species range), and g is the number of generations between Y_0 and Y_T . The Haldane H thus measures the shift in temperature in units of standard deviation per generation and can be viewed as the evolutionary rate of future shift in temperature necessary to maintain the species by adaptation. Thus, we may think of these H values as the predicted Haldanes for the future.

To calculate H , we assumed 2–3 years of generation time for most amphibians, and thus used g values ranging from 40 to 50 by 2080–2100. But the main challenge in calculating H is the estimation of σ , the species environmental tolerance, which can be underestimated by the temperatures observed across the species geographical ranges. This is because species may not

¹ <https://www.iucnredlist.org/resources/spatial-data-download>; <https://amphibiaweb.org/>

necessarily occupy (by historical or ecological reasons) their entire potential climatic range (Munguía et al. 2012), which is particularly challenging for small range species (and, for instance, about 37% of species in our dataset occupy a single cell of the grid). On the other hand, adaptations will happen within populations at the more local scale, so the tolerance across the entire species' range may not necessarily represent the variance available within populations for adaptation (see Discussion). As pointed out by Diniz-Filho et al. (2019), more studies are necessary to evaluate the balance between over and underestimation of σ using geographic range data due to these two factors. On the other hand, experimental studies to establish temperature tolerance and performance curves are done at individual level, for a relatively small number of species (Bennett et al. 2018), and it is difficult to translate the σ for measuring population-level patterns.

For the macroecological generalization provided here we thus assume that σ is correctly estimated by the standard deviation of temperature across species' ranges, at least for broadly distributed species (i.e., species whose geographic range size was > 10 cells in our grid, which corresponds to 28% of the species). There is no phylogenetic signal for σ across the 2028 species with relatively wide ranges (Blomberg's $K = 0.031$, based on the new phylogeny by Jetz and Pyron 2018), so we randomly assigned to the other 5165 species values of σ randomly sampled from the empirical distribution of σ for the 2028 wide ranged species, with a final skewed distribution with median $\sigma = 1.85$ (Fig. 1). We are thus in line with the principle that most species are not in equilibrium with current climate and do not completely fill their fundamental niche (see Munguía et al. 2012, Soberon and Arroyo-Pena 2017).

Once the predicted H for the future is calculated, it is necessary to evaluate if this rate is "high" or "low" (in the sense of being a "plausible" rate). The idea is then to compare the expected values of H with theoretical expectations that allow calculation of the Maximum Sustainable Evolutionary Rates (MSER; see Burger and Lynch 1995, Chevin et al. 2010), derived using genetic and demographic parameters. The idea underlying MSER is to give the rate in which adaptation to moving optimum has to occur to compensate for the reduction in fitness because of environmental shifts and thus maintain a positive population growth rate (and consequently permit species or populations to avoid extinction). Thus, if $H > \text{MSER}$, this indicates that the predicted rate of change is too high to cope with given the population parameters of the species. In this case, persistence is unlikely because extinction will tend to occur before adaptation to the shifting environment (Diniz-Filho and Bini 2019).

There are different models for the calculation MSER and the first one we used here is given by

$$MSER = \sigma_A^2 / \sigma_p \sqrt{\frac{2 \ln \left(\frac{\omega^2}{\sigma_A^2 + V_S} \right)}{\sigma_A^2 + V_S}} \quad (2)$$

where σ_A^2 is the additive genetic variance, σ_p is the phenotypic standard deviation, λ is the maximum rate of population increase in the adaptive optimum (labeled B in the original notation of Kopp and Matuszewski 2014), ω^2 is the fitness landscape, and V_S is the fitness landscape influenced by environmental variance. The additive genetic variance is given by the phenotypic variance times the heritability of the trait (h^2), V_S is the sum of the length of ω^2 and the environmental variance σ_E^2 . We defined $\omega^2 = 50 \sigma_A^2$ for each species, so modeling the process as due to weak selection and more or less corresponding to a fitness reduction of 20% if temperature is at 2.5 standard deviations of the peak. This value of ω^2 generates a function in which there is a reduction in fitness of about 50% at three SD from the optimum. Zero fitness is reached at the limits of the amplitude estimated from the minimum and maximum thermal limits of amphibians, around - 4 and 42.5 °C (see Araújo et al. 2013, Bennett et al. 2018). Values of heritability h^2 are usually low for temperature tolerance, and here we used values randomly sampled from 0.2 and 0.4 (see Cotto et al. 2017, Diamond 2017). Growth rates estimated for amphibian species from Animal Matrix Database COMADRE data (i.e., the first eigenvalue of the Leslie matrix) (Salguero-Gómez et al. 2016) vary between about 0.8 and 1.4, with a mean of 1.18 (excluding the negative growth rate values). But these are empirical observed values, whereas equation 2 requires maximum growth rates at the environmental optimum. Moreover, values lower than 1 will not allow rescue by definition, as populations will decline and go extinct. Thus, we used here values of λ ranging from 1.1 to 1.25, corresponding to maximum intrinsic growth rates (r), as biotic potential, ranging from about 8.6% and 22.3% per generation.

