

RESEARCH ARTICLE OPEN ACCESS

Projecting Untruncated Climate Change Effects on Species' Climate Suitability: Insights From an Alpine Country

Antoine Adde^{1,2}  | Nathan Külling³  | Pierre-Louis Rey²  | Fabian Fopp^{4,5}  | Philipp Brun⁴  | Olivier Broennimann^{2,6}  | Anthony Lehmann³  | Blaise Petitpierre⁷  | Niklaus E. Zimmermann⁴  | Loïc Pellissier^{4,5}  | Florian Altermatt^{1,8}  | Antoine Guisan^{2,6} 

¹Department of Aquatic Ecology, Eawag, Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland | ²Institute of Earth Surface Dynamics, Faculty of Geosciences and Environment, University of Lausanne, Lausanne, Switzerland | ³EnviroSPACE, Institute for Environmental Sciences, University of Geneva, Geneva, Switzerland | ⁴Land Change Science Research Unit, Swiss Federal Institute for Forest, Snow and Landscape Research, WSL, Birmensdorf, Switzerland | ⁵Ecosystems Landscape Evolution, Institute for Terrestrial Ecosystems, Department of Environmental System Sciences, ETH Zurich, Zurich, Switzerland | ⁶Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland | ⁷InfoFlora, Chambésy-Geneva, Switzerland | ⁸Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zürich, Switzerland

Correspondence: Antoine Adde (antoine.adde@eawag.ch)

Received: 30 January 2024 | **Accepted:** 13 August 2024

Funding: This work was supported by the Action Plan of the Swiss Biodiversity Strategy, with financing provided by the Federal Office for the Environment (FOEN) for the ValPar.CH project. This study is part of the SPEED2ZERO Joint Initiative, which received support from the ETH-Board under the Joint Initiatives scheme.

Keywords: biodiversity conservation | climate change scenarios | climate suitability | future projections | niche truncation | species distribution models

ABSTRACT

Climate projections for continental Europe indicate drier summers, increased annual precipitation, and less snowy winters, which are expected to cause shifts in species' distributions. Yet, most regions/countries currently lack comprehensive climate-driven biodiversity projections across taxonomic groups, challenging effective conservation efforts. To address this gap, our study evaluated the potential effects of climate change on the biodiversity of an alpine country of Europe, Switzerland. We used a state-of-the-art species distribution modeling approach and species occurrence data that covered the climatic conditions encountered across the full species' ranges to help limiting niche truncation. We quantified the relationship between baseline climate and the spatial distribution of 7291 species from 12 main taxonomic groups and projected future climate suitability for three 30-year periods and two greenhouse gas concentration scenarios (RCP4.5 and 8.5). Our results indicated important effects of projected climate changes on species' climate suitability, with responses varying by the taxonomic and conservation status group. The percentage of species facing major changes in climate suitability was higher under RCP8.5 (68%) compared to RCP4.5 (66%). By the end of the century, decreases in climate suitability were projected for 3000 species under RCP8.5 and 1758 species under RCP4.5. The most affected groups under RCP8.5 were molluscs, algae, and amphibians, while it was molluscs, birds, and vascular plants under RCP4.5. Spatially, by 2070–2099, we projected an overall decrease in climate suitability for 39% of the cells in the study area under RCP8.5 and 10% under RCP4.5, while projecting an increase for 50% of the cells under RCP8.5 and 73% under RCP4.5. The most consistent geographical shifts were upward, southward, and eastward. We found that the coverage of high climate suitability cells by protected areas was expected to increase. Our models and maps provide guidance for spatial conservation planning by pointing out future climate-suitable areas for biodiversity.

Florian Altermatt and Antoine Guisan should be considered joint senior authors.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Author(s). *Global Change Biology* published by John Wiley & Sons Ltd.

1 | Introduction

Climate change effects on ecosystems have been documented across biomes and are poised to further escalate over the course of the 21st century (IPCC 2023). Although current biodiversity loss is primarily attributed to land and water resource exploitation, it is expected that climatic changes will surpass them as the dominant drivers in the coming years (Maxwell et al. 2016; IPBES 2019; Jaureguiberry et al. 2022). Therefore, it is imperative to formulate evidence-based biodiversity conservation strategies that are robust under forthcoming climate conditions (Lawler, Watson, and Game 2015; IPBES 2019; Chauvier-Mendes et al. 2024). Developing such strategies involves various challenges, including uncertainties in climate change projections, a dynamic and non-linear biodiversity response, and socio-economic trade-offs (Knutti and Sedlacek 2013; Santangeli et al. 2016; Pecl et al. 2017), but it is indispensable for ensuring the efficiency of resulting conservation initiatives (Groves et al. 2012; Reside, Butt, and Adams 2017; Arneith et al. 2020). To maximize their utility, biodiversity assessments should be conducted at spatial scales aligned with the policy units, typically countries (Jackson et al. 2016; Vihervaara et al. 2017; Carroll et al. 2023; Külling et al. 2024). However, there is a limited number of studies comprehensively addressing the range of fauna and flora within target countries, and the research on the effects of climate change on biodiversity is marked by taxonomic bias (Lenoir and Svenning 2015; Feeley, Stroud, and Perez 2017; Lenoir et al. 2020).

Species distribution models (SDMs) that incorporate climate data offer valuable tools for predicting and mapping both current and prospective species distributions within the context of climate change scenarios (Elith and Leathwick 2009; Austin and Van Niel 2011; Araujo and Peterson 2012). SDMs projections operate under the assumption that existing species distributions reflect their environmental preferences, which are expected to persist into the future (Franklin 2010; Peterson et al. 2011; Guisan, Thuiller, and Zimmermann 2017). Despite their limited ability to account for mechanisms such as evolutionary processes and their rare consideration of impacts from other changing environmental variables like land use and cover, climate-driven SDMs are useful for providing a general assessment of how species may respond to future climate (Araujo and Peterson 2012; Guisan et al. 2013; Urban et al. 2016; Araujo et al. 2019). Prior research using SDMs to project the effects of climate change on biodiversity across large geographical scales has consistently unveiled coherent trends across taxonomic groups. Predominantly, these trends manifest as range dislocation, losses, and contractions, with a particular vulnerability at mountain tops (Midgley et al. 2002; Thomas et al. 2004; Thuiller et al. 2005; Fitzpatrick et al. 2008; Pompe et al. 2008; Cheung et al. 2009; Pereira, Navarro, and Martins 2012; Telwala et al. 2013; Newbold 2018; Guisan et al. 2019; Herrera-R et al. 2020). Moreover, results from comparable studies have also shown that anticipated temperature increases are projected to speed up the occurrence of biological invasions (Bellard et al. 2013; Petitpierre et al. 2016; Shrestha and Shrestha 2019). Yet it is unclear how these large-scale trends apply to smaller, diverse, and topographically complex regions like alpine countries, recognized as

biodiversity hotspots (Antonelli et al. 2018; Hoorn, Perrigo, and Antonelli 2018; Rahbek et al. 2019).

To accurately model species responses to climate and project potential future distributions, the modeling data should ideally cover the full spectrum of climate conditions in which the species occurs globally (Sanchez-Fernandez, Lobo, and Hernandez-Manrique 2011; Titeux et al. 2017; Scherrer et al. 2021). When restricted geographic data are used for SDM fitting, spatial niche truncation may arise, leading to potentially biased estimates of the species-climate relationship, resulting in inaccurate predictions, particularly when the model is applied to different spatiotemporal contexts (Barbet-Massin, Thuiller, and Jiguet 2010; Gallien et al. 2012; Chevalier et al. 2021, 2022). This concern holds particular relevance for local- and regional-scale SDM applications, because species often inhabit a broader range of bioclimatic conditions than those represented within the study area. Recent research has shed light on methods to address spatial niche truncation problems in SDM contexts (Fournier et al. 2017; Mateo et al. 2019; Bellamy et al. 2020; Goicolea et al. 2024), and practical solutions have emerged to handle it. In particular, the Nested-Species Distribution Modeling (N-SDM) software (Adde, Rey, Brun, et al. 2023), an end-to-end SDM platform designed for high-performance computing cluster, has been developed to enable the integration of two models fitted with global-level (encompassing the full species range) and regional-level (within the study area extent) data.

Switzerland is a highly diverse, topographically structured, alpine country directly facing the consequences of climate change, making it an ideal study area for climate-biodiversity research in mountainous regions. In Switzerland, the 2013–2022 decade recorded an average temperature 2.5°C higher than the late pre-industrial 1871–1900 period, and projections indicate that if global greenhouse gas concentrations continue to rise, Switzerland can expect drier summers, increased annual precipitation, more tropical days, and less snowy winters (Bader et al. 2023). One of the primary consequences of these changes for Swiss biodiversity are shifts in species' distributions (Pearman, Guisan, and Zimmermann 2011; Vittoz et al. 2013; Vitasse et al. 2021; FOEN 2023). Tracking these shifts may become increasingly challenging for several species whose habitats are currently fragmented across intensively used landscapes, with ecological discontinuities (FOEN 2023). Especially, cold-adapted species are prone to be negatively affected, putting many alpine species at risk (Engler et al. 2011; Dullinger et al. 2012; Theodoridis et al. 2018). However, these changes may also be advantageous for warm-tolerant species, with opportunities to expand their ranges to higher elevations (Engler et al. 2009; Vitasse et al. 2021; Gebert et al. 2022). For instance, Alpine plant diversity has seen an increase due to the upward movement of several species (Roth, Plattner, and Amrhein 2014), the average altitudinal distribution of breeding birds in Switzerland rose by 24m between 1990 and 2010 (Knaus et al. 2018), and many aquatic insect species are also extending their range to higher elevation (Gebert et al. 2022).

Switzerland currently lacks comprehensive climate-driven biodiversity projections that account for niche truncation, posing a significant challenge for guiding effective conservation

efforts. Our study addresses this gap by evaluating the potential impact of climate change on all possible Swiss species across many taxonomic groups for which sufficient data were available, using a climate envelope modeling approach and species occurrence data that covered the climatic conditions encountered across species' ranges. This comprehensive evaluation, along with the consideration of niche truncation, constitutes a significant advancement in the field of conservation biology. First, we quantified the relationship between the baseline climate (1981–2010) and the spatial distribution of 7291 species, covering almost all taxonomic groups. Second, we projected future climate suitability for three 30-year future periods (2020–2049, 2045–2074, and 2070–2099) using climate projections based on two scenarios of future greenhouse gas concentrations. Finally, we evaluated percentage changes in projected climate-suitable areas, examined geographical shifts, and presented illustrative maps for main taxonomic and Red List groups.

