Red List criteria underestimate climate-related extinction risk of range-shifting species

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Abstract

Climate change causes global species redistribution and elevates extinction risk, making early identification of vulnerable species critical for timely conservation. The IUCN Red List provides guidelines for assessing climate-related extinction risk using species distribution models (SDMs) and spatially explicit population models (SEPMs). However, a systematic evaluation of these guidelines is currently missing. Using simulations of virtual species with diverse life-history traits and range dynamics, we found that SDMs consistently underestimated extinction risk for range-shifting species. This was due to a concave relationship between population size and habitat loss, which contradicts the linear assumption in the Red List guidelines. For range-contracting species, SDMs provided adequate warning times. Probabilistic extinction estimates from SEPMs provided delayed warning for all species, particularly for highly threatened ones. Our results reveal key limitations of current Red List guidelines under climate change. Based on our findings, we provide tentative recommendations for updating the IUCN Red List guidelines.

Keywords: IUCN Red List, extinction risk, species distribution models, climate change, virtual species, spatially explicit population models

Introduction

Climate change poses a major threat to biodiversity, affecting virtually all biological processes[1] and potentially elevating extinction risk for many species[2,3]. Species dynamically respond to climate change, for example by tracking suitable habitat[4], which has been projected to lead to substantial global redistribution of species[5]. To protect biodiversity before declines become irreversible, early identification of the most threatened species is essential. Conservation assessments should hence provide sufficient warning time, defined as the time between identification of a threatened species and its extinction without any interventions[6].

The IUCN Red List for Threatened Species (Red List hereafter) is the most widely used framework for assessing extinction risk and informing conservation and policy decisions[7,8]. It classifies species into one of three threatened categories (Vulnerable, Endangered, Critically endangered) based on five quantitative criteria (A-E) that are derived from the theory of extinction trajectories for single populations[7,9,10]. The five different criteria provide alternative ways of assessing a species in the Red List, with qualifying for a threatened category under one criterion being sufficient to classify species in the category. The assessment of the species is mostly based on population size and trends, as well as geographic range area[9]. Originally designed to identify species already in decline, the IUCN has since introduced guidelines for assessing future extinction risk under climate change. These recommend species distribution models (SDMs) to infer habitat loss, and spatially explicit population models (SEPMs) to infer population loss or estimate extinction probability[11,12].

Despite their growing use, the predictive performance of SDMs under climate change remains debated[13–15]. SDMs are correlative models that relate observed species occurrences to prevailing environmental conditions and use this species-environment relationship to predict the suitable habitat under future climatic scenarios[16]. However, SDMs omit key biological processes, such as dispersal limitations, which can lead to an overprediction of future range size[17,18]. Nevertheless, SDMs currently constitute the most pragmatic approach for projecting potential future climate impacts. The Red List guidelines suggest to use SDM-predicted changes in habitat suitability as a proxy for population size reduction under criterion A3[8(p.102)]. This approach assumes a linear relationship between population loss and SDM-predicted habitat loss, which is acknowledged in the Red List guidelines as a source of uncertainty[8(p.99)]. Beyond simply causing uncertainty, this assumption actually lacks empirical validation[19,20], and could be influenced by the non-uniform distribution of species in the

landscape[21], extinction debts[22], and extinction thresholds related to minimum viable population sizes[23].

SEPMs, in contrast, simulate demographic and dispersal processes over space and time, potentially offering more realistic predictions of species responses to climate change[24,25]. Yet, wider application of these models has been hampered by technical and data challenges[26,27] and they have thus been rarely used for assessing climate-related future extinction risk of species[28]. A key open question is whether SEPMs provide more accurate or timely extinction risk estimates than SDMs, particularly for species with different range dynamics under climate change. So far, only a single case study has compared these modelling approaches in the context of IUCN assessments[29] while a systematic evaluation of modelling approaches across varying life histories and range dynamics is missing. This gap prevents evidence-based improvements to current Red List guidelines.

In this study, we aim to test the Red List guidelines for assessing species threatened by climate change. Specifically, we test (i) whether the assumed linear relationship between habitat loss and population decline holds across species and range dynamics, and (ii) whether model-based assessments differ in their ability to identify extinction risk early enough for conservation action. Due to the lack of data regarding climate change-driven extinctions, we chose a simulation approach[30,31]. We generated virtual species with contrasting life-history and dispersal traits (niche position, niche breadth, growth rate and dispersal distance)[32] and used a spatially explicit modelling framework[33] to project population and range dynamics under climate change across three different artificial landscapes (Fig. 1). Finally, we compared the performance of SDMs and SEPMs for assessing extinction risk, focusing on their ability to provide timely warnings for species with varying life history traits and undergoing either range contraction or range shift.