We also obtained the MSER incorporating phenotypic plasticity (Chevin et al. 2010), given by

$$MSER_p = \sqrt{\frac{2 \log()}{\omega^2 + \sigma^2 T} \frac{h^2 \sigma^2}{|B - b|}} \quad (3)$$

where B is the rate of environmental change, b is a parameter controlling phenotypic plasticity (i.e., how much of the total response is due to plasticity in respect to the overall change), and T is the generation length. We set $B = 1$ and b is thus the proportion of variance in relation to the expected rate of environmental change of the species (i.e., the variance of tolerance). We set a limit to $b = 0.2$, but as shown below, results for $MSER_p$ are very conservative (in the sense that increasing b would give a much more optimistic scenario in terms of evolutionary rescue).

We can then compare H with both MSER and $MSER_p$ for the mean temperature within the species distribution of the 7193 species. However, we lack the precise demographic and genetic parameters necessary to calculate MSER. We therefore obtained 1000 values for MSER for each species by randomly sampling each parameter from a uniform distribution within the limits discussed above, generating statistical distributions of MSER and $MSER_p$ that account for uncertainty in model parameters. The expected H

is then compared with these distributions of MSER and MSER_p, allowing us to estimate the probability (frequency) of evolutionary rescue for each species (i.e., how many times $H < MSER$ or $H < MSER_p$). Finally, we build the distribution of probability of rescue for the 7193 species and defined two key thresholds: that species with values lower than 0.05 indicate species that will hardly be able to adapt to climate changes, whereas values higher than 0.95 indicate high confidence in rescue for the species.

We also analyzed the geographical patterns of evolutionary rescue in different ways. First, we just separated the species by biogeographical regions and observed the distribution of probability of rescue for each one. Second, we also compared richness patterns based on species ranges for the two “categories” of species (i.e., those with clear adaptation failure and those with high probability of evolutionary rescue). We did this by excluding from the presence-absence matrix the species with low probability of rescue and recalculating richness without these species. Then we divided this reduced richness by overall richness. We did the same for the species with high probability of evolutionary rescue.

All analyses and simulations were performed in R (R Core Team 2018).

Results

The median shifts in mean temperature within the geographic ranges of the 7193 species for the alternative warming scenarios of CCSM vary between 1.12°C in the most optimistic scenario up to 3.75°C in the more pessimistic scenario (Table 1). The median expected evolutionary change expressed in Haldanes for all species increase for more pessimist scenarios, as expected (as the difference between current and future temperature increases). Accordingly, by comparing the predicted Haldanes with the distribution of MSER and MSER_p, we found that, with 95% confidence intervals, the probability of evolutionary rescue is smaller for the more pessimistic scenario (RCP8.5). In all cases, the proportion of species rescued increased by adding phenotypic plasticity to the model, with the same pattern of increasing of probability of evolutionary rescue from RCP2.6 to RCP8.5.

To conserve space, only results for the more pessimistic emission scenario RCP8.5 will be shown in

more detail below, as it provides the most cautionary results, generating lower probabilities of evolutionary rescue, as shown in Table 1. The mean temperature shifts for this scenario vary between near-zero and 6°C within the geographic ranges of most species, with a median shift equal to 3.75°C (Fig. 2). The Haldanes predicted for the future have a median equal to 0.046, varying between zero and 0.4 for most species, with a widely right-skewed distribution (Fig. 3).

By comparing the predicted Haldanes with the distribution of MSER and MSER_p, we found that, with 95% confidence intervals, the probability of evolutionary rescue is smaller than 0.05 for about 45% of the species (Fig. 4A), such that the predicted shift in mean temperature would be unlikely for almost half of the species. Additionally, only 12% of the species have a probability of rescue higher than 0.95. For the model incorporating plasticity, this last value increases to about 44% of the species (Fig. 4B). The probabilities of rescue based on MSER and MSER_p across species are related by a strongly curvilinear relationship, with plasticity-based probability higher than strictly

