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Warning times for species extinctions due to climate change

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Abstract

Climate change is likely to become an increasingly major obstacle to slowing the rate of species extinctions. Several new assessment approaches have been proposed for identifying climate-vulnerable species, based on the assumption that established systems such as the IUCN Red List need revising or replacing because they were not developed to explicitly consider climate change. However, no assessment approach has been tested to determine its ability to provide advanced warning time for conservation action for species that might go extinct due to climate change. To test the performance of the Red List system in this capacity, we used linked niche-demographic models with habitat dynamics driven by a 'business-as-usual' climate change scenario. We generated replicate 100-year trajectories for range-restricted reptiles and amphibians endemic to the United States. For each replicate, we categorized the simulated species according to IUCN Red List criteria at annual, 5-year, and 10-year intervals (the latter representing current practice). For replicates that went extinct, we calculated warning time as the number of years the simulated species was continuously listed in a threatened category prior to extinction. To simulate data limitations, we repeated the analysis using a single criterion at a time (disregarding other listing criteria). Results show that when all criteria can be used, the Red List system would provide several decades of warning time (median = 62 years; >20 years for 99% of replicates), but suggest that conservation actions should begin as soon as a species is listed as Vulnerable, because 50% of replicates went extinct within 20 years of becoming uplisted to Critically Endangered. When only one criterion was used, warning times were substantially shorter, but more frequent assessments increased the warning time by about a decade. Overall, we found that the Red List criteria reliably provide a sensitive and precautionary way to assess extinction risk under climate change.

Keywords: climate change, IUCN Red List, linked demographic-habitat models, probability of extinction, Red List Categories and Criteria, threatened species

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Introduction

Global climate change is widely recognized as one of the major threats to biodiversity in the 21st century (Millennium Ecosystem Assessment, 2005). Identifying components of biodiversity that are most vulnerable to the effects of climate change is essential for prioritizing conservation actions to minimize biodiversity loss. The most widely used system for identifying species at risk of extinction is the IUCN Red List, which categorizes species based on population-level symptoms of endangerment such as population size and trends, spatial distribution, and fragmentation (Mace *et al.*, 2008; IUCN, 2012, 2014). IUCN Red List criteria have been shown to be effective for identifying the current compendium of factors threatening species today (Hutchings & Reynolds, 2004; Keith *et al.*, 2004; Dulvy *et al.*, 2005; Hayward, 2011; Harris *et al.*, 2012); and provide ample warning for action (Stanton, 2013; Keith *et al.*, 2014) even if recognition of threat status does not always halt deterioration of populations (Butchart *et al.*, 2004). The Red List has also proven to be a useful tool in tracking the status of global biodiversity (Hoffmann *et al.*, 2010) and the effectiveness of conservation action (Butchart *et al.*, 2006; Rodrigues, 2006).

Although the IUCN Red List has proven to be a highly useful conservation tool for a number of threats encountered by species today, it has been suggested that the criteria as they stand may not provide sufficient warning to protect species impacted by slow acting and persistent threats such as global climate change

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(Thomas *et al.*, 2004; Thuiller *et al.*, 2005). Red List threat classifications are made on the basis of either recent data indicating the species is already headed toward extinction (criteria A1, A2, B, C, and D) or evidence that projects a high risk of extinction in the future (criteria A3, A4, and E). A serious concern is that climate change may already be impacting species, but so gradually that waiting until observable signs of decline are evident may prove to be too late to take effective conservation action (Hannah, 2012). The horizons over which the IUCN Red List criteria are assessed may therefore be too short (Thomas *et al.*, 2004), especially for short-lived species (Akçakaya *et al.*, 2006). Criteria A3 and A4 consider declines projected for the next three generations or 10 years, whichever is longer. For many species, this means that only changes in the next 10–30 years are considered in assessing risks based on projected losses due to climate change and other threats. Criterion E is based on risk of extinction in the next 10–100 years. However, criterion E requires a quantitative estimate of the probability of extinction (e.g., using population viability analysis), and thus can be applied to only a few well-studied species. For most species, the three-generation time period considered in the criteria may mean that they are identified as threatened for a relatively short time before they go extinct, and this may not be long enough for conservation measures to take effect and prevent extinction.

Several alternative methods for identifying species as vulnerable to climate change have been proposed recently (Thomas *et al.*, 2011; Young *et al.*, 2012; Foden *et al.*, 2013). These methods are based on variables used in the IUCN Red List, as well as additional variables such as whether there is direct linkage between population decline and climate change (Thomas *et al.*, 2011), occurrence of bottlenecks in recent evolutionary history (Young *et al.*, 2012), and dependence on interspecific interactions that are likely to be disrupted by climate change (Foden *et al.*, 2013). In practice, such variables are based on expert opinion. These approaches have not been quantitatively tested to determine if they provide a longer period of warning compared to the IUCN Red List criteria.

In a recent study, Keith *et al.* (2014) used a linked ecological niche-demographic model of a short-lived frog species to show that the lead times between initial listing in a threatened category based on IUCN Red List criteria and predicted extinction varied from 40 to 80 years, depending on data availability, demonstrating that IUCN Red List may provide adequate warning time for short-lived species. However, this study was limited to a single species, thus limiting the ability to draw general conclusions. Moreover, Keith *et al.* (2014) applied the IUCN Red List criteria to the average trajectory over all replicates of a stochastic model; here, we apply the criteria to the individual stochastic trajectories. Each individual model replicate simulates the year-to-year variability that a real population might display, and thus our approach is a more realistic simulation of the trajectory of Red List assessment through time. In addition, using the average trajectory eliminates the population fluctuations, resulting in much more uniform red list categories over time, and thus potentially overestimating warning times (as was speculated in Keith *et al.*, 2014).