2 | Materials and Methods

2.1 | Study Area

Our core study area was Switzerland (projection extent), with a total area of $\approx 41,000 \text{ km}^2$. To encompass as much as possible of the climatic conditions encountered throughout the species' ranges, we used an extended bounding box covering the European continent and a portion of Northern Africa (ranging from 32.60°N to 71.70°N , and from 28.56°W to 40.21°E) for extracting species and climate data (calibration extent). The projection and calibration extents were the same for all species, chosen as a tradeoff to accommodate most climatic niches while managing computational costs, which increase with the size of the study area. Furthermore, including data from distant continents could introduce more uncertainty due to data consistency issues and taxonomic divergences. Additionally, this extent balanced spatial scale and model accuracy, avoiding niche truncation for widely distributed species while maintaining accuracy for those confined to specific locations.

2.2 | Species Data

Two sets of species occurrence records for inside and outside of Switzerland were used. For Switzerland, validated occurrence records for 21,290 species aggregated at 25-m resolution for the 1980–2021 period were provided by the Swiss Species Information Center InfoSpecies (www.infospecies.ch) on August 23, 2021 (<https://doi.org/10.15468/htjezm>). To avoid modeling issues related to low sample size (e.g., model convergence, number of covariates, etc.) only species with a minimum of 50 remaining records were retained for the analyses, for a total of 7291 species (Appendix S1). Species were classified into 12 main taxonomic groups: algae ($n = 10$), amphibians ($n = 18$), arthropods (all but Ephemeroptera, Plecoptera, Trichoptera, Odonata; EPTO) ($n = 1888$), aquatic arthropods (EPTO) ($n = 258$), birds ($n = 180$), ferns and mosses ($n = 553$), fishes ($n = 34$; note that these are less than one-third of all fish species in Switzerland, with cold-adapted and often endemic lake species being largely not included),

fungi ($n = 1679$), mammals ($n = 73$), molluscs ($n = 162$), reptiles ($n = 15$), and vascular plants ($n = 2421$). When available, International Union for Conservation of Nature (IUCN) Red List status for each species in Switzerland (Klaus, Cordillot, and Künzle 2023) were provided by InfoSpecies, resulting in seven groups: critically endangered (CR) ($n = 49$), endangered (EN) ($n = 226$), vulnerable (VU) ($n = 668$), near threatened (NT) ($n = 688$), least concern (LC) ($n = 3998$), data deficient (DD) ($n = 45$), and not evaluated (NE) ($n = 1617$). Occurrence records for outside of Switzerland for all matching species and the same 1980–2021 period were obtained from the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>) on January 11, 2023 (<https://doi.org/10.15468/dl.fktyas>). The extracted GBIF records were tested and filtered for coordinate validity, which included identifying equal latitude/longitude values, rounded coordinates, and zero values (Zizka et al. 2019). Additionally, we filtered for spatial and temporal outliers by extracting occurrences only within the area defined by a shapefile covering the target European domain and specifying the same period as the Swiss data (1980–2021). Further information on the processing of GBIF data and matching with InfoSpecies species names is provided in Appendix S2. Sampling bias correction was done by applying a spatial filter approach consisting of thinning the two sets of occurrence records. Spatial thinning of species occurrences has been proven useful for reducing sampling biases by mitigating observation clusters (Boria et al. 2014; Aiello-Lammens et al. 2015; Steen et al. 2020). We used level-specific minimal distances between two observations for spatial thinning. Inside Switzerland, we used a distance of 500 m, while outside Switzerland, the distance was set at 1 km. Ideally, these values should be determined by the species' biology, the environmental heterogeneity of the area, and previous research on the study system, including knowledge on sampling patterns (Fourcade et al. 2014; Aiello-Lammens et al. 2015; Lamboley and Fourcade 2024). However, such comprehensive information was unavailable for the full spectrum of species considered. Here we opted for a tradeoff, considering the spatial resolution of the covariate data (i.e., 25 m inside Switzerland and 30 arcseconds outside; see section 2.3 for details) and to be conservative enough (i.e., rather large than small) to allow for efficient spatial disaggregation. For each species and occurrence set, 10,000 background absences were randomly generated across the target areas to contrast the observations.

2.3 | Climate Data

2.3.1 | Baseline Climate (1981–2010)

We retrieved data for the 19 WorldClim bioclimatic variables (<https://www.worldclim.org/data/bioclim.html>) over the baseline period 1981–2010. This period was the effective standard 30-year normal for the current period at the time of our analysis, as defined by the World Meteorological Organization (WMO 2017). Normal periods are updated every 10 years, ensuring that they accurately represent the current climate of a region despite ongoing climate change. The WorldClim bioclimatic variables were specifically created to provide more biologically meaningful indicators than raw temperature and precipitation values and are widely used in ecological and

SDM studies (Hijmans et al. 2005; Booth et al. 2014; Fick and Hijmans 2017). As for species data, we used specific climate data sources for inside and outside of Switzerland to benefit from best-available products. For Switzerland, bioclimatic variables were extracted from the CHclim25 dataset (10.5281/zenodo.7871115) which gathers newly available Swiss-wide climate layers downscaled at 25-m resolution. For outside of Switzerland, we used 30-arcsecond CHELSA layers (Karger et al. 2017). An analysis aimed at comparing the CHclim25 and CHELSA data with independent weather station data revealed that CHclim25 was accurate at both low and high elevations, while CHELSA data could be less accurate at high elevation, resulting in potentially higher differences between the two datasets in these areas. Bioclimatic variable values were extracted individually from the CHclim25 and CHELSA databases at the location of InfoSpecies and GBIF species occurrence records, respectively, and then pooled together to form a unique model matrix.

2.3.2 | Climate Projections (2020–2099)

Swiss-wide projections for the 19 bioclimatic variables averaged for four coupled global and regional climate models (GCM-RCM) (CLMCOM-CCLM4/HADGEM, DMI-HIRHAM/ECEARTH, MPICSC-REMO2/MPIESM, and SMHI-RCA/IPSL) and three future intervals (2020–2049, 2045–2074, and 2070–2099) were retrieved from the CHclim25 dataset (10.5281/zenodo.7871115). These four GCM-RCM were the only ones available through CHclim25, as they were the sole models provided by the CH2018 initiative EURO-CORDEX simulation (Fischer et al. 2022), use as input for CHclim25, at a finer resolution of 0.11° (EUR-11, approximately 12.5 km), compared to others available at a resolution of approximately 50 km. The 12.5 km resolution was the only one relevant for achieving the 25-m downscaling target of CHclim25. To reduce the computational cost of the study, predictions from GCM-RCM were averaged for each period and scenario. We included two greenhouse gas concentration trajectories or representative concentration pathways (RCPs) (van Vuuren et al. 2011), RCP4.5 (“Low Carbon”), and RCP8.5 (“High Carbon”). In RCP4.5, moderate emissions peak around the 2040s and then decline. RCP8.5 assumes that emissions will continue to increase throughout the 21st century. No climate projection data were retrieved for outside of Switzerland (i.e., biodiversity projections were only computed for Switzerland).

2.4 | Climate Suitability Models

2.4.1 | N-SDM Software

To reveal changes in biodiversity patterns in Switzerland across time and climate change scenarios, we quantified the response of each species to baseline climate conditions and project potential changes in their climate-suitable areas. To do so, we used the newly available N-SDM software (Adde, Rey, Brun, et al. 2023). In brief, N-SDM is an end-to-end SDM platform built around a spatially-nested framework intended at facilitating the combination of a global model quantifying the species response to the bioclimatic conditions that can

be found across its full distributional range, with a regional model fitted with fine-scale habitat covariates. In this study, since we only targeted bioclimatic conditions (i.e., global level), N-SDM was run in a single-level mode (i.e., no local-level). The N-SDM “settings.csv” file used to run N-SDM and the ODMAP reporting protocol (Zurell et al. 2020) can be found in Appendix S3 and S4, respectively.

2.4.2 | Covariate Selection

The covsel embedded covariate selection procedure (Adde, Rey, Fopp, et al. 2023) included in N-SDM was used to select the best subset of the 19 bioclimatic variables for modeling each species. In short, covsel is a two-step selection procedure that combines a collinearity-filtering algorithm with model-specific embedded regularization techniques. We used covsel default values with a Pearson correlation coefficient ($|r|$) threshold for identifying collinear variable pairs $\text{corcut} = 0.7$, a target number of variables selected as the final modeling set $n_{\text{cov}} = \text{ceiling}(\log_2(\text{number of occurrences}))$, and $n_{\text{covmax}} = 12$. Covariate selection results were summarized by reporting the selection frequency of the candidate variables.

2.4.3 | Model Fitting and Selection

The five modeling algorithms available in N-SDM—Generalized Linear Model (GLM) (McCullagh and Nelder 1989), Generalized Additive Model (GAM) (Hastie 2017), Maxnet (MAX) (Phillips et al. 2017), Random Forest (RF) (Breiman 2001), and light gradient boosted machine (GBM) (Ke et al. 2017) – were fitted using their default N-SDM values for hyperparameter tuning. To account for class imbalance, background pseudo-absences and occurrences were weighted equally in the models. Model accuracy was evaluated using a split-sample approach repeated 100 times with 30% of the data kept for validation. For each model, the best combination of hyperparameters was identified using the average “Score” of three evaluation metrics including the area under the curve’ (AUC’) (or Somers’ D , such as $\text{AUC}' = \text{AUC} \times 2 - 1$) (Somers 1962), the maximized True Skill Statistic (maxTSS), and the Continuous Boyce Index (CBI) (Hirzel et al. 2006). We graphically summarized the cross-validated accuracy of the selected models using boxplots. In addition, we reported the individual importance of the climate variables in average for the five modeling algorithms.

2.4.4 | Spatial Projections

For each species, climate suitability values (ranging from 0 to 100) were projected for the baseline period and three future intervals \times two RCPs. Results from the five modeling algorithms were individually mapped over a 25-m resolution grid of 64,007,390 cells covering Switzerland and ensembled together by averaging the five maps. To facilitate between species comparisons, we computed binarized version of the projection maps (suitable or unsuitable cell) by using species-specific thresholds maximizing the TSS value (maxTSS) of the baseline models.