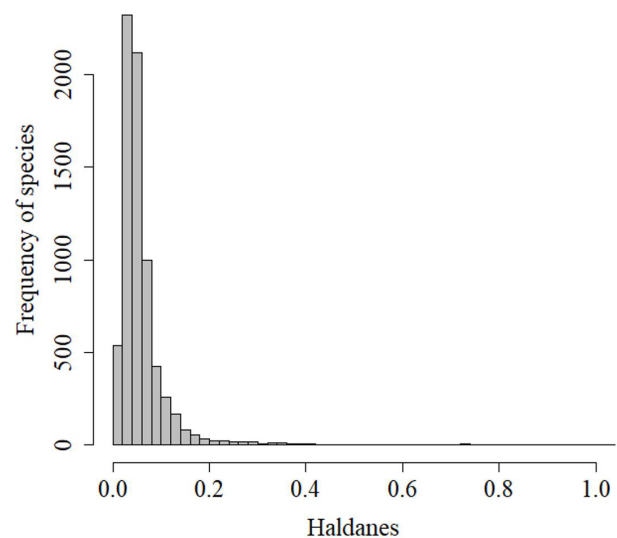


Figure 3. Distribution of the evolutionary change expected in mean annual temperature within the geographic range of 7193 species of amphibians worldwide (in Haldanes) between current and future climates (CCSM RCP8.5).

Table 1. Probability of evolutionary rescue (P - purely genetic and P_p - with phenotypic plasticity) for 7193 amphibian species at temperature peaks (°C) with the global mean temperature increase for alternative CCSM AOGCM warming scenarios.

Emission Scenario	Mean Temperature	Haldane median	Probability Rescue < 0.05	Probability Rescue > 0.95	Probability Rescue (plasticity) < 0.05	Probability Rescue (plasticity) > 0.95
RCP 2.6	1.12	0.013	4	84	2	94
RCP 4.5	1.94	0.023	11	55	5	84
RCP 6.0	2.37	0.029	17	40	8	75
RCP 8.5	3.75	0.046	45	12	21	44

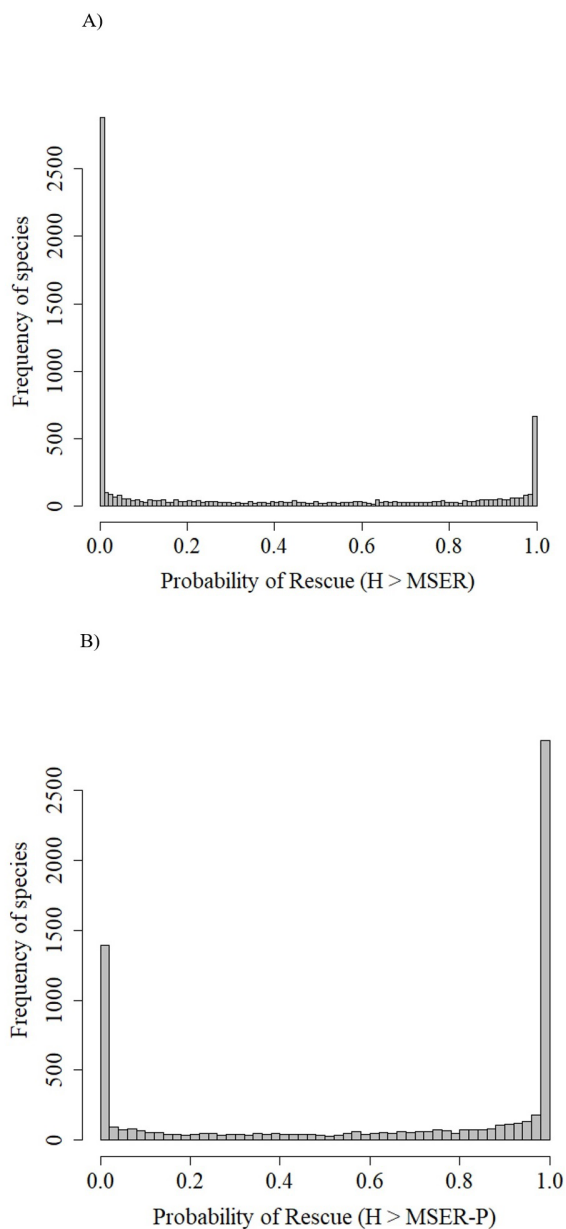


Figure 4. Probability of rescue for the 7193 species of amphibians worldwide, by comparing evolutionary change expected expressed in Haldanes (H) with maximum sustainable evolutionary rates $MSER$ (A) and maximum sustainable evolutionary rates incorporating phenotypic plasticity $MSER_p$ (B) for 1000 simulations within each species.

genetic-based probability for all species (Fig. 5). So, for further spatial analyses, only results comparing H with $MSER$ (i.e., without considering plasticity) are shown, as results for $MSER_p$ are less pessimistic, in the sense that more species persist globally.