To evaluate how climate change might influence the effectiveness of the IUCN Red List criteria as a tool for identifying species at risk, we used a set of models developed previously to forecast extinction risk due to climate change for endemic North American reptiles and amphibians (Pearson *et al.*, 2014). We evaluated individual stochastic model replicates run under a climate change scenario by applying IUCN Red List criteria at each annual timestep. For trajectories that went extinct within the simulated time period, we calculated the length of time spent in each threat category prior to extinction. We refer to the time between red-listing of a species and its extinction (assuming no conservation action) as the 'warning time' because it gives an estimate of the time that would be available for conservation measures to prevent the extinction of climate-impacted species. These calculations allowed us to also determine the relative length of time spent in different threat categories, which has been used before to infer the effectiveness of conservation actions (Brooke *et al.*, 2008). We also calculated the number of years listed as threatened for trajectories that did not go extinct, as a way to identify false alarms. To examine how the results are affected by data limitations, we repeated the analysis using each criterion separately. Finally, we tested whether predictor variables (life history traits and spatial variables) explain the variation in the number of years continuously listed as threatened prior to extinction.

Materials and methods

Population models

We used population models that were developed by Pearson *et al.* (2014), which coupled ecological niche models (ENM) with demographic models to forecast population dynamics under three climate change scenarios: no climate change; a reduced carbon emissions scenario that assumes policy intervention (Policy scenario); and a high emissions scenario that assumes no substantial mitigation (Reference scenario). Pearson *et al.* (2014) generated ENM based on occurrence data for 36 North American endemics under current climate and other environmental variables (including land cover, hydrography, and land surface form), and then projected those distributions to annual future climate modeled variables, thus generating 36 unique spatial trajectories of potential habitat to the year 2100. Those spatial models were then paired with age- and stage-structured generic life history (GLH) models designed to encompass the range of demographic parameters representing a typical snake, small salamander, large salamander, turtle, tortoise, or lizard (see Appendix S1 for a brief overview of the GLH models). Pearson *et al.* (2014) sampled within the parameter space to generate 40–50 different spatially explicit demographic metapopulation models for each paired GLH and ENM. The spatial structure of each metapopulation model was calculated using the Spatial Data module in the RAMAS GIS software package (Akcakaya, 2012) based on the time series of habitat suitability maps. A 'patch' was defined as the area of habitat that potentially supports one subpopulation of the modeled species. Each patch consists of a cluster of contiguous grid cells that have habitat suitability values above a threshold. The initial abundance in the patches was determined based on a map of the occurrence records. The carrying capacity of patches was based on the total habitat suitability (sum of the habitat suitability values for all grid cells constituting a patch).

The GLH approach allows generalization beyond the species for which occurrence data are available. Because the demographic models we had assembled are representative of six major groups of amphibians and reptiles, our study represents the first systematic analysis of warning times under climate change. This modeling framework generated 9720 individual population models representing realistic species scenarios with annual time steps tracking the impact of climate change. This previous study aimed to explore what measurable life history traits and recent trend indicators might be useful for identifying species most at risk of extinction under climate change (Pearson *et al*., 2014). Here, we test how well the IUCN Red List criteria might perform in predicting extinctions due to climate change by applying the criteria to individual model trajectories. To do this, we reran each population model, recording information on the population size and number and spatial distribution of subpopulations in each time step of each replicate. We determined the IUCN Red List status annually for 10 stochastic replicates of each population model run under the Reference ('business-as-usual') climate scenario (CO_2 concentration of 750 ppm; WRE750; Wigley *et al.*, 1996). Overall, there were 1680 models run for a total of 16 800 individual replicates analyzed. The models did not simulate any anthropogenic threat other than climate change, any conservation action, or any climate mitigation action. We thus focus only on climate change, both because climate change was poorly understood as a threat to species at the time the current IUCN rules were developed (in early 1990s) and revised (in 1999–2001), and because, as described in Introduction, the applicability of IUCN criteria to climate change has been questioned, leading to proposals for alternative systems to identify vulnerable species.

IUCN Red List assessments

We evaluated each simulated trajectory separately against the IUCN Red List criteria (Fig. S1), which allocate species to categories of extinction risk (see below) using simple quantitative rules based on species-specific information such as population size, range area, and rates of population and range declines (Table S1). Details of the listing criteria and guidelines for their use are available from IUCN (2012, 2014; for summary table see http://www.iucnredlist.org/documents/2001CatsCrit_Summary_EN.pdf). In one analysis, we applied all the criteria. In another analysis, we applied only one criterion (separately for each of criteria A, B, C, and D), and combinations of two criteria, to examine the effect of lack of information that results in only one or two criteria to be applied (as is often the case in IUCN Red List assessments). We applied the criteria at annual, 5-year and 10-year time steps for each model replicate (see Appendix S2). Thus, for each replicate we applied the IUCN criteria 100 times (annually), 20 times (5-year intervals), and 10 times (10-year intervals), for a total of roughly 24 million applications of the criteria. For each of these applications, we only considered the information available up to and including the time step under evaluation, without consideration for the future or the ultimate fate of the trajectory (Fig. S1). To avoid circularity, we did not consider Red List criteria A3, A4, or E, which involve making future projections. Details regarding the calculations used to determine the threat status based on the Red List criteria are available in Appendix S2.

Analysis of projected changes in red list status

We recorded the time step at which one or more Red List criteria were met for each threat category, as well as the number of years spent in each category before advancing to the next category or going extinct. We analyzed trajectories ending in extinction separately from trajectories that did not result in extinction prior to the end of the simulation to see if they showed substantial differences in Red List categorization trends.