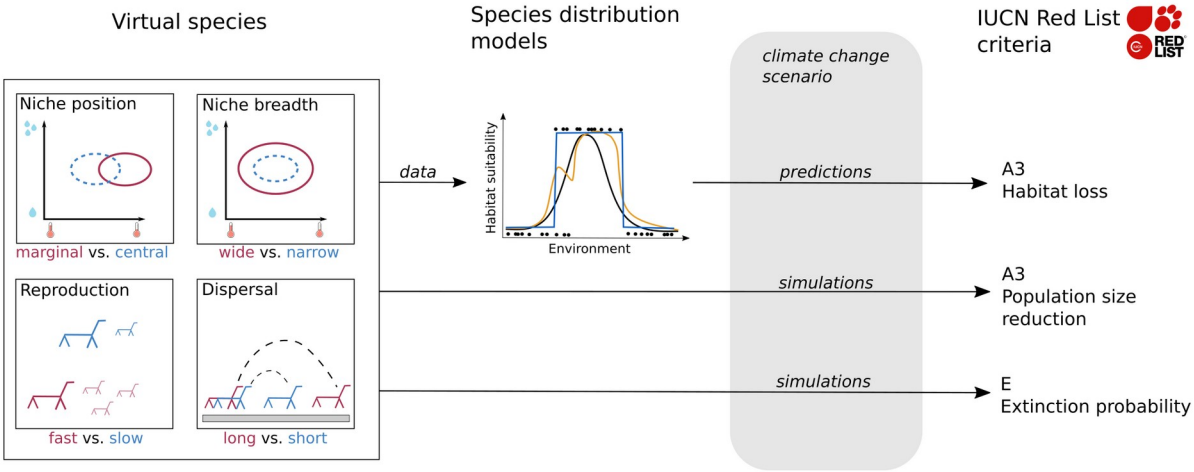

Figure 1: Conceptual figure of the modelling workflow. We simulated virtual species under climate change using a spatially explicit individual-based model. Species varied in four traits, which resulted in a variety of range distributions and dynamics. Before climate change set in, distribution data were sampled from the simulations as input to train correlative species distribution models (SDMs). SDMs were then used to predict habitat loss under climate change. Finally, Red List classifications under climate change were compared for SDM-derived habitat loss and simulation-derived population size reduction and extinction probability.

Results

Population dynamics and SDM performance

The considered trait combinations led to distinct differences in range and population dynamics. Notably, species with marginal niche position mainly occurred at the “northern” edge of the landscape and their ranges contracted towards that edge under climate change, while species with central niche position had centrally located ranges and exhibited range shifting before going extinct under climate change (Fig. 2). As could be expected, species with slow growth, narrow niches and short dispersal went extinct earlier than species with fast growth, wide niches and long dispersal (Fig. S1). The differences in temporal dynamics between species with different trait values were more pronounced for range-shifting species than for range-contracting species.

We sampled species occurrence from the simulations before climate change set in, and fitted three different SDM algorithms and an ensemble model. The SDM ensembles showed high pre-climate change predictive accuracy for all species and landscapes (AUC: 0.95 ± 0.02; TSS: 0.78 ± 0.06). The predictive performance was slightly lower for species with

central compared to marginal niches and for species with short compared to long dispersal (Fig. S2 + S3). Under climate change, SDMs correctly predicted range loss of range-contracting species, but they underestimated the range loss of dispersal-limited range-shifting species (Fig. 2). This pattern was consistent across replicate landscapes (Fig. S1).