As shown in Fig. 4A, the frequency distribution of evolutionary rescue for amphibian species globally, based on $MSER$ alone, shows that most species (almost 50%) have a small probability of resisting climate change. The same pattern is observed in all

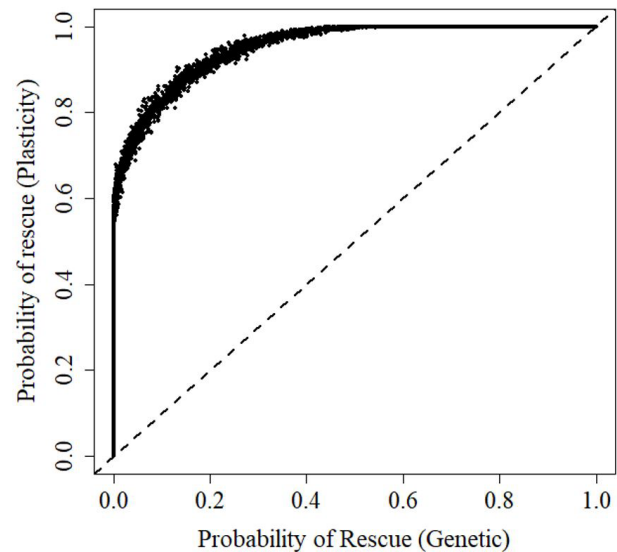


Figure 5. Relationship between probability of rescue for the 7193 species of amphibians worldwide obtained using maximum sustainable evolutionary rates $MSER$ (Genetic), and $MSER_p$ (Plasticity) showing how incorporating phenotypic plasticity increases probability of evolutionary rescue.

biogeographic domains (Fig. 6). However, the number of species with a low probability of rescue is quite a bit higher in the Neotropics, Afrotropic, and Australasia regions than in the Indo-Malaya, Nearctic, Palearctic, and Oceania regions.

Mapping richness patterns of species with high and low probabilities of rescue reveal similar patterns. Overall species richness is higher in the tropics, especially in the rainforests of the Neotropics, Afrotropic and Indo-Malaya (Fig 7A). Species richness for species with low probability of rescue is also concentrated in these more diverse regions (Fig 7B), with the exception of the Southeast Asian continental region and the Atlantic rainforest of Brazil. On the other hand, the richness of rescued species tends to be higher in the Atlantic Forest of Brazil, in the regions of the Andes cordillera, in the rainforests of Southeast Asia, in the east of Afrotropical region and Madagascar, and in the east of Australia (Fig 7C). In relative terms, the proportion of species with a high chance of evolutionary rescue is higher in the Indo-Malaysian region and in the high latitudes of the Nearctic, Palearctic, except for Siberia (Fig. 8A). On the other hand, the proportion of species with low probability of rescue tends to be concentrated in the tropical regions and in the Mediterranean region, as well as in the tropical islands of the Caribbean and Southeast Asia - except for Papua New Guinea (Fig. 8B).

Discussion

Evolutionary rescue in global amphibians

We have provided for an entire animal clade – the amphibians – a first macroecological generalization of the approach recently offered by Diniz-Filho et al.