For analysis of trajectories that resulted in extinction, we removed the trajectories that were categorized as Critically Endangered (CR) at the time of initial listing (after burn-in; see below). Including these trajectories would have biased the results, because any species that is currently listed as CR would have already been listed as Endangered (EN) or Vulnerable (VU) for several years; therefore, the number of years listed as threatened in the simulations would underestimate the time such a species would have been listed as threatened (at any category). Trajectories that did not result in extinction introduce a different type of bias. Many of these trajectories, although not extinct by year 2100, represented very small and restricted populations that have been declining over the last several generations. If we had continued the simulations for another few decades, many of them would have gone extinct. To partially correct for this bias, when analyzing trajectories that did not go extinct, we did not consider assessments made within the final 20 years of the simulation.

Following established rules (IUCN, 2012, 2014), if an assessment met the criteria for 'up-listing' from a less threatened category (e.g., VU to EN), the species was moved to the more threatened category. However, if an assessment met the criteria for 'down-listing' to a less threatened category, the species remained in the higher threat category pending a reassessment 5 years later (or, in the case of an annual re-evaluation interval, five continuous down-listing recommendations). The decision to down-list was only made if upon reassessment the species continued to meet the conditions for down-listing, in accordance with standard IUCN practice (IUCN, 2012, 2014). Note that 5-year reassessments were conducted even when we were simulating a 10-year re-evaluation interval (and these interim assessments did not reset the regular 10-year evaluation schedule). Also, note that a category can be skipped if the population status changes quickly compared to the assessment interval. All models include a 10 year spin-up period for model calibration which we excluded from the Red List analysis. All simulation models were run using RAMAS GIS 6.0 (Akcakaya, 2012) and all subsequent analysis was performed using R (R Core Team, 2013).

On the basis of the results of Red List assessments, we calculated the number of years each trajectory was continuously listed in any category VU and above (i.e., listed as threatened; we label this as 'VU+'), in category EN and above (labeled as 'EN+', i.e., EN or CR), and in category CR, before extinction or the end of the simulation, whichever came first. Based on the histogram of times for which trajectories were continuously listed, we calculated the median number of years listed before extinction, as well as the proportion of trajectories that were listed for fewer than 20 years before extinction. We used the 20 years as a threshold, assuming that a shorter period would have provided insufficient warning to conservation practitioners. For trajectories that did not go extinct, we calculated the proportion that were listed for more than 50 years, assuming that listings longer than that would constitute a 'false alarm' to conservation practitioners.

For replicates resulting in extinction, we calculated the number of years of the 'warning period' [i.e., listed as threatened (VU+) continuously prior to extinction] spent in each specific threat category, VU, EN, and LC. We did this calculation separately for trajectories differing in initial listing status, to gain insight into the time a species heading toward extinction is expected to spend in each category in the absence of conservation action.

The procedures described above resulted in a data table of extinct replicates (one for each model) and a data table of non-extinct replicates, with columns representing potential response variables (e.g., number of years continuously listed as CR under IUCN Red List criterion C) and potential predictor variables (e.g., initial abundance, generation length). To test whether warning time can be predicted on the basis of species-level data commonly available to researchers, we quantified relationships between predictor variables and the response variables using a random forest (RF) algorithm (Cutler *et al.*, 2007). RF is a machine learning method that combines predictions from multiple independent regression trees (recursive partitioning algorithm) into a robust ensemble model that can accommodate nonlinear, context–dependent interactions among multiple, correlated predictor variables (Prasad *et al.*, 2006; Olden *et al.*, 2008) We performed RF analyses using the party package in R (Hothorn *et al.*, 2014), which implements a nonparametric, distribution-free RF algorithm that uses conditional inference trees in place of standard regression tree algorithms (Hothorn *et al.*, 2006).

We used RF, and single conditional inference trees (also implemented in party), to assess which variables best predict the length of warning time (total time continuously listed before extinction) provided by the IUCN Red List criteria under climate change. We produced 1000 conditional trees, each using a random subset of 50% of the data (sampled without replacement), with each split of each tree based on a different random subset of five variables. Variable importance values were determined by computing the prediction error for the out-of-bag sample for each tree, and assessing the degree to which out-of-bag prediction error increases when the indices are randomly permuted for each predictor variable (Strobl *et al.*, 2008). The importance value therefore accounts for main effects and interactions (the number of recursive partitions, or tree 'depth', was not constrained in these analyses, allowing for consideration of high-order interactions). Predictions were made by averaging across all trees in the forest.

To assess RF model performance and predictive ability, and thereby assess the extent to which the warning time (in years) provided by IUCN Red List criteria under climate change could be explained by measurable variables (suggesting that the IUCN Red List could potentially be modified to better account for climate-related risks), we used a leave-one-out cross-validation scheme in which one species at a time was withheld from the fitting algorithm as an independent validation set (models were trained based on remaining species, following Pearson *et al.*, 2014). The predictor variables (see Table S2) included those that are incorporated into IUCN Red Lists system directly (such as occupied area) or indirectly (such as generation length), as well those that are not explicitly incorporated but are hypothesized to influence climate-related extinction risk (such as niche breadth). We used species as a data partition instead of random partitioning methods (such as a standard tenfold cross-validation) to challenge the modeling algorithm against truly independent data. We used proportion of explained variance (R^2) and root mean squared error as the performance metrics, which we computed for the full model (all data used for training) and for cross-validation sets (data from species other than the one being predicted were used to build the model).

Results

Of the 16 800 replicates, 5071 (30.2%) resulted in extinction, and the rest (11 729 replicates, 69.8%) did not. After filtering 626 trajectories (3.7%) that started as CR in the first time step, the analysis is based on the remaining 4445 extinct trajectories, and the 11 729 extant trajectories. When all Red List criteria were applied, both extinct and extant trajectories were listed under (i.e., met the thresholds of) all four criteria, although trajectories were listed more frequently under criterion B (Table 1). Generation times ranged from 3.51 to 17.8 years; thus criterion A2 was evaluated for periods of 11–53 years.