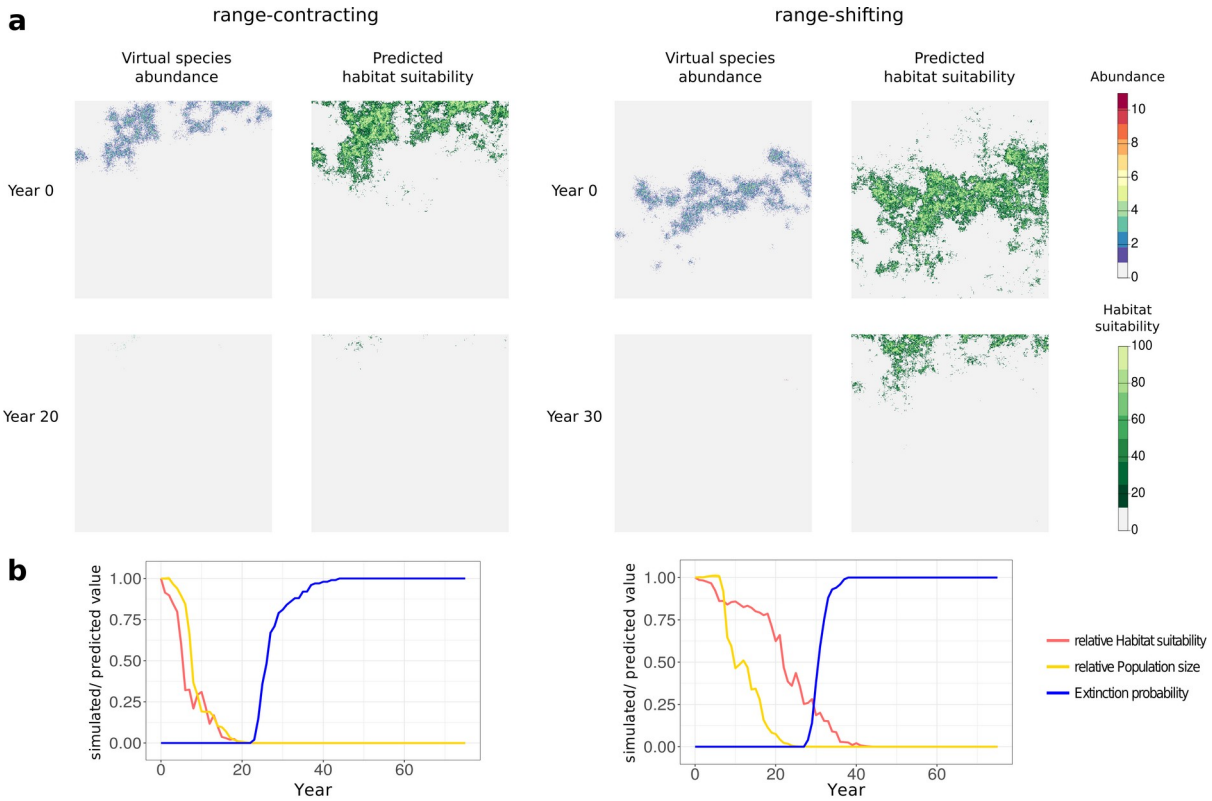

Figure 2: Distribution of virtual species and SDM-predicted habitat suitability for two example species. Top panels (a) show the maps of simulated „true“ species abundance and maps of habitat suitability predicted by SDMs for one replicate run under equilibrium conditions (year 0) and under climate change (year 20 / 30) in one example landscape. Bottom panels (b) show the corresponding time trajectories of the relative change in habitat suitability sums predicted from SDMs and in simulated population size, both averaged over ten selected replicate runs, as well as simulated extinction probability. Results are shown for two example species differing in their range dynamics (i.e., in marginal vs. central niche position). Both species have a narrow niche, slow growth rate, and short dispersal.

Population size - habitat loss relationship

For all species and replicate landscapes, the relationship between relative population size and SDM-derived habitat loss deviated from the linear assumption proposed in the Red List guidelines (Fig. 3). For range-contracting species, the relationship was convex with an initial

smaller rate of decline of population size in comparison to habitat loss. Population size steeply declined once habitat loss exceeded 50% across all replicate landscapes (Fig. S4 + S5). In contrast, range-shifting species showed a concave relationship with considerable declines in population size already happening at low rates of habitat loss, and with larger differences between the different replicate landscapes (Fig. 3 + S5). We only found comparatively small differences between the relationships for the other traits, with the variability between the different landscapes often being larger than among the different trait levels (Fig. S4 + S5). A Bayesian generalised mixed-model analysis of covariance showed that the population size - habitat loss relationship significantly differed across all traits, but the effect sizes for niche position (i.e. for range-shifting vs. range-contracting species) were considerably larger than for all other traits (Table S1).