2.5 | Climate Suitability Analyses

2.5.1 | Projected Spatial Changes

To facilitate the interpretation of projected species distributions, we started by mapping average projected changes from baseline for maximum temperature and total precipitation values for the two RCPs and three future intervals. In addition, to further assess the reliability of our projections, we performed a mobility-oriented parity (MOP) analysis on the 19 bioclimatic covariates (sensu Owens et al. 2013), enabling us to assess similarity between current climate conditions (calibration extent) and future conditions (projection extent).

Then, to illustrate projected spatial changes in climate suitability for each taxonomic and red list group, we mapped the average and standard deviation (SD) of the differences between baseline and future periods. To assess whether changes in climate suitability values were associated with specific patterns in temperature and precipitation, we computed bivariate scatter plots and linear models with quadratic terms. These plots and models explored the relationship between changes in habitat suitability values and the two most important temperature and precipitation variables identified from the variable importance analysis of the models. To identify high climate suitability cells for the current period and the end of the century, we isolated and mapped the cells that fall within the top 30% of values from the average maps for all species together and for threatened species (red list groups VU, EN, and CR) individually. We investigated the temporal stability of the high climate suitability cells by computing the proportion of overlapping cells between the baseline and future periods for all species combined, as well as by main taxonomic and red list groups. Finally, to assess the ability of the existing network of protected areas (PAs) to incorporate high climate suitability cells, we calculated the proportion of these cells within the PAs, distinguishing between PAs with comprehensive protection and those with partial protection status. Comprehensive protection involves legally binding measures that enforce strict conservation regulations and minimal human impact, while partial protection allows for regulated activities and sustainable use. See Appendix S7 for details on PAs and protection status.

2.5.2 | Percentage Changes in Climate-Suitable Area

To quantify the magnitude of potential changes in climate suitability and provide a clearer picture of how much suitable habitat might increase or decrease in the future, we calculated for each species the percentage change between projected and baseline number of suitable cells over the entire study area. Results were graphically summarized by taxonomic and red list groups by using bar plots displaying for each group the percentage of species projected to experience stable (< 10%), moderate (< 50%), or major (> 50%) changes in climate-suitable area. To assess whether the climate-suitable area in the current period, the red list group, and the taxonomic group had an effect on the class of projected changes in future climate-suitable area, for each period \times scenario combination, we performed ordered (proportional odds) logistic regressions (Venables and Ripley 2002). We included quadratic terms for the predictor “climate-suitable area of the current period”, which was the only continuous one (the

others were categorical). In addition, we computed the overall proportion of cells affected by losses or gains (> 10%) in climate suitability. We explored the distribution of these losses or gains at the Swiss level and by major biogeographic region (FSO 2018).

2.5.3 | Geographical Shifts

To better identify the extent and the direction of projected shifts in climate-suitable cells, for each species, we quantified their average altitudinal, latitudinal, and longitudinal position. Results were graphically summarized at the taxonomic and red list group levels by using line plots displaying the average altitude, latitude, and longitude projected for each interval and scenario. Statistical significance of pairwise differences between periods were assessed using Dunn tests (Dunn 1964), with the magnitude and direction of changes assessed using the resulting Z score.

3 | Results

3.1 | Climate Change Projections

Average projected changes from the baseline maximum temperature and total precipitation values for the three 30-year periods and two RCPs are mapped in Appendix S6: Figure S6.1. An increasing warming gradient was evident from 2020–2049 to 2070–2099. Compared to baseline values, the greatest increases in the maximum temperature, $\approx +4.5^\circ\text{C}$, were expected during the 2070–2099 period under RCP8.5. Switzerland was also projected to experience increased annual precipitation, with the greatest changes ($\approx +30\%$) in the easternmost quarter for the 2070–2099 period under both RCPs. Decreased precipitation ($\approx -5\%$) was projected for the first two periods in the central area of the country under RCP4.5. The MOP analysis revealed that under projected future conditions a maximum of 0.007% of the cells will experience non-analog climate compared to the current conditions across the calibration extent. This maximum was found under RCP8.5 for the 2070–2099 period.

3.2 | Climate Suitability Models

N-SDM was successfully run for all 7291 species. The mean \pm SD cross-validated Score value was 0.89 ± 0.04 , indicating rather high model performances. The mean number of climate covariates included in the final models was 6.58 ± 0.72 . The models for the 7291 species included 19 distinct climate covariates (all were selected at least once). The average importance for the temperature and precipitation covariates was 0.60 ± 0.24 and 0.27 ± 0.12 , respectively. More details on model assessment and covariate selection results are available in Appendix S5.

3.3 | Climate Suitability Projections

3.3.1 | Projected Spatial Changes

For all species combined and categorized by taxonomic and red list groups, average and SD maps of projected climate suitability values for the baseline and three prospective periods under the

two RCPs can be found in Appendix S6: Zip S6.1 in both .tif and .png formats (<https://doi.org/10.6084/m9.figshare.25046312>). We illustrated with maps showing the difference between the baseline and the 2070–2099 period for the 12 taxonomic groups (Figure 1). Visual inspection of the maps suggested that the most consistent change in climate suitability across groups was an increase in the southern part of the country (i.e., the Alps). For some groups (e.g., amphibians, birds, and fungi), this increase was particularly noticeable in the East. Visual analyses underscored that projected changes in climate suitability were more pronounced under the RCP8.5 scenario in comparison to the RCP4.5.

Figure 2a shows the spatial distribution of high climate suitability cells (top 30% of values) for the current period and the end of the century, distinctively for all species and for threatened species. Analogous figures displaying the results for each taxonomic group are available in Appendix S6: Figures S6.2–S6.13. On average for all species, compared to the current period, our results suggested that future high climate suitability cells were expected to emerge or persist in high-altitude regions, particularly in the south-east of the country (i.e., the Alps) and on the north-western border of Switzerland (i.e., the Jura). In contrast, for all species, high climate suitability cells currently located in low-elevation areas, particularly in the south-west and north-north-east of the country, were no longer included in the top 30%. For threatened species, changes in high climate suitability cells were less evident, with fewer emerging in the southeastern part of the country and a large portion persisting in the southwestern quarter.

Analysis aimed at investigating the temporal stability of the high climate suitability cells revealed that under RCP8.5, the

three taxonomic groups with the least overlap of cells with high climate suitability between the baseline period and the end-of-century were fungi (10.1% of the high climate suitability cells), arthropods (EPTO) (15.8%), and arthropods (non-EPTO) (19.8%). Under RCP4.5, the least overlap was also for fungi (39.9%), arthropods (EPTO) (47.1%), and arthropods (non-EPTO) (54.6%). Conversely, the three groups with the most overlapping cells under RCP8.5 were fishes (71.6%), ferns and mosses (54.2%), and birds (43.2%). Under RCP4.5, the groups with the most overlap were fishes (86.5%), algae (79.0%), and amphibians (76.1%). The same analyses done for red list groups showed that under the RCP8.5 scenario, the three least stable groups were NE (7.8% of the high climate suitability cells), LC (20.1%), and DD (21.2%). The three most stable groups were EN (47.9%), CR (46.7%), and NT (33.8%). Under the RCP4.5 scenario, the three least stable groups were NE (40.2%), LC (50.4%), and DD (52.9%). The three most stable groups were CR (75.4%), EN (73.5%), and VU (64.0%).

From the perspective of the coverage of high climate suitability cells by the current network of PAs (Figure 2b), our results for both all species and threatened species indicated that PAs should contain more high climate suitability cells under future climate scenario. Currently, for all species, the proportion of high climate suitability cells in the PA network was 5.5% and 12.4%, which increased to 12.5% and 20.0% by 2070–2099 under RCP8.5 for PAs with comprehensive and partial protection statuses, respectively. For threatened species, the current proportion of high climate suitability cells in PAs was of 4.8% and 10.5%, which increased to 8.4% and 16.3% by 2070–2099 under RCP8.5 for PAs with comprehensive and partial protection statuses, respectively.

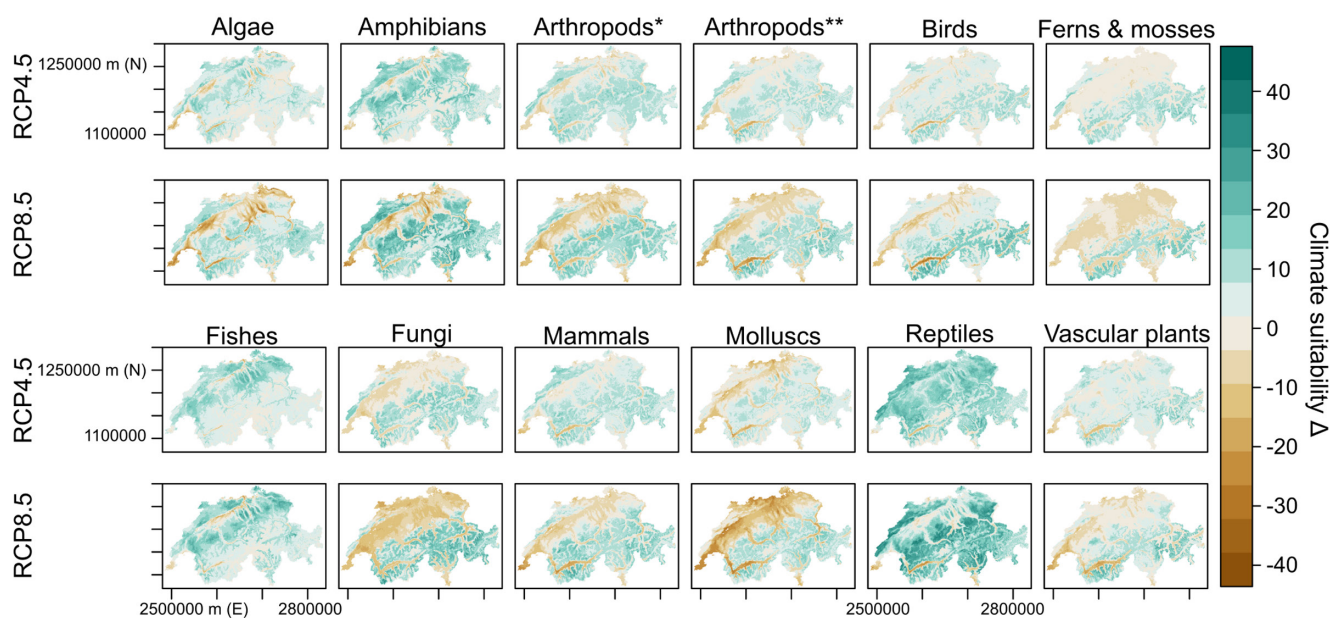
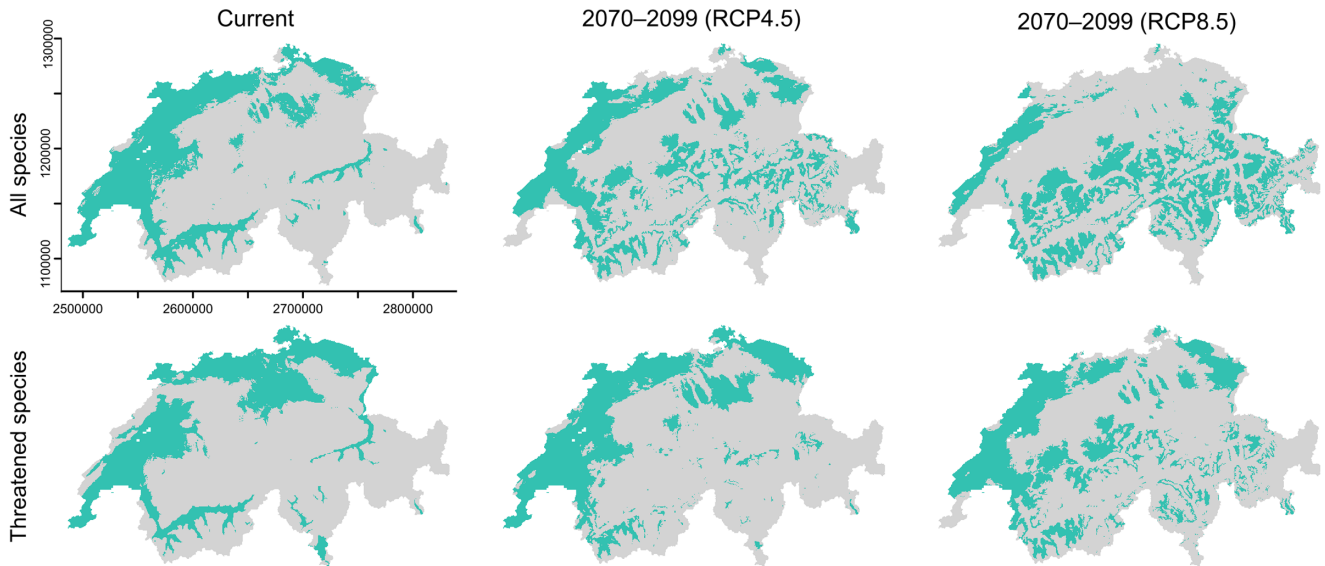