The extinct trajectories were continuously listed as threatened (VU+, i.e., in category CR, EN, or VU) for an average of 60.4 years (median = 62 years) prior to extinction, with only 0.16% continuously listed as threatened for shorter than 20 years (Fig. 1). When all the criteria were applied, the interval between assessments (1, 5, or 10 years) made little difference in the distribution of the times listed as threatened: with 10-year intervals, the proportion of trajectories that were listed as threatened for <20 years prior to extinction was 1.15% (for sensitivity of results to the 20-year threshold, see Tables S3 and S4).

As expected from the nested nature of the IUCN threat categories, the extinct trajectories were continuously listed at higher threat categories for substantially shorter periods. The median number of years listed as EN or CR (i.e., EN+) prior to extinction was 50, with 11% of trajectories continuously listed at these two higher threat levels for shorter than 20 years (Fig. 2b). Extinct trajectories were continuously listed as CR for a median of only 21 years prior to extinction (Fig. 2c).

Using a single criterion substantially decreased the warning time. The proportion of extinct trajectories listed as threatened (VU+) for less than 20 years prior to extinction was 51.3%, 33.8%, 23.3%, and 2.4%, when only criterion A, B, C, and D was used, respectively (Fig. 3, left panel). When only a single criterion was used, annual (instead of 10-year) assessments made more of a difference in terms of increasing warning times (Fig. 3, right panel) than when all criteria were used (Fig. 1). For example, when only criterion C was used, making assessments at annual instead of 10-year intervals resulted in a substantial decrease in the proportion of trajectories listed as threatened for less than 20 years prior to extinction, from 23.3% to 4.2% (Fig. 3c). When a single criterion was used, median times listed as threatened prior to extinction were over 40 years with 10-year assessments, and over 50 years with annual assessments, except under criterion A, under which median times were 20–25 years (Fig. 3). When two criteria were used, warning times varied depending on the combination (Fig. S2); all combinations except A + C resulted in median warning times of greater than 50 years, and for combinations with D, <2% of warning times were <20 years (Fig. S2).

Extinct replicates that started at a higher threat category spent less time in lower threat categories prior to extinction (compared to those that started at a lower category); however, extinct replicates spent about the same amount of time as CR before they went extinct, regardless of their initial listing category (Fig. 4). Replicates that started as not threatened (LC or NT) and went extinct within 100 years spent less time as VU than as CR or EN (Fig. 4, top bar).

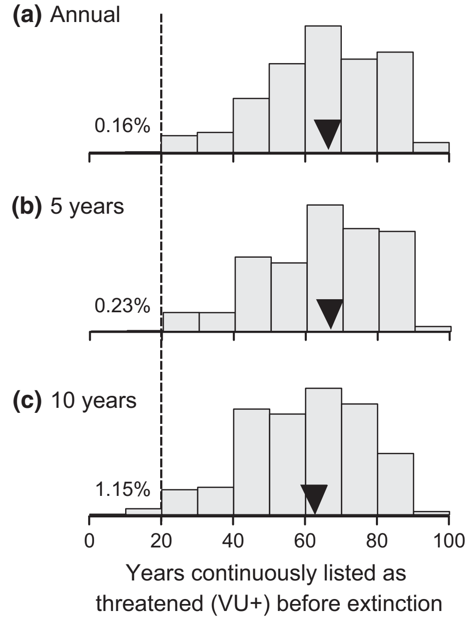

Fig. 1 Histogram of time continuously listed as threatened (VU+; i.e., as VU, EN or CR) prior to extinction for trajectories simulating range-restricted North American reptiles and amphibians under climate change, on the basis of IUCN Red List criteria with (a) 1, (b) 5, and (c) 10-year evaluation intervals. The vertical dashed line indicates threshold duration (20 years) below which the IUCN listing process might have provided insufficient warning to conservation practitioners. The percentage of total simulations listed as threatened for less than 20 years prior to extinction is shown to the left of the dashed line. Black triangles indicate the median duration for which species were continuously listed as threatened prior to extinction.

Table 1 For simulated species listed under each IUCN Red List category, the proportion of listings under which each of the listing criteria (A–D) were met

IUCN Red List category	Extinct runs (%)				Nonextinct runs (%)			
	A	B	C	D	A	B	C	D
CR	26.7	58.5	53.9	41.8	25.1	86.1	25.8	14.4
EN	33.9	29.7	22.5	14.0	40.6	70.3	45.0	17.5
VU	39.0	65.7	66.7	79.3	42.9	58.5	52.7	53.8
NT	42.1	96.9	63.0	80.3	45.7	82.8	50.2	68.2

CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened.

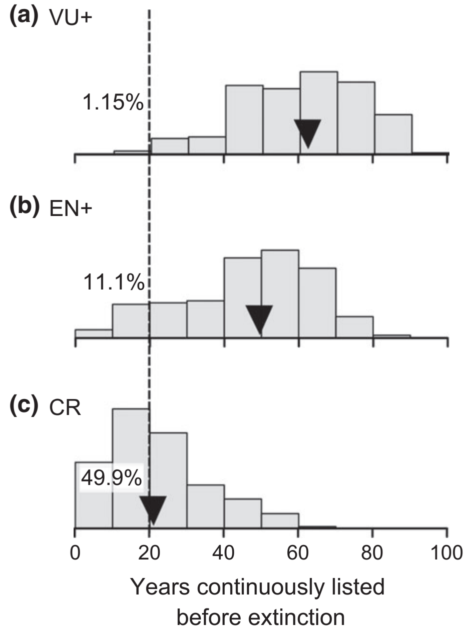

Fig. 2 Histogram of time continuously listed as (a) threatened (VU+), (b) endangered or above (EN+), and (c) Critically Endangered (CR) prior to extinction for trajectories simulating range-restricted North American reptiles and amphibians under climate change, on the basis of IUCN Red List criteria with a 10 year evaluation interval. The percentage of total simulations listed for <20 years is shown to the left of the dashed line. Black triangles indicate the median duration for which species were continuously listed prior to extinction.