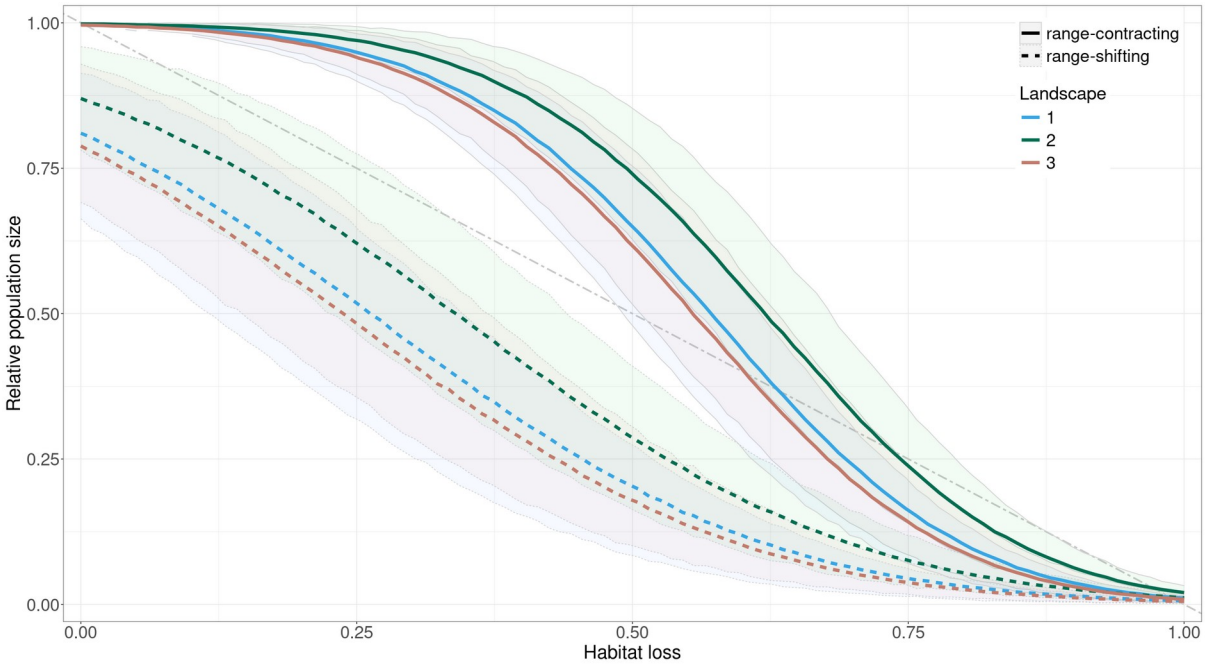

Figure 3: Population size - habitat loss relationship for the different range dynamics. Relative population size was obtained from the simulation (observed true data for virtual species) and habitat loss was predicted by the SDMs. The dot-dash grey line shows the assumption of a linear relationship between population size and habitat loss as proposed by the Red List guidelines. The relationships are displayed using an ordered beta regression model, in which landscape was included as a random effect. Lines indicate the mean model predictions and the transparent bands the 95% confidence interval. We only show results here for the trait niche position, resulting in range-contracting and range-shifting species, while results for the other traits are displayed in Fig. S4.

Red List classification

An important question is to which extent SDM-derived habitat loss under climate change can be used for assessment in the Red List. To answer this, we determined the time at which a species would be classified into the three threatened categories VU, EN and CR (Vulnerable, Endangered, and Critically endangered) of the Red List. Specifically, we compared assessments against criterion A3 when i) applied to the true (simulated) population size and ii) to the sum of habitat suitability derived from SDMs as recommended by the Red List guidelines[8(pp.101-111)]. Additionally, we compared these to the assessment under criterion E based on the quantitative extinction probability extracted from our simulation. Since all species went extinct during the 90 years of climate change, all of them qualified for all threatened categories throughout their life span. Again, we found the strongest differences between range-contracting and range-shifting species reflecting the differences in the population size - habitat loss relationship (Fig. 4 + Fig. S6).