FIGURE 1 | Projected average climate suitability changes between the baseline period (1981–2010) and 2070–2099 for the 12 taxonomic groups under the low (RCP4.5) and high (RCP8.5) greenhouse gas scenarios in Switzerland. Arthropods*: All but Ephemeroptera, Plecoptera, Trichoptera, Odonata (EPTO). Arthropods**: Aquatic arthropods (EPTO). See <https://doi.org/10.6084/m9.figshare.25046312> for average and SD maps of projected climate suitability values for the baseline and three prospective periods under the two RCPs for all species combined and categorized by the taxonomic and red list groups. Climate suitability values are ranging between 0 and 100. The labels on the x and y-axes represent the coordinates in meters (m) in the Swiss coordinate system CH1903+/LV95.

(a) High climate suitability cells



(b) Protected areas cover

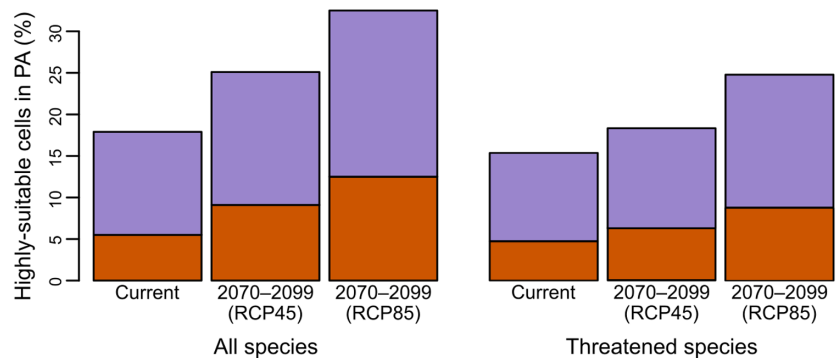
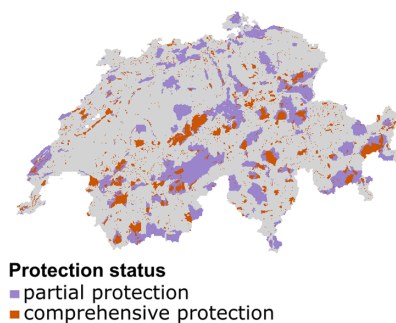


FIGURE 2 | Spatial distribution of high climate suitability cells and coverage by protected areas (PAs). (a) Maps of high climate suitability cells (in green) that fall within the top 30% of values from the average maps for all species together and for threatened species individually (red list groups VU, EN, and CR) for the current period and the end of the century under RCP4.5 and 8.5. (b) Map of PAs in Switzerland, by protection status, and bar plots showing the coverage of high climate suitability cells under current and future conditions for all species together and for threatened species (red list groups VU, EN, and CR). See Appendix S6: Figures S6.2–S6.13 for the results for individual taxonomic groups. See Appendix S7 for more details on PAs and conservation status. The labels on the x and y-axes of the maps represent the coordinates in meters (m) in the Swiss coordinate system CH1903+/LV95.

Results from the bivariate analyses aimed at assessing whether changes in climate suitability values were associated with specific patterns in temperature and precipitation indicated statistically significant associations between the two most important temperature and precipitation variables identified from the variable importance analysis of the models (BIO1: Annual mean temperature, BIO4: Temperature seasonality, BIO12: Annual precipitation, and BIO18: Precipitation of warmest quarter) and changes in climate suitability ($p < 0.001$). The bivariate plots revealed skewed and scattered patterns, as illustrated in Appendix S6: Figure S6.14. For temperature, identifiable patterns included minimal changes in climate suitability at the coldest pixels, an increase at mid-range temperatures, and a decrease at the warmest. For precipitation, patterns displayed either an increase or a decrease in climate suitability at the lowest precipitation levels, with a trend towards fewer changes at higher precipitation levels.

3.3.2 | Percentage Changes in Climate-Suitable Area

The overall percentage of species projected to experience major changes in climate-suitable area ($> 50\%$ decrease or increase) was higher under RCP8.5 (68.5%) than RCP4.5 (65.7%). On average for the two RCPs, this percentage increased over time with values of 62.3% for 2020–2049, 65.8% for 2045–2074, and 71.1% for 2070–2099.

3.3.2.1 | Negative Changes. Averaged across all species, by the end of the century (2070–2099), we projected an overall decrease ($> 10\%$) for 39.5% of the cells of the study area under RCP8.5 and 9.6% under RCP4.5. Results stratified by main biogeographic regions (Appendix S6: Figure S6.15) showed that the regions with the highest proportion of cells projected to experience decreases in climate suitability under RCP8.5 were the Plateau (87.1% of the cells) and the Jura (49.0%), and under RCP4.5 the Plateau (21.4%) and the western Alps (15.5%).

At the species level, we projected decreases in climate suitability for 3000 species under RCP8.5 and 1758 under RCP4.5. Among these species, 44 and 85 were projected to lose their entire climate-suitable area (100%) under RCP4.5 and RCP8.5, respectively. It included primarily arthropods ($n=16$ and 29), vascular Plants ($n=13$ and 37), and molluscs ($n=3$ and 5), from the LC ($n=16$ and 27), NE ($n=10$ and 22), and VU ($n=2$ and 14) red list groups. Relative to the current baseline, by the end of the century (2070–2099) and under RCP8.5, the three groups with the largest proportion of species forecasted to experience decreases in climate-suitable area were molluscs (70.4%), algae (60%), and amphibians (55.6%) (Figure 3). For RCP4.5, the three groups with the largest proportion of species forecasted to experience decreases were molluscs (48.8%), birds (29.4%), and vascular plants (28%) (Figure 3). Analogous figures for other periods and stratifying the results by red list groups are available in Appendix S6: Figures S6.16–S6.21. By the end of the century (2070–2099) and under RCP8.5, the red list groups with the highest proportion of species projected to experience the greatest losses in climate-suitable areas were EN (32.7%), NE (29.9%),

and VU (27.2%). Under RCP4.5 (2070–2099), these groups were CR (22.4%), NE (16.3%), and VU (14.4%).

3.3.2.2 | Positive Changes. In contrast, averaged across all species, by the end of the century (2070–2099), we projected an overall increase (>10%) for 50.3% of the cells under RCP8.5 and 73.1% under RCP4.5. The regions with the highest proportion of cells projected to experience an increase under RCP8.5 were the eastern Alps (80.5% of the cells) and the northern Alps (72.3%) (Appendix S6: Figure S6.15). Similarly, under RCP4.5, these regions were projected to experience gains for 92.7% and 88.4% of their cells, respectively.

At the species level, we projected increases for 3878 species under RCP8.5 and 5007 under RCP4.5. For RCP8.5, the three groups with the largest proportion of species forecasted to experience increases were reptiles (80.0%), ferns and mosses (69.8%), and fungi (68.1%) (Figure 3). For RCP4.5, the three groups with the largest proportion of species forecasted to experience increases were reptiles (86.7%), fishes (82.4%), and ferns and mosses (81.2%) (Figure 3).