When all criteria were used, 71.4% of the trajectories that did not go extinct were listed as threatened (VU+) for more than 50 years prior to year 80; the proportion listed as EN or VU (i.e., EN+) was 29.7%, and the proportion listed at the highest threat category was 10.1% (Fig. 4; for sensitivity of results to the 50-year threshold, see Table S5). When a single criterion was used, the proportion listed for more than 50 years was 19–31% at the VU+ level, and 5–16% at the EN+ level (Fig. 5, left and right panels, respectively).

Analysis of factors contributing to warning time had very poor predictive performance; the R^2 for cross-validation was negative (−0.36, compared to R^2 = 0.73 for the full model), indicating predictive power worse than that of the null model. The most important variable was spatial correlation of variability (Fig. S3), and all variables (including generation length) contributed very little to explain the variability in the number of years listed as threatened prior to extinction.

Discussion

Our results show that IUCN Red List criteria can provide decades of warning time for species that would go extinct due to climate change. When information is available to use all four Red List criteria, very few trajectories that go extinct were listed for less than 20 years, and half were listed for 62 years or more. In addition, the assessment interval did not make a substantial difference in the length of the warning period (Fig. 1).

The warning time necessary for effective conservation of species threatened with extinction is difficult to determine, as it depends on the specific mechanisms through which climate change is affecting the species, the nature of conservation actions that are feasible, and social, institutional and economic constraints, among other factors. There is no systematic review of how quickly different types of conservation projects can result in positive outcomes. Jones & Merton (2012) report times ranging from 14 to 30 years (median = 20 years) for the recovery of bird species in re-introduction programs. In *Global Re-Introduction Perspectives* (Soorae, 2013), most of the successful re-introduction projects involving amphibians, reptiles, and birds are reported to have taken <20 years. Thus, for most situations, a warning time of several decades might be considered sufficient.

For replicates which ultimately resulted in extinction, the Red List criteria considered here did provide advance warning. Based on these results, we conclude that it would be unlikely for a species to go from a non-threatened category to extinction in <20 years, and thus within the recommended Red List assessment interval of 10 years, when climate change is a major threat. However, if conservation action is delayed until a species is listed in the highest threat category, there may not be sufficient time for saving the species (Fig. 2c), even if information is available to use all the IUCN criteria. This suggests that conservation actions should be initiated as soon as a species is listed as threatened in any category, and at the very latest when it is listed as Endangered (Fig. 2b). In addition, our results are based on simulated effects of only one threat, climate change. Whether warning times are longer or shorter, when species are impacted by multiple interacting threats remain to be investigated.

When lack of data and uncertainty in available data result in only one criterion being applied, the Red List system still provided long warning times (median >40 years; Fig. 3), unless criterion A2 is the only criterion used, in which case median warning time was only about 20 years (Fig. 3a). One reason criterion A2 did not provide as much warning is because, unlike for the other criteria, we did not use all parts of criterion A. In particular, to avoid circularity, we did not use criteria A3 and A4 (or criterion E). These criteria require projections into the future; thus applying them to simulated

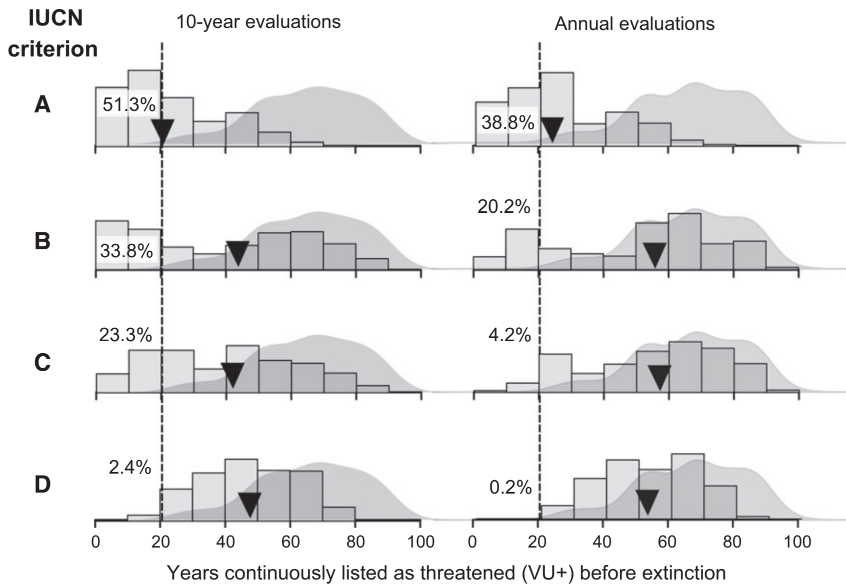

Fig. 3 Histogram of time continuously listed as threatened (VU+) prior to extinction for range-restricted North American reptiles and amphibians under climate change, on the basis of IUCN Red List criteria A, B, C, and D, respectively (using 10-year evaluation interval). The percentage of trajectories listed for <20 years is shown to the left of the dashed line. Black triangles indicate the median duration for which species were continuously listed prior to extinction. The shaded region is a simplified representation of the histogram of listing durations when all four IUCN Red List criteria are used.