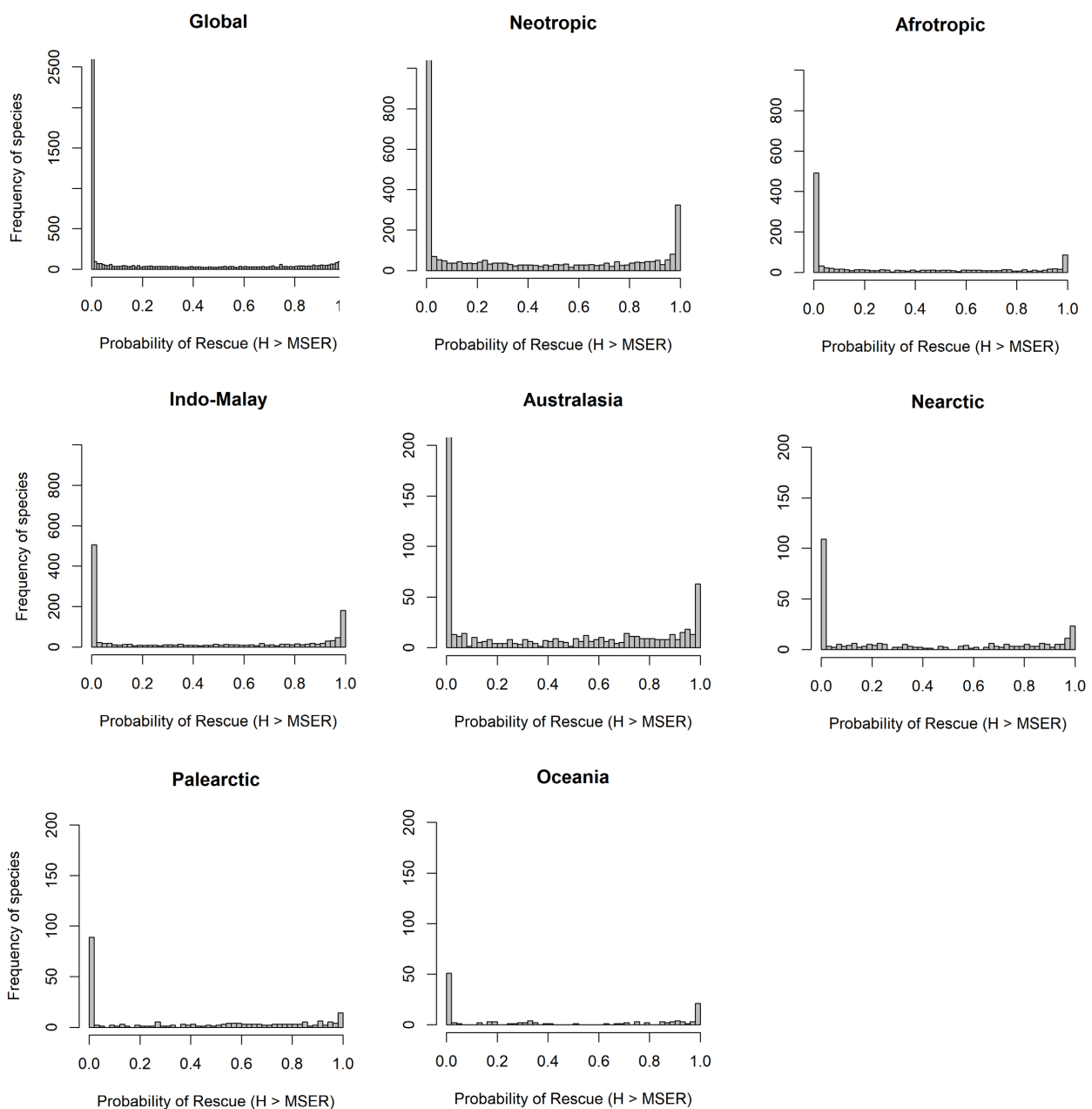


Figure 6. Frequency distribution of probability of evolutionary rescue for amphibian species from around the World and for different biogeographic regions.

(2019; see also Skelly et al. 2007) for comparing expected evolutionary rates under climate change, measured in Haldanes, with theoretical expectations based on different evolutionary models (Burger and Lynch 1995, Chevin et al. 2010). For high emission scenarios, our analyses suggest that the probability of rescue (i.e., a successful shift in mean temperatures) is smaller than 5% for almost half of the species, and higher than 95% only for about 12% of the species. In short, the change in temperature within the current species' range under the RCP8.5 emission scenario

of the CCSM model is too high to allow adaptation, which is coherent with many studies of evolutionary rescue (Diniz-Filho and Bini 2019). If phenotypic plasticity is incorporated into MSER, more optimistic figures appear, in the sense of increasing probability of rescue, as found by Diniz-Filho et al. (2019). However, the ecological significance of these results depends on several assumptions about the way Haldanes and MSER are calculated, in terms of likelihood of extinction and failure to adapt to the predicted climate change for the vast majority of species (see below).