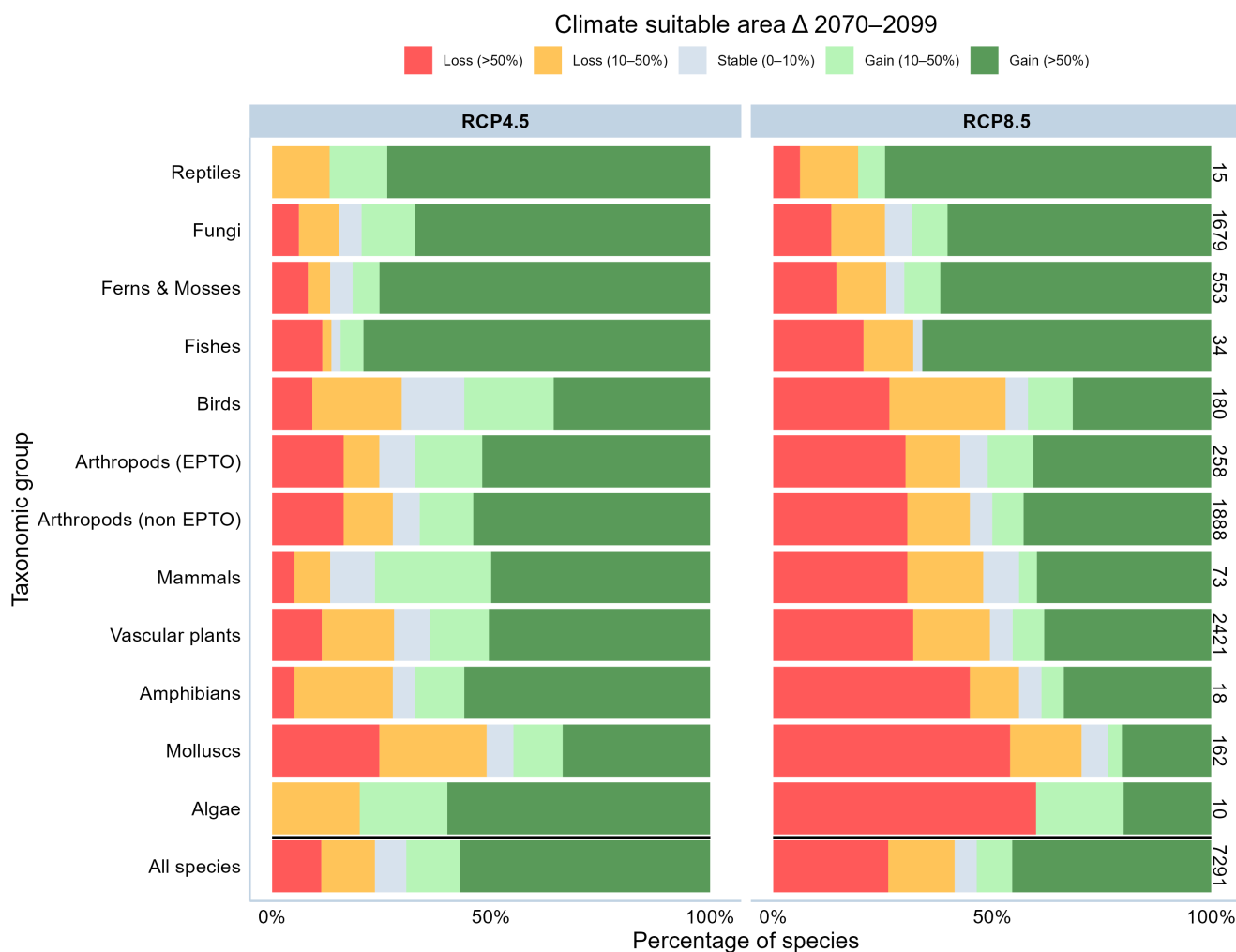
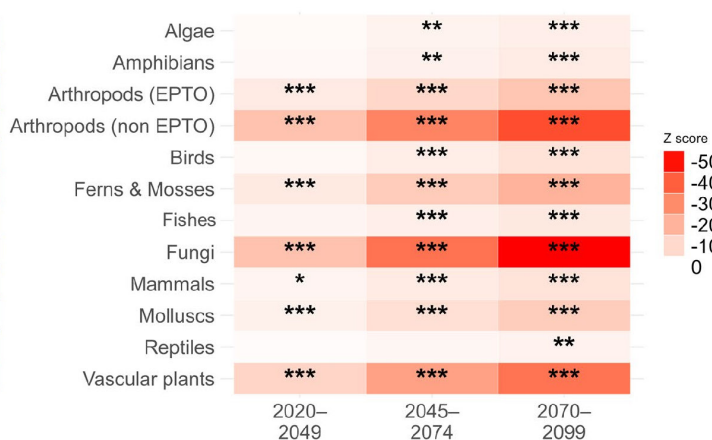
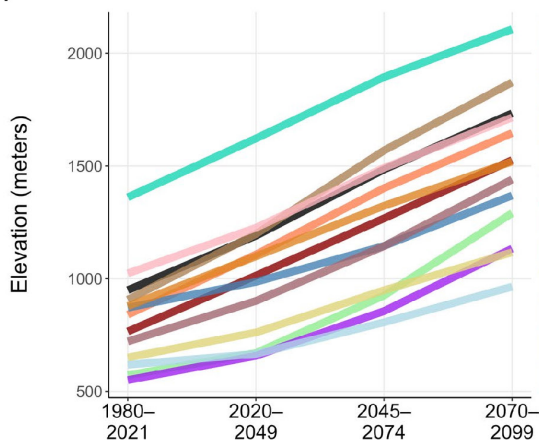


FIGURE 3 | Percentage changes in projected species' climate suitability in Switzerland from baseline (1981–2010) values for the 2070–2099 period under “low” (RCP4.5) and “high” (RCP8.5) greenhouse gas concentration trajectories by taxonomic group. Numbers on the right indicate the species count by taxonomic group. Note that for fish species, these are less than one-third of all species in Switzerland, with cold-adapted and often endemic lake species being largely not included. Taxonomic groups are ordered by the percentage of species in each group projected to undergo a major loss (>50%) in climate-suitable area under RCP8.5, from low to high percentages. See Appendix S1 for the detailed species list and Appendix S6: Figures S6.16–S6.21 for the results for all periods and red list groups.

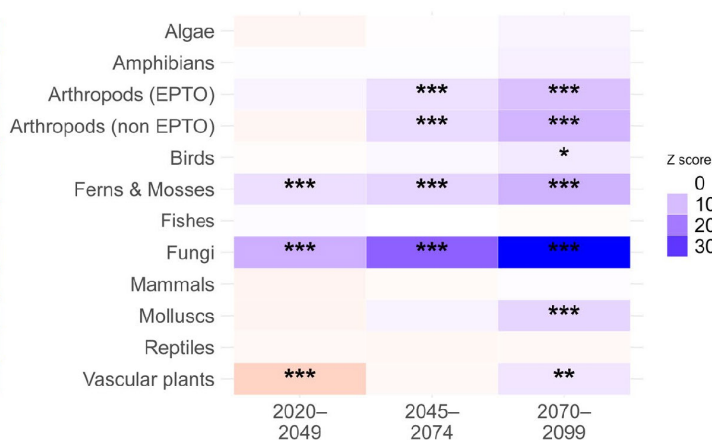
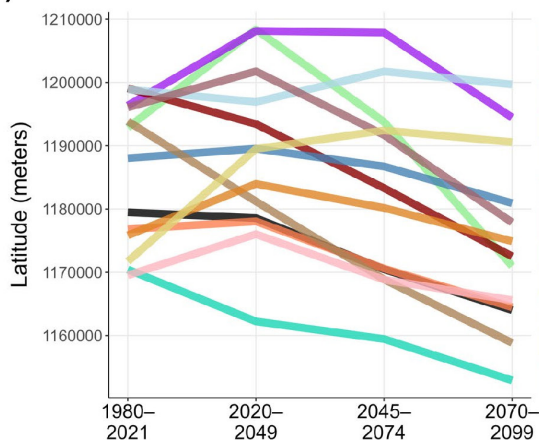
3.3.2.3 | Effects of Current Climate-Suitable Area, Red List Group, and Taxonomic Group on Projected Changes. The climate-suitable area in the current period was significantly and consistently associated with the class of projected change in future climate-suitable area (Appendix S6 Figure S6.22 and Table S6.1). This association revealed that species with a small

climate-suitable area in the current period were more likely to experience substantial changes in the future (loss or gain of > 50%), while those with a current climate-suitable area of intermediate or large size were less prone to major changes. The red list group had little effect on the class of projected changes, except for DD and NT, which were both significantly associated with an increase

(a) Elevation



(b) Latitude



(c) Longitude

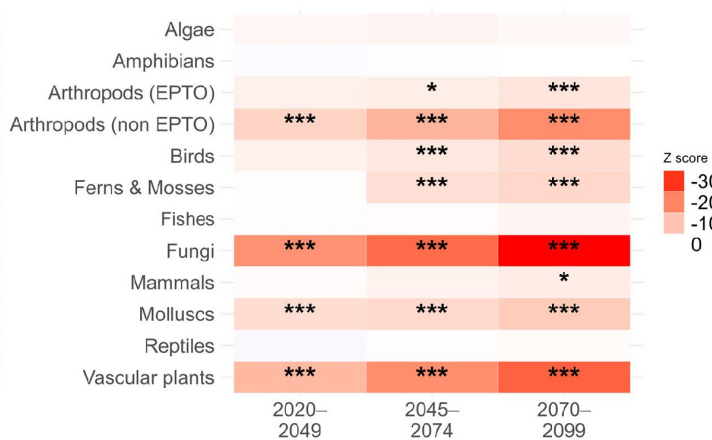
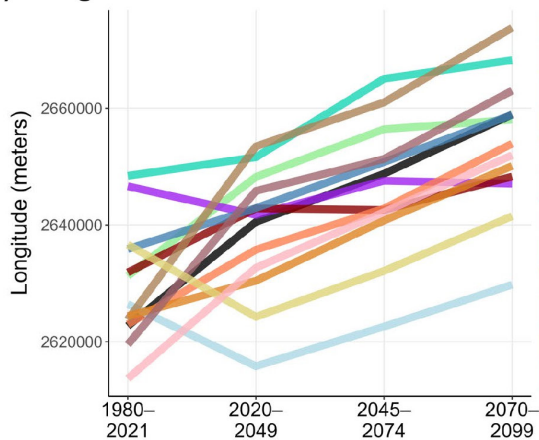


FIGURE 4 | Projected geographical shifts in species' climate-suitable area in Switzerland. Left: Average (a) elevation, (b) latitude, and (c) longitude of species' climate-suitable area for the baseline (1981–2010) and three 30-year future periods (2020–2049, 2045–2074, and 2070–2099) under the “high” (RCP8.5) greenhouse gas concentration trajectory by taxonomic group. The black lines indicate the average values across all species. Right: Magnitude and significance of changes from baseline period for the three future intervals. Statistical significance of pairwise differences between periods were assessed using Dunn tests and the magnitude and direction of changes using the resulting Z score, with *** $p < 0.001$, ** $p < 0.01$; * $p < 0.05$; none: Non-significant. See Appendix S6: Figures S6.23–S6.26 for the results for RCP4.5 and red list groups.

in projected future climate-suitable area. Taxonomic groups had varying effects: reptiles, ferns and mosses, fishes, and fungi were significantly associated with an increase in projected future climate-suitable area under RCP8.5 for the two periods 2045–2074 and 2070–2099. In contrast, arthropods (non-EPTO), molluscs, and vascular plants were associated with a decrease under both RCPs for the 2020–2049 period.