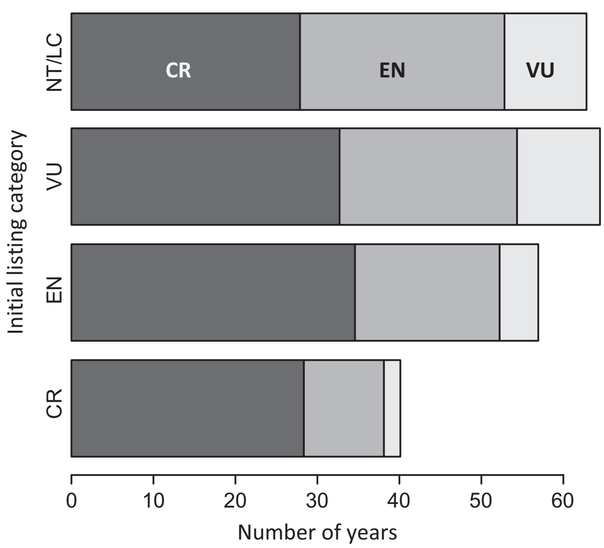

Fig. 4 Number of years listed in each threat category. Each bar illustrates, for those replicates that go extinct, the mean total 'listed' time (VU+) spent in each IUCN category: CR (black), EN (dark gray), and VU (light gray). Each bar summarizes results for a set of species that start off at a specific threat category. Only one species is initially listed as LC and goes extinct within 100 years, thus the top bar pools species that are initially listed either as LC or as NT.

trajectories must either use the information from the rest ('future') of that simulated trajectory, or apply these criteria in incomplete ways. The first option would overestimate warning times, and the second option would add ambiguity to the process that does not exist in real assessments. In actual Red List assessments, criteria A3 and A4 are used to calculate future population reductions based on, for example, expected future decline in potential habitat (although, so far, only for a few amphibians and reptiles that are threatened by climate change; see below). In the case of climate change, such declines are often calculated based on results of ENM using projections of global climate models (see IUCN, 2014, section 12.1). For example, almost all of the reef-building coral species threatened by climate change and local impacts were listed under criterion A4 (Carpenter *et al.*, 2008). Thus, our results underestimate the ability of criterion A to identify species vulnerable to climate change.

Criteria other than A2, when used singly, provided <20 years of warning time for up to a third of extinct replicates (Fig. 3, left panel), indicating that warning times may be too short for a substantial proportion of poorly known species impacted by climate change. Unlike the case with using all the criteria, when using a single criterion, the assessment period made a substantial difference, with annual intervals adding about 10 years to the warning time (Fig. 3, right panel). Thus, one way to lessen the negative effects of data shortage might be to perform more frequent assessments.

There was some variability among the extinct trajectories in terms of the length of the warning time

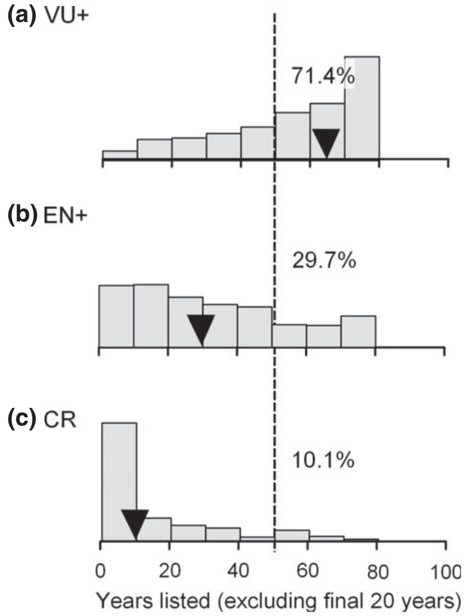

Fig. 5 Histogram of time continuously listed as (a) threatened (VU+), (b) endangered or above (EN+), and (c) Critically Endangered (CR) for range-restricted North American reptiles and amphibians under climate change, for simulation runs that did NOT terminate in extinction, on the basis of IUCN Red List criteria with a 10 year evaluation interval. The vertical dashed line indicates a threshold duration (50 years) above which the IUCN listing process would have provided a 'false alarm' to conservation practitioners. The percentage of total simulations above this threshold is listed to the right of the dashed line. Black triangles indicate the median duration for which species were continuously listed for nonextinct runs. Note that the final 20 years of simulations were not considered for this analysis, since many of these simulated species may have gone extinct soon after the end of simulations (and therefore should not be considered a 'false alarm').

(Fig. 1), which brings up the question of whether any information currently available can be used to predict the length of time a species will be listed as threatened before it goes extinct. If so, it would be possible to identify species that would be listed for shorter periods before they go extinct that would also be valuable information for prioritizing conservation actions. Our analyses showed that the predictive model performed very poorly, suggesting that none of the predictor variables included in this study could be used to improve the performance of the IUCN Red List criteria under climate change. In particular, generation time contributed almost no predictive power, indicating that the length of warning time provided by the Red List criteria may not be shorter for short-lived species. This is likely because generation time determines the Red List assessment period, and is thus already incorporated into the Red List system.

The number of years extinct replicates spent in different threat categories was unexpected. Replicates that started as not threatened (LC or NT) and went extinct within 100 years spent less time at lower threat category (VU) than at higher categories (CR or EN; Fig. 4, top bar). Assuming that the trajectory toward extinction is sequential through all categories and that the rate of extinction is constant, Brooke *et al.* (2008) estimated that the number of years spent in each category should decrease with increasing threat level. Here, we found the opposite pattern, implying that the assumptions outlined for this estimation were not met. This raises an important issue, because species remaining at threat categories longer than anticipated might be attributed to the effects of conservation actions, when it is possible there was little impact of conservation – only a mistaken assumption of how long the progression toward extinction should take. For example, Brooke *et al.* (2008) compared their calculations to the rate of movement of species through IUCN categories to make conclusions about effectiveness of conservation efforts. Our results indicate that such conclusions may be invalid, at least for species threatened by climate change. The different amounts of time spent in different categories are likely a result of a species' response to threats (i.e., the external processes), rather than a direct result of the thresholds or the other characteristics of the Red List system. We conclude that, in the absence of knowledge about the details of a particular species, the specific threats it is facing, and the measured results of conservation actions taken (Butchart *et al.*, 2006; Rodrigues, 2006), the more conservative approach of not assuming an expected trajectory or timeline (Hoffmann *et al.*, 2010) may be advisable, particularly when the primary threats include climate change.