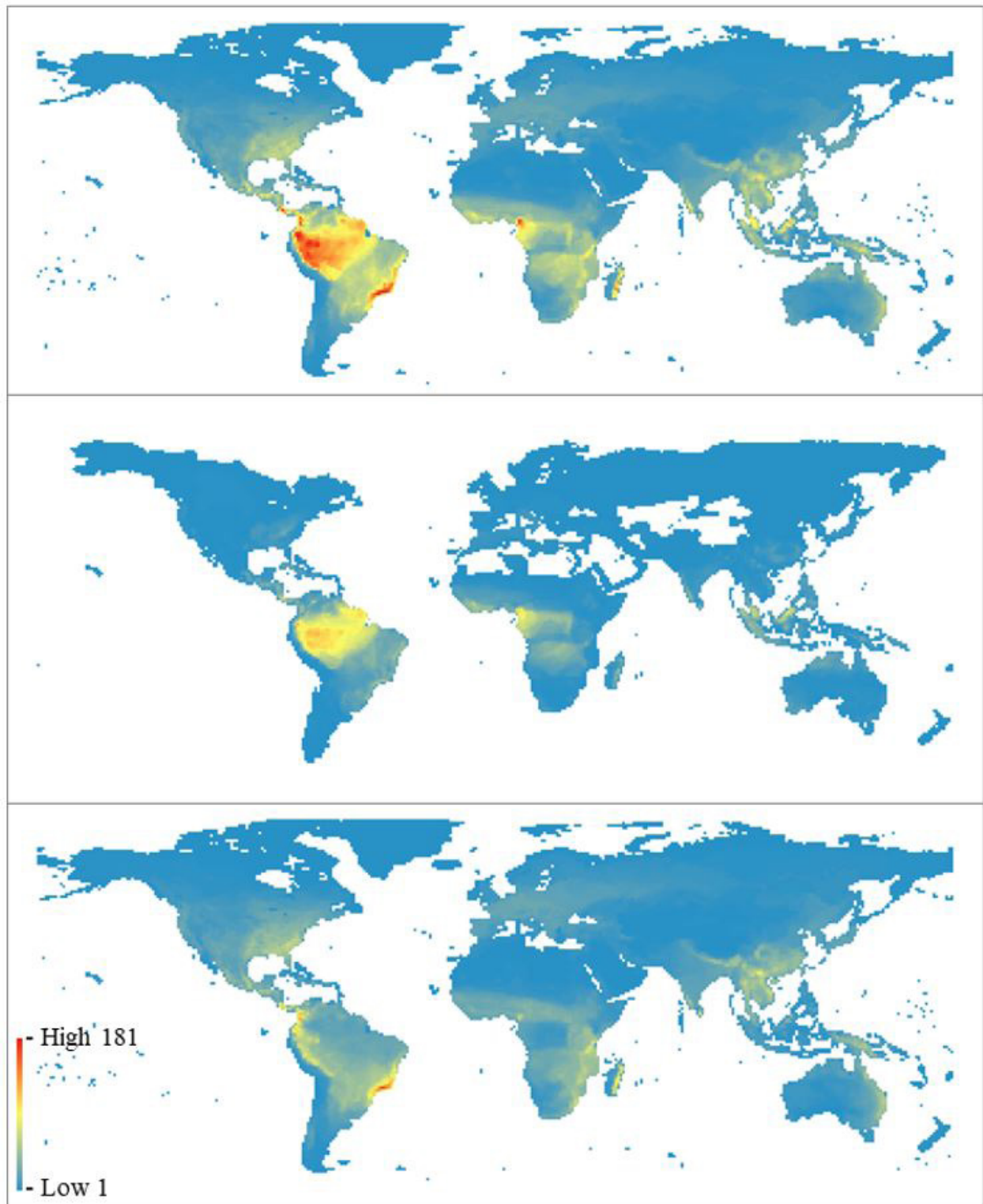


Figure 7. Current species richness of amphibian in the world (a), species richness excluding species with low probability of rescue (b) and species richness with high probability of evolutionary rescue (c). Maps use a WGS84 Mercator projection.

Anyway, it is important to consider that, given our current knowledge of adaptive potential and physiological responses to temperature changes in amphibians (i.e., Ficetola and Maiorano 2016; Bovo et al. 2018), our approach may be only a first approximation toward

a macroecological evaluation of global patterns of potential evolutionary rescue in relation to the threats posed by climate change. More refined experimental approaches to better define demographic and genetic parameters, as well as their phylogenetic patterns,