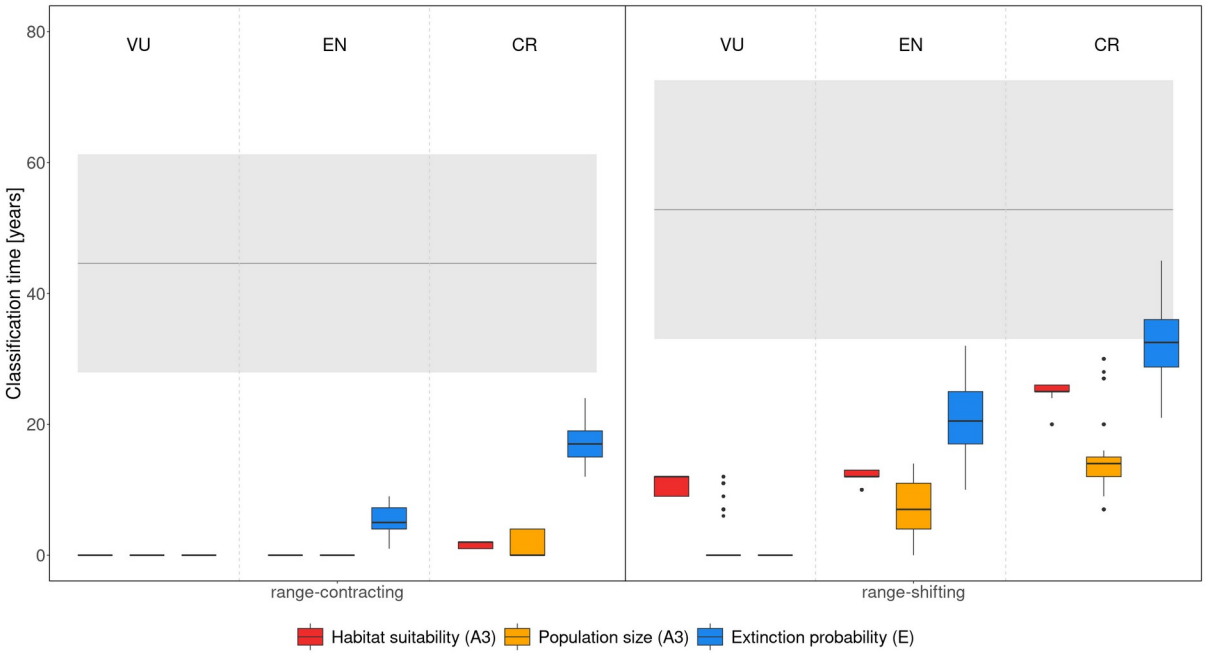

Figure 4: Classification times for listing species in different IUCN Red List threatened categories. Results are shown separately for range-contracting (left) vs. range-shifting species (right). Classification time refers to the years when species would be classified into the three different threatened categories (Vulnerable, Endangered, Critically endangered) using true population size or SDM-derived habitat loss against criterion A3, and simulated extinction probability against criterion E. Note that all species went extinct during the 90 years of climate change, thus qualifying for all threatened categories throughout their life span. The grey line shows the mean year of extinction across species and the grey bands the 95% confidence interval. Sampling size per box plot is n=240 (8 species x 3 replicate landscapes x 10 replicate runs).

For range-contracting species, the classification time did not differ between true population size and SDM-derived habitat loss. By contrast, for range-shifting species SDM-based risk classification was substantially later than for true population size because range loss was underestimated by the SDMs. This resulted in a very short warning time for range-shifting species when using SDM-based risk classification (Fig. 4 + Fig. S6). In a sensitivity analysis, we tested whether SDM-based predictions of range-shifting species could be improved by including simple dispersal assumptions but found no effect (Fig. S7). Other traits did not result in pronounced differences in classification times (Fig. S6). Interestingly, we found that for higher threatened categories (EN, CR) quantitative estimates of extinction probability and listing under criterion E resulted in considerably later classification time, and thus very short warning time, than information on population size and listing under criterion A3 (Fig. 4 + S6). The Red List guidelines indicate that criteria A-D are more precautionary than criterion E[8(p.17)]. Still, our results show that listing under these criteria can differ by up to 20 generations for our virtual species (Fig. 4).

Discussion

Based on idealised simulated species, we systematically evaluated the guidelines of the Red List for assessing species-level extinction risk under climate change. Our results revealed that the effectiveness of current Red List criteria strongly depend on expected range dynamics. SDM-based assessment provided sufficient warning time only for range-contracting species. For range-shifting species, warning time was substantially shorter mainly because of the highly non-linear relationship between population size and SDM-predicted habitat loss. Other life-history traits had comparatively little effect on warning times. Further, model-based assessment based on probabilistic extinction estimates led to considerably shorter warning times than when based on predicted population sizes.

The strong effect of range dynamics stems from fundamental differences in how population size relates to predicted habitat loss. For range-contracting species we found a convex relationship, meaning that species initially retained stable population sizes despite ongoing habitat loss while population sizes dropped very suddenly for higher rates of habitat loss. This is consistent with a non-uniform distribution of individuals in the landscape, where sparsely populated edge habitats are lost first during range-contraction[21,34]. Additionally, the curve is indicative of an extinction threshold, a critical amount of habitat beyond which population size declines steeply[23]. Crossing the threshold can initiate the extinction vortex, in which reinforcing processes such as inbreeding depression and genetic drift increase

population decline, ultimately leading to species extinction[35]. Even though we did not consider species genetics or stage-structured populations in our simulation, we still observed an extinction threshold. In our simulations, this threshold was around 50% habitat loss, but empirical evidence shows that these thresholds are highly case specific and species dependent[23]. A convex shape of population decline over time was already reported for several species[36], but research on the exact relationship between population size, habitat loss and extinction risk remains limited[20]. While the linear assumption in Red List guidelines is violated in these cases, our results suggest that SDM-based assessment still offer sufficient warning time for range-contracting species.

In contrast, range-shifting species exhibited a concave relationship indicating a strong underestimation of range loss by SDMs. This likely reflects the inability of some species to fully track shifting climates due to dispersal limitations[37,38] and time lags[39,40]. The underestimation resulted in shorter warning time for SDM-based assessment of species in comparison to true population size. Because effective conservation measures often require several decades of advance warning, SDM-based assessment may not leave enough warning time to protect range-shifting species from extinction[29]. Stronger dispersal ability is expected to improve climate tracking and the survival of range-shifting species under climate change[32,41]. Interestingly, we found no such influence of dispersal ability on the classification time of range-shifting species but found delayed warning for all range-shifting species. As inclusion of simple dispersal assumptions did not change these results, our study suggests that SDMs will not be adequate for assessing extinction risk in range-shifting species threatened with climate change. For these species, spatially explicit population models are likely more adequate.