3.3.3 | Geographical Shifts

Figure 4 illustrates changes in average elevation, latitude, and longitude of climate-suitable areas by taxonomic group under the RCP8.5 scenario. Corresponding figure for the RCP4.5 scenario can be found in Appendix S6: Figure S6.24.

Under both scenarios, projections indicated that the climate-suitable area for all groups will shift to higher elevations during the study period. Statistically significant shifts between the baseline period (1981–2010) and the end of the century (2070–2099) ranged from 314 ± 504 m for fishes to 962 ± 286 m for fungi under the RCP8.5 scenario (Figure 4a). Under RCP4.5, the upward elevation shifts were less prominent, with values of 97 ± 188 and 498 ± 253 for these two groups, respectively.

Results revealed statistically significant decreases in average latitude (indicating southward shifts) for all groups except algae, amphibians, fishes, mammals, and reptiles under RCP8.5, when comparing the baseline (1981–2010) to the end of the century (2070–2099) (Figure 4b). Mean latitudinal shifts varied between $-3540 \pm 38,360$ m for vascular plants to $-34,841 \pm 31,201$ m for fungi. Statistically significant southward shifts were projected under RCP4.5 only for ferns and mosses, fungi, mammals, and vascular plants.

Conversely, a significant increase in average longitude (indicating eastward shifts) was projected for all groups except algae, amphibians, fishes, and reptiles under RCP8.5 throughout the study period (Figure 4c). These longitudinal shifts between the baseline period (1981–2010) and the end of the century (2070–2099) ranged from $16,831 \pm 40,124$ m for arthropods (EPTO) to $49,954 \pm 50,144$ m for fungi. Under RCP4.5, statistically significant eastward shifts were projected only for fungi, vascular plants, arthropods (non EPTO), birds, and molluscs.

For both RCPs, detailed figures stratifying the results by red list groups can be found in Appendix S6: Figures S6.25–S6.26. By the end of the century, under the RCP8.5 scenario, the red list groups projected to experience the most significant elevational shifts included NE (810 ± 410), LC (787 ± 364), and VU (740 ± 437). The most substantial southward shifts were projected for LC ($-20,575 \pm 32,554$), DD ($-18,002 \pm 41,429$), and VU ($-10,544 \pm 42,819$), while the highest eastward shifts were projected for LC ($40,267 \pm 46,143$), NE ($35,406 \pm 51,827$), and DD ($29,442 \pm 53,173$).

4 | Discussion

With many areas projected to continue to become warmer and changes in precipitation regime (Bader et al. 2023), and

assuming that species will conserve their current climatic niche, future climate will likely shift the ranges of many species in Switzerland. Our study, by including over 7000 individual species from 12 major taxonomic groups, represents by far the most comprehensive climate change–biodiversity assessment available for Switzerland, providing insight into the changes in biodiversity patterns across the century under two climate change scenarios. Our results indicated that projected climate changes could have important effects on species' climate suitability, with 41% of species projected to experience decreases and 53% increases, on average for all future periods and scenarios, with different responses based on taxonomic groups. The overall percentage of species projected to experience major changes in climate suitability was higher under RCP8.5 (68.5%) compared to RCP4.5 (65.7%). By the end of the century (2070–2099), decreases in climate suitability were projected for 3000 species under RCP8.5 and 1758 species under RCP4.5. Spatially, by 2070–2099, we projected an overall decrease in climate suitability for 39% of the cells in the study area under RCP8.5 and 10% under RCP4.5, while projecting an increase for 50% of the cells under RCP8.5 and 73% under RCP4.5. The most consistent geographical shifts were upward, southward, and eastward, leading to an increase in high climate suitability cells in high-altitude regions and a decline in low-elevation areas. These trends are consistent with other observational and modeling studies that focused on Switzerland (Vittoz et al. 2013; Petitpierre et al. 2016; Vitasse et al. 2021; Gebert et al. 2022). Changes in both latitude and longitude are likely to be associated with altitudinal effects (Pearson's r of -0.53 , $p < 0.001$ between elevation and latitude, and 0.29 , $p < 0.001$ between elevation and longitude), as the regions with the highest elevations in Switzerland are also in the south and east. Additional potential explanations for the eastward shifts involve increased levels of precipitation in the eastern region and the filling of species' suitable areas that were vacant because of incomplete post-glacial recolonization (Svenning and Skov 2007; Qian, Badgley, and Fox 2009; Baselga et al. 2012).

Climate change has been shown to have clade-specific effects given distinct climatic preferences, dispersal abilities, or adaptive capacity (Lavergne et al. 2010; Fei et al. 2017; Nogués-Bravo et al. 2018). Here, assuming niche conservatism under climate change, we also show distinct consequences. On average for the two RCPs, the three groups with the highest proportion of species projected to experience decreases in climate-suitable area were molluscs, arthropods, and vascular plants. This is a particularly concerning result, as most of the species making up these groups are not very mobile, or immobile, and should have difficulty keeping up with climate velocity, or the speed at which a species must migrate to keep pace with climate change (Loarie et al. 2009). Even more alarmingly, 44 (RCP4.5) and 85 (RCP8.5) species were projected to lose their entire climatically suitable range in Switzerland, including primarily arthropods, vascular plants, and molluscs. In contrast, for several species, climate suitability was projected to expand in high-elevation areas, but not necessarily contract in the lowlands, resulting in increased total suitable area. Reptiles, ferns and mosses, and fishes where the three groups most affected in this way. However, it is important to note that not all these groups were equally well represented. While virtually all reptile species in Switzerland

were covered, only about one-third of the fish species could be included, resulting in less robust findings.

From an red list group perspective, we showed that the threatened VU and EN categories were also those with the highest number of species projected to experience losses. This finding is concerning and can be viewed as an additional threat, given that the consequences of climate change are often inadequately accounted for in the current red list status (Keith et al. 2014; Trull, Böhm, and Carr 2018; Foden et al. 2019). On average, for all species together and specifically for threatened ones, an increasing proportion of high climate suitability cells was projected to fall within the PA network under both future climate scenarios. This suggests that the PA network in Switzerland would remain robust against projected changes in climate suitability. This finding aligns with results from several similar recent studies (Hoveka et al. 2022; Mi et al. 2023; Zhang et al. 2024). Swiss PAs are mainly at higher altitudes, which are projected to become more climate-suitable in the future, but individual species may still face significant losses outside PAs, with some losing both climate-suitable areas and PA coverage (Engler et al. 2011; Vincent et al. 2019).

Predicting biodiversity responses to climate change for a delimited area such as a country can be challenging due to spatial niche truncation (Barbet-Massin, Thuiller, and Jiguet 2010; Gallien et al. 2012; Chevalier et al. 2022). In addition to being pioneering for Switzerland in terms of the number and diversity of species considered, this study is also innovative in its effort to integrate species occurrence data outside of the core study area (i.e., across Europe). This was done to cover the full range of bioclimatic conditions that the species encounters within its distribution range, and thus obtaining an untruncated estimate of the response of the species to future climate. The MOP analysis conducted in an attempt to evaluate the degree of non-analog climate conditions in future projections revealed that this objective was successfully met, with less than 0.01% of the cells of the Swiss projection extent identified to be non-analogous in the future compared to the current conditions across the whole European calibration extent. The seamless integration of European and Swiss species and climate data was facilitated by the use of the N-SDM modeling platform (Adde, Rey, Brun, et al. 2023). N-SDM was specifically designed to tackle the niche truncation issue and has the key advantage of being designed to be run on high-performance computing structures, which is indispensable for modeling so many species simultaneously in an acceptable timeframe. Integrating data from species that extend beyond the national framework could explain why we ended up with a greater number of “winners” than “losers”, whereas the opposite is generally the case in comparable studies (Guisan and Theurillat 2001; Randin et al. 2010; Velásquez-Tibatá, Salaman, and Graham 2013; Ferreira et al. 2016; Dyderski et al. 2018). Indeed, most of the species evaluated in this study have a current range that extends well beyond Switzerland and may evolve in temperature conditions that are already warmer than those projected for the end of the century in Switzerland (as already shown for bird species; (Chevalier et al. 2022)). Furthermore, it should be noted that our study focused only on species already present in Switzerland, but the patterns predicted for the major taxonomic groups could differ

somewhat if we consider the arrival of new species for which bioclimatic conditions across Switzerland could become favorable in the future (Lawler et al. 2009; Blois et al. 2013; Chan et al. 2018).

Worldwide, an expanding number of species occurrence data has recently become available, primarily due to the multiplication of community science initiatives (Dickinson, Zuckerberg, and Bonter 2010; Amano, Lamming, and Sutherland 2016; Pocock et al. 2017; Oliver et al. 2021). Despite the considerable efforts of the Swiss biodiversity centers (www.infospecies.ch) to collate and curate the numerous data received each year, these data remain highly heterogeneous in terms of the sampling protocol and are subject to imperfect detection due to spatial-temporal variation among observers, in environmental conditions, and in species' behaviors. In order to limit the potential issues related to these characteristics, we applied a correction strategy consisting of performing a spatial disaggregation of the occurrence records, which is useful for getting rid of observation clusters (Kramer-Schadt et al. 2013; Vollering et al. 2019; Steen et al. 2020). The quality of the input data will also influence on the reliability of the output map, and this is difficult to control when so many species are modeled at once. In particular, for species with few occurrence points, it could be difficult to discern whether a species is rare or under-sampled. In order to avoid having to make this distinction, we chose to focus on species for which a minimum of 50 occurrence points were available. This choice was also motivated to use a method applicable to all species. In particular, to model the rarest species, it would have been possible to use the ensembles of small models approach (Lomba et al. 2010; Breiner et al. 2015, 2018), but this would have prevented the comparability of the output maps. We acknowledge that a major caveat of our study is that a critical part of Switzerland's biodiversity—the under sampled or rare one—is excluded from our study, and that a specific assessment for these species is still necessary. For example, nearly all narrow endemic fish species, many limited to just one lake, were excluded upon applying the spatial disaggregation and minimum number of occurrence filters. Despite their significance for biodiversity conservation, many of these rare species are frequently excluded from SDM studies for modeling purposes (Gaston 1998; Grenyer et al. 2006; Wiens and Zelinka 2024). We emphasize the importance of interpreting our results with the awareness that we did not cover the rarest species.