A large proportion of the replicates that did not go extinct were nonetheless categorized as threatened, some for over 50 years (Figs 5 and 6). This would imply that the Red List may occasionally do a poor job of discriminating between replicates that are threatened and those that are not, and raising false alarms. However, threat listings for replicates that did not result in extinction before the end of the simulation do not necessarily indicate, for several reasons, that the Red List is in general overly precautionary. First, it should be noted that a large proportion of the threatened listings for the lower risk models were listed under the spatial-based criteria (B1, B2, as well as D for VU and NT; Table 1). This may indicate a bias particular to the species these models were constructed after. Many of the species selected for inclusion in this study were done so because they are North American endemics, many with relatively small ranges. This may have predisposed these models toward meeting the criteria based in part on spatial parameters (note that B1 and B2 require additional indicators to be present in addition to the spatial thresholds).

Second, the fate of these replicates beyond the timeframe of the simulation is not known. Although these replicates are not extinct by the end of the simulation, many represent situations with very small and restricted populations, which, had the simulation been run for another 100 years, might have gone extinct. We tried to address this bias by not considering the last 20 years of the trajectories that did not go extinct. However, this is only a partial solution; a more comprehensive solution would be to run simulations for longer periods, perhaps for 200 years. However, high uncertainty in projections beyond the year 2100 makes this currently ill-advised.

The third reason why these results do not necessarily cast the Red List as overly precautionary is that the proportion of nonextinct trajectories that were listed as threatened is very small when only a single criterion is used (Fig. 6). For example, when only criterion D is used, a very small proportion the nonextinct trajectories are listed as EN+ for more than 10 years. For any criteria, less than a third of the nonextinct trajectories are listed as threatened for more than 50 years. Considering that many of these might be headed toward extinction soon after the end of the simulated period (as discussed above), we conclude that although the IUCN Red List system does appear precautionary, the overall proportion of false alarms is likely to be small.

Amphibians are not only highly threatened but their status is also deteriorating fast. Globally, 41% of amphibians (range 36–56%) and 19% of reptiles (range 15–36%) are listed as threatened (VU+) (iucnredlist.org; Böhm *et al.*, 2013). Between 1980 and 2004, the total number of category changes in all amphibians is calculated as equivalent to 30% of species being uplisted by one threat category each (Butchart *et al.*, 2005). A similar long-term calculation of status change is not yet available for reptiles. In the short term (from 2006 to 2014), the Red List category of a total of 18 reptile and 10 amphibian species have changed due to genuine change in status (IUCN Red List Summary Table 7, in http://www.iucnredlist.org/about/summary-statistics#Table_7). Climate change has been identified as a threat for 334 threatened species of reptiles and amphibians, but only 14 of these (4%) are listed under criterion A4 (future reduction). Among North American reptiles and amphibians, 24 of the 131 species that have been assessed (18%) are threatened (VU+). For 20 of the 131

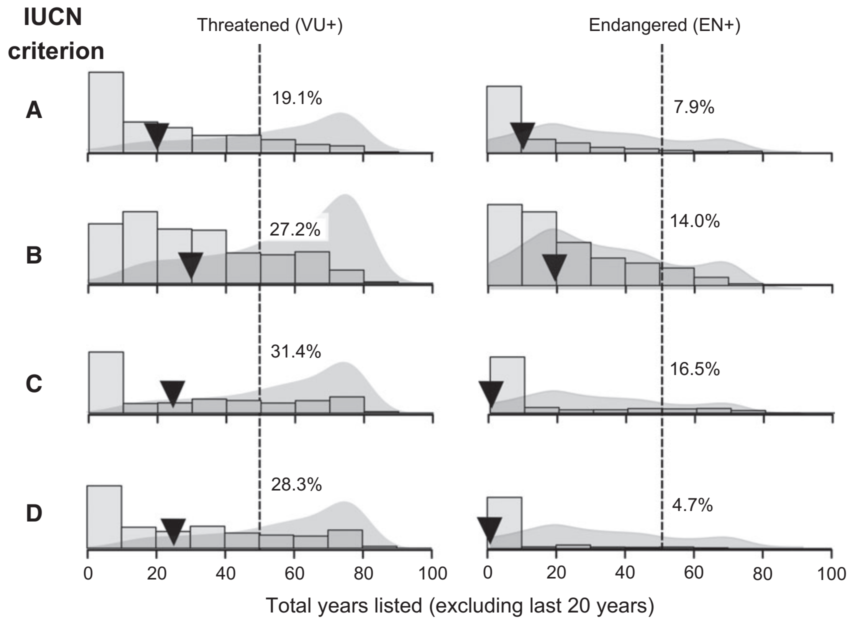

Fig. 6 Histogram of total years listed as threatened (VU+) or endangered or above (EN+) for range-restricted North American reptiles and amphibians under climate change, for simulation runs that did NOT go extinct, on the basis of IUCN Red List criteria A, B, C, and D, respectively (using 10-year evaluation interval). The vertical dashed line indicates a threshold duration (50 years) above which the IUCN listing process might have provided a 'false alarm' to conservation practitioners. The percentage of simulations that were listed for longer than 50 years is shown to the right of the dashed line. Black triangles indicate the median duration for which species were continuously listed. The shaded region is a simplified representation of the histogram of listing durations when all four IUCN Red List criteria are considered. Note that the final 20 years of simulations were not considered for this analysis, since many of these simulated species may have gone extinct soon after the end of simulations (and therefore should not be considered a 'false alarm').