Our results further revealed that Red Listing based on probabilistic extinction estimates under criterion E led to delayed classifications and insufficient warning times for all species, particularly those most at risk. This aligns with previous findings that criterion E often results in less precautionary extinction risk status in comparison to other criteria[42]. In our study, the short warning time resulted from steep, sigmoidal extinction risk curves, which led to rapid population collapse and abrupt extinction of species. Such curve shapes have been shown to realistically describe species' survival probabilities under changing environmental conditions[43,44]. In stochastic population models, sigmoidal extinction curves typically emerge when full parameter knowledge during the model building process is available[45]. With higher parameter uncertainty the extinction risk curves are expected to become more shallow[45], which consequently influences the classification time in the Red List. Interestingly, a previous study[29] reported that criterion A leaves less warning time in comparison to listing

against criterion E when using a coupled SDM-population model approach with a real species. It is thus unclear whether a higher parameter uncertainty in the model building process for criterion E might leave more warning time or may introduce additional biases. As a more robust approach for species threatened by climate change, especially those undergoing range shifts, we recommend estimating expected minimum abundance (EMA) from SEPMs. Our results suggest that assessing extinction risk based on these projections provides a more reliable basis for classification than relying on quantitative extinction probabilities alone.

Our simulations were idealised, with full knowledge of the true population and range dynamics, perfect data to fit SDMs, and simplified assumptions. In practice, missing data and sampling biases as well as environmental and demographic stochasticity could introduce additional uncertainties in the assessment process[45–47]. Here, we want to echo the Red List guidelines in stressing transparency regarding uncertainties in the assessment process to minimize their effect[8(pp.23-25)]. Additionally, simulating realistic climate change scenarios and more detailed species characteristics, such as stage-structured populations, stochastic movement dispersal and density-dependent traits could lead to more diverse responses of species influencing the assessment process. Furthermore, climate change is known to not only influence the distribution of species but also have diverse effects on species[48], which we did not consider in our study. Nevertheless, our results revealed that even under idealised conditions, current Red List criteria are highly sensitive to species range dynamics under climate change.

To improve assessment, we recommend including a screening step into model-based Red List assessments. In this initial screening, SDMs can serve to assess whether a species is likely to experience exclusive range contraction or to shift its range. For range-shifting species, we strongly recommend using spatially explicit population models and assess extinction risk based on expected minimum abundance, rather than extinction probabilities. While adjusting probability thresholds may improve assessments in some cases, further research is needed to define thresholds that offer both realism and sufficient warning time. For range-contracting species, SDMs may be appropriate to assess the extinction risk of species. Still, the assumption of a linear relationship between population size and habitat size should be treated with caution as our results show that sudden population reductions can cause delayed warning by SDMs. Furthermore, the known limitations of SDMs should be kept in mind[18] and the assessment based on SDMs should follow community standards[49,50] to avoid wrong classifications. To further guide the novelization of the Red List

under climate change, we recommend empirically testing our results for a variety of species for which adequate range loss and population loss data are available.

Methods

We used the RangeShifter framework[33,51,52] to simulate population dynamics of virtual species under equilibrium conditions and under climate change in three different artificial landscapes. Species differed in four traits: niche position (central vs. marginal), niche width (narrow vs. wide), growth rate (slow vs. fast) and dispersal (short vs. long), leading to 16 (2^4) different species to cover all trait combinations. Niches were defined by two environmental variables that could be interpreted as temperature and precipitation. Species occurrence data and climate data were extracted from the simulation at equilibrium before climate change set in. Based on these data we fitted species distribution models (SDMs) and predicted habitat suitability under climate change. From the simulations, we observed population size across the entire time frame of 90 years of climate change and estimated extinction probability per year. We ran simulations for 90 years to ensure the extinction of all species. From the SDMs, we derived the predicted habitat suitability values for each year and compared these to true population size. Last, we applied the Red List criteria to each of these three metrics to classify species into different threatened categories.

Virtual species

In our simulation approach, we first modelled the population dynamics of the 16 virtual species in the three artificial landscapes under climate change. The artificial landscape consisted of two environmental variables (temperature and precipitation) with a spatial extent of 512 x 512 cells at 1000 m resolution. The environmental layers were generated using the package “NLMR”[53]. Temperature was represented by a latitudinal gradient with spatially auto-correlated noise. For this the arithmetic mean of a landscape with a linear gradient and a landscape built with midpoint displacement with a Hurst exponent of 0.96 was taken. To create spatially auto-correlated precipitation patterns, we generated a landscape using midpoint displacement with a Hurst exponent of 0.75. Landscape values ranged between 0 and 1. We derived three replicate landscapes using the same settings (Fig. S8).