Climate-only SDMs depend on the assumption that patterns in species' distribution are at least partially determined by climatic conditions and thus may be modeled using climate covariates (Heikkinen et al. 2006; Hijmans and Graham 2006; Araujo and Peterson 2012). These models ignore multiple other variables and mechanisms that could play key roles in mediating species' responses to climate, including land use and cover, demographic shifts, species interactions, and evolution (Guisan et al. 2013). Furthermore, our analyses do not incorporate dispersal constraints (Soberon and Peterson 2005), which depend on geographical and historical limitations. Consequently, projected gains in climate-suitable areas will not necessarily be reflected in terms of gains in distribution areas, or even in habitat suitability. However, for species projected to lose most of their climate-suitable areas, we have

information that their primary climate requirements are unlikely to be fulfilled. Climate suitability is not the most detailed information that could have theoretically been accessed from our results and analyses of spatio-temporal beta diversity patterns, including species turnover, taxonomic heterogenization or homogenization, would have been necessary for a more comprehensive assessment of the future biodiversity situation. Considering the heterogeneity and the number of species modeled in this study, along with the numerous sources of uncertainties related to future projections, we believe that remaining at this fairly coarse and aggregated level of analysis has allowed us to draw more robust conclusions about the targets we set. Since input climate data are the only covariates feeding these models, their quality is important. In this study, the use of N-SDM (Adde, Rey, Brun, et al. 2023), which allows the combination of covariate data from different sources and with varying spatial resolutions for the regional (i.e., Switzerland) and global (i.e., Europe) levels, made it possible to take advantage of the best climate data available at each level. In particular, for Switzerland, the use of the 25-m resolution downscaled CHclim25 dataset (Broennimann 2021) allowed us to capture locally relevant climatic processes. We recognize that these climate data are only including air and not water measurements, which is probably an important limitation for the modeling of aquatic species, although relationships have already been established between air and water temperatures (Caissie 2006; Seekell and Pace 2011; Isaak et al. 2012).

5 | Conclusion

By using a modeling approach explicitly designed to account for niche truncation, our study provides state-of-the-art projections for biodiversity in Switzerland, addressing the lack of comprehensive climate-driven biodiversity data for guiding effective conservation efforts. We alarmingly revealed that about half of the ~7000 species evaluated could experience decrease in climate-suitable areas, and that several species could even potentially lose their entire climatically-suitable range in Switzerland by the end of the century. These estimates are likely conservative, as we did not model species that are already rare (i.e., for which less than 50 occurrence points were available). Climate suitability layers made available along this study can serve as biodiversity indicators to be evaluated alongside other socioeconomic sectors of national importance such as energy, agriculture, and tourism. Once these trade-offs are identified, additional work will be necessary to assess the climate change resilience of the national ecological infrastructure and plan adaptation solutions.

Author Contributions

Antoine Adde: conceptualization, data curation, formal analysis, methodology, software, validation, visualization, writing – original draft, writing – review and editing. **Nathan Külling:** conceptualization, data curation, formal analysis, methodology, validation, visualization, writing – review and editing. **Pierre-Louis Rey:** conceptualization, data curation, methodology, validation, writing – review and editing. **Fabian Fopp:** conceptualization, data curation, methodology, validation, writing – review and editing. **Philipp Brun:** conceptualization, data curation, methodology, validation,

writing – review and editing. **Olivier Broennimann:** conceptualization, data curation, methodology, validation, writing – review and editing. **Anthony Lehmann:** conceptualization, data curation, methodology, validation, writing – review and editing. **Blaise Petitpierre:** conceptualization, data curation, methodology, validation, writing – review and editing. **Niklaus E. Zimmermann:** conceptualization, data curation, methodology, validation, writing – review and editing. **Loïc Pellissier:** conceptualization, data curation, methodology, validation, writing – review and editing. **Florian Altermatt:** conceptualization, data curation, funding acquisition, methodology, resources, supervision, validation, writing – review and editing. **Antoine Guisan:** conceptualization, data curation, funding acquisition, methodology, resources, supervision, validation, writing – review and editing.

Acknowledgments

The Swiss Species Information Center InfoSpecies (www.infospecies.ch) supplied Swiss-level species occurrence data and expertise on species' ecology, and we acknowledge their support regarding the database. This research was enabled in part by the support provided by the Scientific Computing and Research Unit of Lausanne University (www.unil.ch/ci/dcsr).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available from Figshare at <https://doi.org/10.6084/m9.figshare.25046312>. European and Swiss-level climate data can be accessed from their source repositories, <https://chelsa-climate.org/> and <https://doi.org/10.5281/zenodo.7871115>, respectively. European-level species data can be accessed from the Global Biodiversity Information Facility at <https://doi.org/10.15468/dl.fktyas>. Swiss-level species data is available from InfoSpecies (www.infospecies.ch) and may be supplied to researchers on request. An anonymized version of both the Swiss- and European-level species data and climate model data is available from FigShare at <https://doi.org/10.6084/m9.figshare.27178728>. The species distribution modeling software N-SDM is available from Zenodo at <https://zenodo.org/records/10604559>, and GitHub at <https://github.com/antadde/N-SDM>, where complementary instructions for installation and example data are provided. The N-SDM 'settings.csv' file used to run N-SDM and the ODMAP reporting protocol can be found in Appendix S3 and S4, respectively.

References

- Adde, A., P. L. Rey, P. Brun, et al. 2023. "N-SDM: A High-Performance Computing Pipeline for Nested Species Distribution Modelling." *Ecography* 2023: e06540.
- Adde, A., P.-L. Rey, F. Fopp, et al. 2023. "Too Many Candidates: Embedded Covariate Selection Procedure for Species Distribution Modelling With the Covsel R Package." *Ecological Informatics* 75: 102080.
- Aiello-Lammens, M. E., R. A. Boria, A. Radosavljevic, B. Vilela, and R. P. Anderson. 2015. "spThin: An R Package for Spatial Thinning of Species Occurrence Records for Use in Ecological Niche Models." *Ecography* 38: 541–545.
- Amano, T., J. D. L. Lamming, and W. J. Sutherland. 2016. "Spatial Gaps in Global Biodiversity Information and the Role of Citizen Science." *Bioscience* 66: 393–400.
- Antonelli, A., W. D. Kissling, S. G. A. Flantua, et al. 2018. "Geological and Climatic Influences on Mountain Biodiversity." *Nature Geoscience* 11: 718.