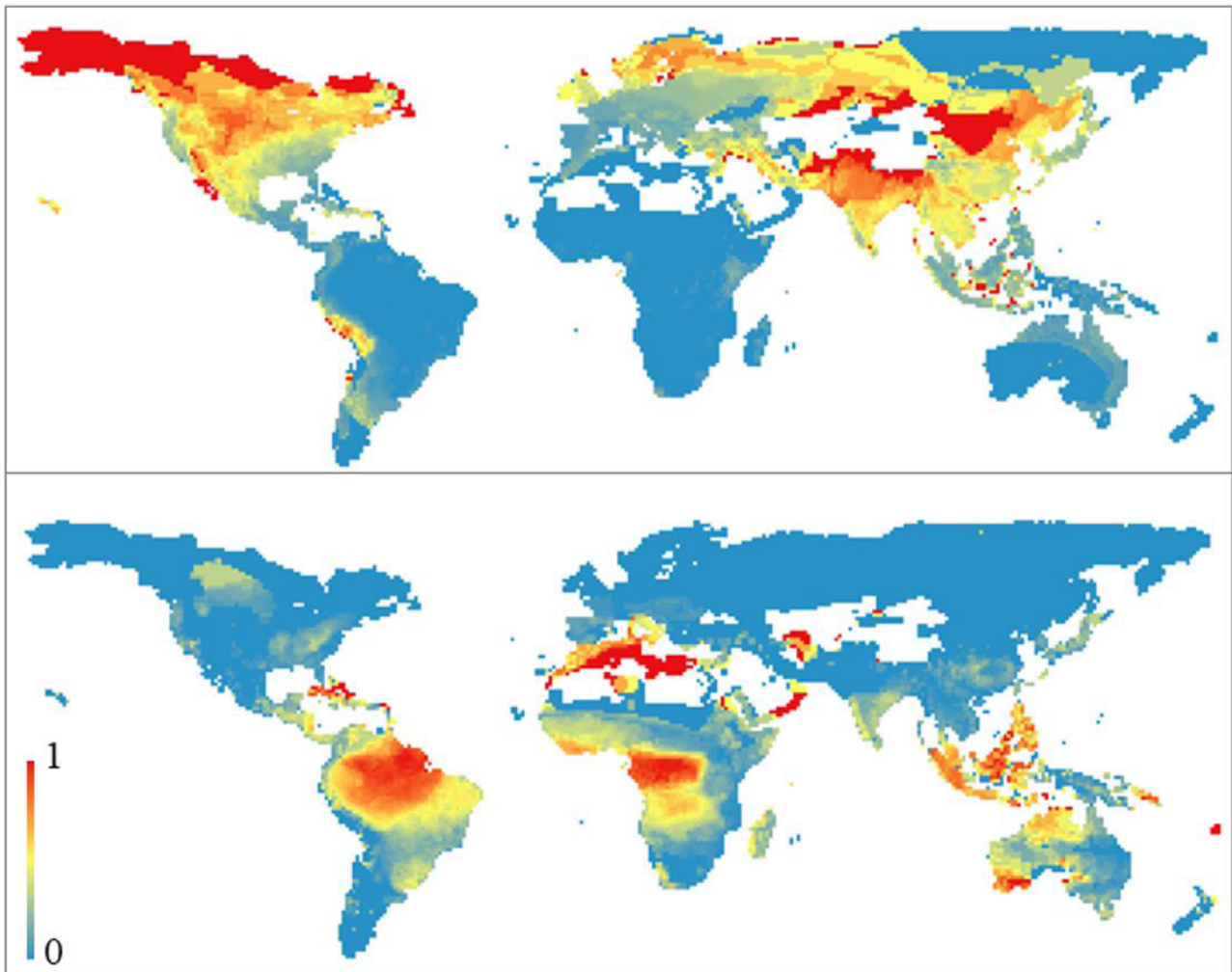


Figure 8. Proportion of species richness excluding species with a low likelihood of evolutionary rescue ($P < 0.05$) (a) and the proportion of species richness with high probability of evolutionary rescue ($P > 0.95$) (b), in respect to current overall richness. Maps use a WGS84 Mercator projection.

may help in improving the first results shown here and help clarify the conservation status of many species (see Nori et al. 2018). But as things stand, building the distribution of MSER models based on a wide range of parameters may help in assessing the probability of evolutionary rescue for multiple species and for evaluation of their geographical patterns.

In a geographical context, both interspecific analysis (i.e., separating species by biogeographic regions) and spatially explicit analyses of species richness suggest that failure of evolutionary rescue will be concentrated in the tropical regions, as previously found by Sunday et al. (2011) based on tolerance analyses. However, it is important to remember that our analyses are assuming limited dispersal, as pointed out before, as we are not considering potential range shifts under climate changes. Consequently, failure to adapt and low probability of rescue do not necessarily mean that species will go extinct, as they may be capable of moving towards more suitable regions close to their current range limits. Also, our analyses

are considering only the species peak in temperature, and do not account for the possibility that different populations within large-ranges species will be able to adapt and persist (see Diniz-Filho et al. 2019). So, our maps in Fig. 7 and 8 indicate only where species will fail to adapt and not necessarily the final richness after potential extinctions. On the other hand, these analyses based on species' peaks in temperature may provide reasonable first approximations considering that most amphibians have very small geographical ranges, so the patterns shown in Fig. 8 may be not far from those predicted under more complex population models. Finally, note that Munguia et al. (2012) showed that in the Neotropics the species tend to occupy a small proportion of their realized ranges, but this cannot explain the geographical patterns in Fig. 8 as we used a random sample of standard deviations and not the ones empirically observed.

On the other hand, counterbalancing the pessimistic extinction scenario, it is important to highlight that even moderate levels of phenotypic plasticity increase

species probability of persistence (see Urban et al. 2014). So, further analyses, incorporating more explicitly the dispersal potential and range shifts under niche conservatism may provide more accurate estimates of the extinction expected in scenarios of a failure of evolutionary rescue. Moreover, considering the generally low dispersal potential of amphibians and the strong effects of habitat loss, it may be unrealistic to factor in significant range shifts within SDM for amphibians. Hence, our results may be considered as a warning of strongly geographically-structured species' loss under climate changes. Further analyses accounting for these combined effects of adaptive potential, dispersal and habitat loss are necessary for more comprehensive generalizations and to allow a better evaluation if species will be able or not to deal with multiple threats (Nori et al. 2018).