species (11 of which are threatened), climate change has been identified as a threat (data downloaded from iucnredlist.org on 12 June 2014). However, interpreting the information about species threatened with climate change is complicated by several issues: (1) not all reptile species have been assessed; (2) because the IUCN criteria are based on symptoms of endangerment, the causes of endangerment are not always determined comprehensively (it is easier to know that a species is declining than to know why), and, in general, the identification of threats do not affect a species' threat status; (3) climate change may be identified as a potential threat, even if the species is not threatened; (4) identification of climate change as a threat is often based on inferring the impacts of past climate change (as evidenced by the small proportion of climate change-threatened amphibian and reptile species that are listed under A4), and thus not comparable to our results, which are based on projected climate change in the 21st century.

Species distribution models, such as Maxent, are subject to a number of well-documented limitations (Pearson & Dawson, 2003; Peterson *et al*., 2011). Uncertainties arise due to reliance on the assumption that current species' ranges reflect their fundamental environmental requirements, which limits the model's ability to predict into novel climates (Sax *et al*., 2013). We here took a conservative approach of using clamping in our niche models (Phillips *et al*., 2006) to restrict predictions into novel (no-analog) climates, but future work to incorporate more mechanistic distribution models could reduce uncertainties (Kearney & Porter, 2009).

Although this study goes beyond a simple climate envelope approach to risk assessment due to climate change by incorporating realistic life history and dispersal dynamics, there are still some notable avenues whereby species' extinction risks may be impacted by climate change that are not addressed here. Pearson *et al.* (2014) modeled climate change as altering the amount and geographic configuration of habitat in the landscape gradually through time. The suitability values of the habitat patches were also impacted by the shifting bioclimate variables, which impacted the dynamics of the population by altering the carrying capacity. Thus, climate change in this study influenced vital rates through density dependence rather than through physiological tolerances to specific temperature or precipitation extremes (Pörtner *et al*., 2006; Deutsch *et al*., 2008). In addition, changes in temperature or precipitation regimes may affect species in other complex and sometimes unpredictable ways, such as by altering fire regimes (Keith *et al*., 2008; Fordham *et al*., 2012), causing habitat loss because of sea-level rise (Aiello-Lammens *et al*., 2011), reducing the availability of pollinator (Memmott *et al*., 2007), or prey species (Fordham *et al*., 2013), or by increasing predation (Harley, 2011), or disease (Pounds *et al*., 2006). Nor do the models used in this study address the possibility of genetic local adaptation. Many of these complex factors have already shown to be implicated in local extinctions (Cahill *et al*., 2013) and are likely to continue in the future. However, even if such factors may cause a faster decline for some species, it is not clear whether the warning period provided would be shorter. One reason is that some of the bias introduced by these factors may be countered by our conservative approach to dealing with novel climates (see above), which may result in underestimating the range of future environmental conditions that the species may be able to persist in. In any case, incorporating these dynamics into the forecast of extinction risk due to climate change is best addressed on a species-specific basis rather than through a multi-species approach such as this.

Because the effects of climate change are thought to be gradual, but persistent there is concern that species may not manifest the threatened indicators within the time frames used by the IUCN Red List. We found that IUCN Red List will likely provide several decades of warning time for most species. Thus, we conclude that although climate change brings many new conservation challenges, and therefore there is an urgent need to rethink conservation options for many species impacted by climate change, there is no apparent need to invent new systems to assess species vulnerability to climate change.

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Supporting Information

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

Appendix S1. Overview of Generic Life History Models.
Appendix S2. Calculation of Red List criteria based on simulation outputs.
Table S1. Simplified summary of the IUCN Red List Categories and Criteria.
Table S2. Predictor variables used to test whether warning times can be predicted from current information on life history and spatial traits.
Table S3. Percentage of time continuously listed as threatened (VU+; i.e., as VU, EN or CR) for ≤ the designated number of years (row labels) prior to extinction, on the basis of IUCN Red List criteria with 1, 5, and 10-year evaluation intervals (column labels).
Table S4. Percentage of time continuously listed as threatened (VU+), endangered or above (EN+), and Critically Endangered (CR) for ≤ the designated number of years (row labels) prior to extinction, on the basis of IUCN Red List criteria with a 10-year evaluation interval.
Table S5. Percentage of time continuously listed as threatened (VU+), endangered or above (EN+), and Critically Endangered (CR) for ≥ the designated number of years (row labels) for replicates that did not end in extinction, on the basis of IUCN Red List criteria with a 10-year evaluation interval.
Figure S1. Schematic illustrating IUCN Red List analysis as applied to a single model replicate. Height of bars indicates the category the replicate would be classified under that model year considering data available up to and including that year. The black line is the listing category, which takes into account the 5-year waiting rule for down-listing (this is the information used in calculating warning times). The dots at the top indicate the criteria determining the Red List classification. IUCN categories used in this analysis, in order of increasing extinction risk, are: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), and Extinct (EX).
Figure S2. Histogram of time continuously listed as threatened (VU+) prior to extinction for range-restricted North American reptiles and amphibians under climate change, on the joint basis of IUCN Red List criteria A&B, A&C, A&D, B&C, B&D, and C&D (using 10-year evaluation interval). The percentage of trajectories listed for <20 years is shown to the left of the dashed line. Black triangles indicate the median duration for which species were continuously listed prior to extinction. The shaded region is a simplified representation of the histogram of listing durations when all four IUCN Red List criteria are considered.
Figure S3. Importance values from random forest analysis of warning time as a function of predictor variables (see Table S2 for descriptions of the variables).