The virtual species niche was modelled using the package “virtualspecies”[54]. First, Gaussian-shaped response curves for both environmental variables were simulated. The mean of the response curve for temperature was adapted to the respective niche position (marginal: 0.27, central: 0.5), the mean of the precipitation response curve was set to 0.5. To model different niche breadths, the standard deviation of both response curves was adapted

based on the respective niche breadth (narrow: 0.045, wide: 0.055). We then used the product of both response curves to map the virtual species niche in the artificial landscapes.

To simulate climate change, temperature was linearly increased over 90 years, while precipitation remained static. We selected a time frame of 90 years to model a continuous increase of temperature that would result in no suitable habitat being left at the end of climate change, ensuring the extinction of all species. To the linear temperature increase we also included a temporal autocorrelated noise. For this we used an ARIMA model[55] of the order 0,0,1 and added it to the linear model using the following equations:

$$\eta_t = \theta * \varepsilon_{t-1} + \varepsilon_t$$

$$y_t = \alpha + \beta * t + \eta_t$$

Where, η_t represents the time series obtained from the ARIMA model with θ set to 0.5 and ε representing the residuals at the respective time points. This time series was then added to a linear model with α set to 0.5, β set to 0.6, and t representing the respective year. The time series was rescaled between 0 and 0.9 and added to the temperature value of every cell in the artificial landscape. Values that were larger than 1 were reduced to 1 to stay within the range of 0 to 1.

To model the population dynamics of the virtual species, we used the spatially explicit and individual-based modelling platform RangeShifter[33,51], operated via the package "RangeShiftR"[52]. We implemented a cell-based model using the previously created maps of the virtual species niche with the resolution set to 1000 m and the carrying capacity set to 0.05 ind/ha. We modelled the virtual species as an asexual species with non-overlapping generations meaning that each individual only lived for one year. The competition coefficient was set to 1 (i.e. no over- or undercompensation) and the value for the maximum growth rate was adapted according to the growth rate (slow: 3, fast: 5). After reproduction the adults died and the offspring dispersed. Dispersal is modelled explicitly in three phases in RangeShifter: emigration, transfer, and settlement. The emigration probability for each individual was set to 0.4 and was density-independent. The transfer was modelled using a negative exponential dispersal kernel. For short-distance dispersal, the mean dispersal distance was set to 5000 m. For long-distance dispersal, a double exponential dispersal kernel was used to include rare long-distance dispersal events. The double kernel is composed of two negative exponential kernels with different means and probabilities of occurrence. The first (shorter) kernel occurred with a probability of 95% and had a mean dispersal distance of 15 000 m, the second (longer) kernel occurred with a probability of 5% and had a mean dispersal distance of 250 000 m. If the arrival point of an individual went beyond the boundaries of the landscape or within the natal cell the dispersal process was repeated. The individual settled in the arrival cell if the cell contained suitable habitat. If the

arrival cell was not suitable, the individual was displaced to one of the eight neighbouring cells, if one of them was suitable, or else died. If a cell became unsuitable due to climate change, all individuals inhabiting that cell died immediately.

The simulation was initialised using the map with equilibrium climatic conditions and individuals were distributed in all suitable cells at half-carrying capacity. The simulation ran for 101 spin-up years to remove any initialisation effect. After the spin-up period, the landscape was changed yearly to represent the virtual species niche shifting northwards in response to climate change. In the following, year 100 will be referred to as year 0 and year 1-90 represent the years under climate change. Each of the 16 species was simulated with 100 replicate runs for each of the three artificial landscapes.

From the output of each simulation, we obtained the population size of the species for each year and replicate run. To calculate the extinction probability for each year, we divided the number of replicate runs without a viable population of that year by the total number of replicate runs.

Species distribution models

At the end of the spin-up period, before climate change set in, we extracted species presence and absence information as well as climate variables from the simulation to fit SDMs. To account for variation between the replicate runs, we randomly selected ten replicate runs from the simulation and fitted separate SDMs to each. This resulted in 480 SDMs (16 species x 3 landscape replicates x 10 replicate runs). For the species data we assumed perfect sampling with no error in detection. Data points were partially thinned by selecting every second cell to avoid spatial autocorrelation using the package “dismo”[56].

Based on the recommendations of the Red List[8(p.108)] we used three distinct modelling algorithms (Generalised Linear Model (GLM), Random Forest and MaxEnt) and further calculated an ensemble model based on the arithmetic mean. For the GLM, linear and quadratic predictors were used with a binomial error distribution. For Random Forest, we fitted 1000 trees with a minimum terminal node size of 20 to fit comparably smooth response surfaces. In the MaxEnt algorithm, we used the feature classes linear, quadratic and hinge. The probability of occurrence was predicted for each of the 90 years under climate change using the ensemble model. The predictive performance of the model algorithms and the ensemble model was evaluated using the 99 replicate runs that were not used for fitting the SDM. For the performance measures we selected the AUC (area under the ROC curve) and TSS (true skill statistics)[16]. The calculated performance measures were averaged over all 99 replicate runs using the arithmetic mean. For the calibration and evaluation of the SDMs we

used the following packages: “randomForest”[57], “maxnet”[58], “gbm”[59], “PresenceAbsence”[60] and “lhs”[61].