Methodological Issues

From a methodological perspective, it is also important to consider biases in our analyses of evolutionary rates. Let's start by evaluating the aspects in our analyses that can be considered too pessimistic, in the sense that the likelihood of adaptations and probability of persistence must be higher than predicted here. First of all, we have compared only the mean values within entire species' ranges, which is only representative of a single optimum, with enough gene flow to offset local adaptations (see Kirkpatrick and Barton 1997 for original derivation). On the other hand, it is more likely that some populations that are adapted to hotter conditions within the range should persist. This case is particularly likely for large-ranged species with limited gene flow throughout their range, as expected by the overall low dispersal rates of amphibians as a group.

A second important aspect to consider is whether the purely genetic adaptive model (MSER) is realistic? It is expected that ecological traits such as temperature tolerance can show some degree of plasticity and indeed other factors are known to compensate for thermal tolerance, including morphological, ontogenetic and behavioral adjustments (Bovo et al. 2018). Although we do not know exactly the proportion of variation allowed by phenotypic plasticity, even low levels of b (up to 15% in equation 3) in Chevin et al.'s (2010) model will result in much less alarming patterns (see Urban et al. 2014).

The amount of variation is also related to another important parameter here, the phenotypic variance in temperature tolerance. We assumed that broadly distributed species (i.e., more than 10 cells in our world grid) are in equilibrium with current climate (sensu Araújo and Pearson 2005) so that they occupy the entire geographic range within the species' tolerance range to temperature. However, one can still argue that this is an underestimate of species tolerance and that the fundamental niche for temperature may be broader, as experimental evidence suggests (e.g., Soberón and Arroyo-Peña 2017, Bennett et al. 2018). If this is true, the standard deviations used to calculate Haldanes (and the MSER for the two models) should be larger,

and consequently the probability of rescue estimated here may be much lower than in reality.

Conversely, some other factors suggest that the results presented here may be too optimistic. Firstly, regarding the single optimum, although local adaptations are likely to occur for broad-ranged amphibians (as analyzed by Diniz-Filho et al. 2019 using ecological niche models), most species have very small ranges, so shifts in the peaks tend to encompass the full adaptive potential. Notice that, in this case, we also assumed a large standard deviation sampled from the statistical distribution of the broad-ranged species, supporting the analyses by Munguia et al. (2012; i.e., as the standard deviations used for the analyses are much higher than those we could calculate for their empirical ranges, which tends to zero as they occur in quite restricted areas)). Therefore, although the underestimation of the fundamental niche for temperature may hold, it is difficult to evaluate if small-ranged species will indeed have physiological tolerances as high as assumed here with the bootstrap procedure. For instance, this may be particularly true for mountain species, in which geographic constraints and habitat dynamics will tend to lead species to extinction (Colwell et al. 2008).

Finally, we are assuming here a strongly limited dispersal and have analyzed temperature shifts within the current ranges of the species. Most amphibians are likely to have very small ranges, and empirical observation suggests very low dispersal abilities (see Cayuela et al. 2018). But a few, e.g. invasive species such as *Rhinella marina* and others, have a high dispersal potential, and this may turn out to be the case for other species under strong environmental pressures. This would allow them to colonize new regions where conditions are similar to those in their current range (so no adaptation would be required). For such a scenario it would be possible to follow the proposal of Diniz-Filho et al. (2019) to model evolutionary shifts only in species' trailing edges. However, there are two problems with this approach that are particularly relevant for small-ranged species. First, methodologically it is difficult to use ENMs for these small ranged species because they provide poor estimates of the climatic niche (going back to the issue of underestimating environmental tolerances). In addition, although they could expand to nearby regions within relatively few generations, these populations would still be closer to the original occurrences, showing similar climatic configuration (and again this is unlikely under conditions of general biotic attrition). Second, even if dispersal is possible, climate changes are not the only threat, and dispersal routes may be constrained by human induced changes in land use and loss of natural environments (e.g. Sales et al. 2019).

Concluding Remarks

It remains difficult to evaluate the pros and cons of the above arguments, and further studies aimed at better estimating genetic and demographic parameters for species' responses to climate change are needed. But of course, it may be unrealistic to think of doing this for hundreds or thousands of species and, in

any case, these better estimates will help to improve implementation of more general macroecological approaches, as trialled here. The few more detailed and realistic models for evolutionary responses to climate change available to date tend to provide pessimistic results and hardly suggest adaptation as an easy route for species persistence in the short run (see Franks and Hoffmann 2012, Thuiller et al. 2013, Bush et al. 2016, Cotto et al. 2017, Radchuk et al. 2019; but see Buckley and Kingsolver 2019 and Razgour et al. 2019 for other possibilities of rescue involving plasticity and migration). If we consider the small current range of many amphibian species and the other threats involved and their interaction (see Nori et al. 2018), it may be precautionary to assume that results shown here are not too liberal and that persistence of populations by evolutionary rescue may be generally unlikely.

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