For testing the effect of dispersal assumptions in SDMs on the assessment in the Red List, we first binarized the predictions of each species and landscape replicate using the maxTSS threshold[62]. Around the known presences we created a buffer with the size of the estimated dispersal distance of an individual in the respective time frame and set the predicted habitat suitability outside the buffer to 0 following the recommendation of the Red List guidelines[8(p.110)]. Buffer sizes were determined by the empirical dispersal distances observed from the RangeShifter simulations. For this, we extracted the dispersal distances of all emigrated individuals for year 0 from the simulations, and calculated the arithmetic mean of dispersal distance.

Red List classification

To assess Red Listing of species threatened by climate, we compared the assessment of the species against two different Red List criteria using three metrics. For the criterion A3, we used true population size observed from the RangeShifter simulations and the sum of the SDM-derived habitat suitability values. For the criterion E, we used the extinction probability for every species obtained from the RangeShifter simulations. For the population size, we only used the population size from the ten replicate runs that were selected for fitting the SDMs. To calculate the sum of the habitat suitability values from the SDM predictions we followed the recommendations from the Red List guidelines[8(p.99)]. We first removed cells with values below a certain threshold value, for which we used the maxTSS[62]. We then summed up the predicted habitat suitability of the remaining cells and for every year. For the classification into the different categories of the Red List, different thresholds and time frames apply for the different criteria (see Tab. 1).

Table 1: Thresholds and time frames used to classify species into threatened categories, based on the Red List Criteria[8]

Criterion	Red List Threatened Categories		
	Critically Endangered	Endangered	Vulnerable
A3: future population size reduction / future reduction of sum of SDM-derived habitat suitability	>= 80% in 10 years	>= 50% in 10 years	>= 30% in 10 years
E: probability of extinction	>= 50% in 10 years	>= 20% in 20 years	>= 10% in 100 years

For each species, we determined the time of classification into the three different threatened categories using all three metrics (i.e., population size, habitat suitability and extinction probability). For this, we used a moving window approach, testing for every year if the species would fulfil the Red List criteria in the following years (see Table 1 for considered time spans). This means that if a species was predicted to reach a habitat loss of 30% between year 0 and year 10, the year 0 would be marked as classification time point for listing the species as “Vulnerable” under criterion A3 when using the metric sum of SDM-derived habitat suitability values. If the species was predicted to reach a habitat loss of 30% between year 25 and 35, then the year 25 would be marked as classification time for the “Vulnerable” category. Thereby, the loss of suitable habitat and the population loss was always calculated relative to the starting year of the moving window. As all species continuously experienced population and habitat loss under climate change until their extinction, each species qualified for all threatened categories throughout their life span.

In a sensitivity analysis, the assessment of classification times based on SDM-derived habitat suitability values was repeated for more realistic dispersal assumptions using the buffer approach described earlier.

Statistical analysis

To investigate the relationship between population size and habitat loss, we fitted a generalised mixed-model ANCOVA using an ordered beta regression implemented by the package “ordbetareg”[63,64]. This package is a front-end to the package “brms”[65]. We selected

an ordered beta regression since our response variable (simulated “true” populated size) was continuous with a zero and one inflation. As predictors, we considered habitat loss as continuous variable, the four traits (niche position, niche width, dispersal distance and growth rate) as categorical variable with two levels each, and their pairwise interactions with habitat loss. We further controlled for the landscapes by including them as random intercepts. The best model was selected based on the difference in expected log predictive density. Posterior distributions were estimated using Markov chain Monte Carlo (MCMC) sampling with 4 chains and a delta value of 0.95. Each chain had a length of 6000 iterations, with the first 2000 being used as a warm-up. For the prior, the default was selected.

For the study R 4.2.2[66] was used. In addition to the already mentioned packages the following were used for data preparation and visualization: “scales”[67], “dplyr”[68], “ggplot2”[69], “terra”[70], “gridExtra”[71], “tibble”[72], “RColorBrewer”[73], “doParallel”[74], “foreach”[75], “data.table”[76].

Code availability:

The codes for this study are available at https://doi.org/10.5281/zenodo.16909451

Author Contributions:

RK and DZ conceptualised the study. RK ran all analyses and led the writing. All authors contributed to revising the text.

Competing Interest Statement:

The authors declare that they have no conflict of interest to disclose.

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