- Araujo, M. B., R. P. Anderson, A. M. Barbosa, et al. 2019. "Standards for Distribution Models in Biodiversity Assessments." *Science Advances* 5: eaax4858.
- Araujo, M. B., and A. T. Peterson. 2012. "Uses and Misuses of Bioclimatic Envelope Modeling." *Ecology* 93: 1527–1539.
- Arneth, A., Y. J. Shin, P. Leadley, et al. 2020. "Post-2020 Biodiversity Targets Need to Embrace Climate Change." *Proceedings of the National Academy of Sciences of the United States of America* 117: 30882–30891.
- Austin, M. P., and K. P. Van Niel. 2011. "Improving Species Distribution Models for Climate Change Studies: Variable Selection and Scale." *Journal of Biogeography* 38: 1–8.
- Bader, S., S. Bircher, M. C. Coen, et al. 2023. "Climatological report 2022. Bern, Switzerland."
- Barbet-Massin, M., W. Thuiller, and F. Jiguet. 2010. "How Much Do We Overestimate Future Local Extinction Rates When Restricting the Range of Occurrence Data in Climate Suitability Models?" *Ecography* 33: 878–886.
- Baselga, A., J. M. Lobo, J. C. Svenning, P. Aragon, and M. B. Araujo. 2012. "Dispersal Ability Modulates the Strength of the Latitudinal Richness Gradient in European Beetles." *Global Ecology and Biogeography* 21: 1106–1113.
- Bellamy, C., K. Boughey, C. Hawkins, et al. 2020. "A sequential multi-level framework to improve habitat suitability modelling." *Landscape Ecology* 35: 1001–1020.
- Bellard, C., W. Thuiller, B. Leroy, P. Genovesi, M. Bakkenes, and F. Courchamp. 2013. "Will Climate Change Promote Future Invasions?" *Global Change Biology* 19: 3740–3748.
- Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick, and S. Finnegan. 2013. "Climate Change and the Past, Present, and Future of Biotic Interactions." *Science* 341: 499–504.
- Booth, T. H., H. A. Nix, J. R. Busby, and M. F. Hutchinson. 2014. "BIOCLIM: The First Species Distribution Modelling Package, Its Early Applications and Relevance to Most Current MAXENT Studies." *Diversity and Distributions* 20: 1–9.
- Boria, R. A., L. E. Olson, S. M. Goodman, and R. P. Anderson. 2014. "Spatial Filtering to Reduce Sampling Bias Can Improve the Performance of Ecological Niche Models." *Ecological Modelling* 275: 73–77.
- Breiman, L. 2001. "Random Forests." *Machine Learning* 45: 5–32.
- Breiner, F. T., A. Guisan, A. Bergamini, and M. P. Nobs. 2015. "Overcoming Limitations of Modelling Rare Species by Using Ensembles of Small Models." *Methods in Ecology and Evolution* 6: 1210–1218.
- Breiner, F. T., M. P. Nobs, A. Bergamini, and A. Guisan. 2018. "Optimizing Ensembles of Small Models for Predicting the Distribution of Species With Few Occurrences." *Methods in Ecology and Evolution* 9: 802–808.
- Broennimann, O. 2021. *CHclim25: A High Spatial and Temporal Resolution Climate Dataset for Switzerland (v.1)*. Switzerland: Ecospat laboratory, University of Lausanne.
- Caissie, D. 2006. "The Thermal Regime of Rivers: A Review." *Freshwater Biology* 51: 1389–1406.
- Carroll, C., R. F. Noss, L. M. Dreiss, H. Hamilton, and B. A. Stein. 2023. "Four Challenges to an Effective National Nature Assessment." *Conservation Biology* 37: e14075.
- Chan, F. T., K. Stanislawczyk, A. C. Sneekes, et al. 2018. "Climate Change Opens New Frontiers for Marine Species in the Arctic: Current Trends and Future Invasion Risks." *Global Change Biology* 25: 25–38.
- Chauvier-Mendes, Y., L. J. Pollock, P. H. Verburg, et al. 2024. "Transnational Conservation to Anticipate Future Plant Shifts in Europe." *Nature Ecology & Evolution* 8: 1–13.
- Cheung, W. W. L., V. W. Y. Lam, J. L. Sarmiento, K. Kearney, R. Watson, and D. Pauly. 2009. "Projecting Global Marine Biodiversity Impacts Under Climate Change Scenarios." *Fish and Fisheries* 10: 235–251.
- Chevalier, M., O. Broennimann, J. Cornuault, and A. Guisan. 2021. "Data Integration Methods to Account for Spatial Niche Truncation Effects in Regional Projections of Species Distribution." *Ecological Applications* 31: e02427.
- Chevalier, M., A. Zarzo-Arias, J. Guélat, R. G. Mateo, and A. Guisan. 2022. "Accounting for Niche Truncation to Improve Spatial and Temporal Predictions of Species Distributions." *Frontiers in Ecology and Evolution* 10: 944116.
- Dickinson, J. L., B. Zuckerberg, and D. N. Bonter. 2010. "Citizen Science as an Ecological Research Tool: Challenges and Benefits." *Annual Review of Ecology, Evolution, and Systematics* 41: 149–172.
- Dullinger, S., A. Gatttringer, W. Thuiller, et al. 2012. "Extinction Debt of High-Mountain Plants Under Twenty-First-Century Climate Change." *Nature Climate Change* 2: 619–622.
- Dunn, O. J. 1964. "Multiple Comparisons Using Rank Sums." *Technometrics* 6: 241–252.
- Dyderski, M. K., S. Paz, L. E. Frelich, and A. M. Jagodzinski. 2018. "How Much Does Climate Change Threaten European Forest Tree Species Distributions?" *Global Change Biology* 24: 1150–1163.
- Elith, J., and J. R. Leathwick. 2009. "Species Distribution Models: Ecological Explanation and Prediction Across Space and Time." *Annual Review of Ecology, Evolution, and Systematics* 40: 677–697.
- Engler, R., C. F. Randin, W. Thuiller, et al. 2011. "21st Century Climate Change Threatens Mountain Flora Unequally Across Europe." *Global Change Biology* 17: 2330–2341.
- Engler, R., C. F. Randin, P. Vittoz, et al. 2009. "Predicting Future Distributions of Mountain Plants Under Climate Change: Does Dispersal Capacity Matter?" *Ecography* 32: 34–45.
- Feeley, K. J., J. T. Stroud, and T. M. Perez. 2017. "Most 'global' reviews of Species' Responses to Climate Change Are Not Truly Global." *Diversity and Distributions* 23: 231–234.
- Fei, S., J. M. Desprez, K. M. Potter, J. Io, J. A. Knott, and C. M. Oswalt. 2017. "Divergence of Species Responses to Climate Change." *Science Advances* 3: e1603055.
- Ferreira, M. T., P. Cardoso, P. A. Borges, et al. 2016. "Effects of Climate Change on the Distribution of Indigenous Species in Oceanic Islands (Azores)." *Climatic Change* 138: 603–615.
- Fick, S. E., and R. J. Hijmans. 2017. "WorldClim 2: New 1-Km Spatial Resolution Climate Surfaces for Global Land Areas." *International Journal of Climatology* 37: 4302–4315.
- Fischer, A. M., K. M. Strassmann, M. Croci-Maspoli, et al. 2022. "Climate Scenarios for Switzerland CH2018–Approach and Implications." *Climate Services* 26: 100288.
- Fitzpatrick, M. C., A. D. Gove, N. J. Sanders, and R. R. Dunn. 2008. "Climate Change, Plant Migration, and Range Collapse in a Global Biodiversity Hotspot: The Banksia (Proteaceae) of Western Australia." *Global Change Biology* 14: 1337–1352.
- Foden, W. B., B. E. Young, H. R. Akçakaya, et al. 2019. "Climate Change Vulnerability Assessment of Species." *Wiley Interdisciplinary Reviews: Climate Change* 10: e551.
- FOEN. 2023. *Biodiversity in Switzerland: Status and Trends*. Switzerland: Bern.
- Fourcade, Y., J. O. Engler, D. Rodder, and J. Secondi. 2014. "Mapping Species Distributions With MAXENT Using a Geographically Biased Sample of Presence Data: A Performance Assessment of Methods for Correcting Sampling Bias." *PLoS One* 9: 13.

- Fournier, A., M. Barbet-Massin, Q. Rome, and F. Courchamp. 2017. "Predicting Species Distribution Combining Multi-Scale Drivers." *Global Ecology and Conservation* 12: 215–226.
- Franklin, J. 2010. *Mapping Species Distributions: Spatial Inference and Prediction*. Cambridge, UK: Cambridge University Press.
- FSO. 2018. *Biogeographic Regions of Switzerland and Their Surface Area*. Switzerland: Federal Statistical Office Bern.
- Gallien, L., R. Douzet, S. Pratte, N. E. Zimmermann, and W. Thuiller. 2012. "Invasive Species Distribution Models - How Violating the Equilibrium Assumption Can Create New Insights." *Global Ecology and Biogeography* 21: 1126–1136.
- Gaston, K. J. 1998. "Rarity as a Double Jeopardy." *Nature* 394: 229–230.
- Gebert, F., M. K. Obrist, R. Siber, F. Altermatt, K. Bollmann, and N. Schuwirth. 2022. "Recent Trends in Stream Macroinvertebrates: Warm-Adapted and Pesticide-Tolerant Taxa Increase in Richness." *Biology Letters* 18: 20210513.
- Goicolea, T., A. Adde, O. Broennimann, et al. 2024. "Spatially-Nested Hierarchical Species Distribution Models to Overcome Niche Truncation in National-Scale Studies." *Ecography* e07328.
- Grenyer, R., C. D. L. Orme, S. F. Jackson, et al. 2006. "Global Distribution and Conservation of Rare and Threatened Vertebrates." *Nature* 444: 93–96.
- Groves, C. R., E. T. Game, M. G. Anderson, et al. 2012. "Incorporating Climate Change Into Systematic Conservation Planning." *Biodiversity and Conservation* 21: 1651–1671.
- Guisan, A., O. Broennimann, A. Buri, et al. 2019. "Climate Change Impact on Mountain Biodiversity." In *Biodiversity and Climate Change*, edited by T. E. Lovejoy and L. Hannah, 229–241. New Haven: Yale University Press.
- Guisan, A., and J. P. Theurillat. 2001. "Assessing Alpine Plant Vulnerability to Climate Change: A Modeling Perspective." *Integrated Assessment* 1: 307–320.
- Guisan, A., W. Thuiller, and N. E. Zimmermann. 2017. *Habitat Suitability and Distribution Models, With Applications in R*. Cambridge: Cambridge University Press.
- Guisan, A., R. Tingley, J. B. Baumgartner, et al. 2013. "Predicting Species Distributions for Conservation Decisions." *Ecology Letters* 16: 1424–1435.
- Hastie, T. J. 2017. "Generalized Additive Models." In *Statistical Models in S*, 249–307. New York, NY: Routledge.
- Heikkinen, R. K., M. Luoto, M. B. Araujo, R. Virkkala, W. Thuiller, and M. T. Sykes. 2006. "Methods and Uncertainties in Bioclimatic Envelope Modelling Under Climate Change." *Progress in Physical Geography* 30: 751–777.
- Herrera-R, G. A., T. Oberdorff, E. P. Anderson, et al. 2020. "The Combined Effects of Climate Change and River Fragmentation on the Distribution of Andean Amazon Fishes." *Global Change Biology* 26: 5509–5523.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. "Very High Resolution Interpolated Climate Surfaces for Global Land Areas." *International Journal of Climatology* 25: 1965–1978.
- Hijmans, R. J., and C. H. Graham. 2006. "The Ability of Climate Envelope Models to Predict the Effect of Climate Change on Species Distributions." *Global Change Biology* 12: 2272–2281.
- Hirzel, A. H., G. Le Lay, V. Helfer, C. Randin, and A. Guisan. 2006. "Evaluating the Ability of Habitat Suitability Models to Predict Species Presences." *Ecological Modelling* 199: 142–152.
- Hoorn, C., A. Perrigo, and A. Antonelli. 2018. "Mountains, Climate and Biodiversity: An Introduction." In *Mountains, Climate and Biodiversity*, edited by C. Hoorn, A. Perrigo, and A. Antonelli. Hoboken, NJ: Wiley.
- Hoveka, L. N., van der Bank, M., and T. J. Davies. 2022. "Winners and Losers in a Changing Climate: How Will Protected Areas Conserve Red List Species Under Climate Change?" *Diversity and Distributions* 28: 782–792.
- IPBES. 2019. *Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*, edited by S. Díaz, J. Settele, E. S. Brondizio, et al., 60. Bonn, Germany: Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES).
- IPCC. 2023. "Climate Change 2023: Synthesis Report. Contribution of Working Groups I." In *II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland: Intergovernmental Panel on Climate Change (IPCC).
- Isaak, D., S. Wollrab, D. Horan, and G. Chandler. 2012. "Climate Change Effects on Stream and River Temperatures Across the Northwest US From 1980–2009 and Implications for Salmonid Fishes." *Climatic Change* 113: 499–524.
- Jackson, S. T., C. S. Duke, S. E. Hampton, et al. 2016. "Toward a National, Sustained US Ecosystem Assessment." *Science* 354: 838–839.
- Jaureguiberry, P., N. Titeux, M. Wiemers, et al. 2022. "The Direct Drivers of Recent Global Anthropogenic Biodiversity Loss." *Science*. *Advances* 8: eabm9982.
- Karger, D. N., O. Conrad, J. Böhner, et al. 2017. "Climatologies at High Resolution for the earth's Land Surface Areas." *Scientific Data* 4: 170122.
- Ke, G. L., Q. Meng, T. Finley, et al. 2017. "LightGBM: A Highly Efficient Gradient Boosting Decision Tree." In *31st Conference on Neural Information Processing Systems (NIPS 2017)*, Long Beach, CA, USA.
- Keith, D. A., M. Mahony, H. Hines, et al. 2014. "Detecting Extinction Risk From Climate Change by IUCN Red List Criteria." *Conservation Biology* 28: 810–819.
- Klaus, G., F. Cordillot, and I. Künzle. 2023. *Gefährdete Arten und Lebensräume in der Schweiz: Synthese Rote Listen*. Switzerland: BAFU Bern.
- Knaus, P., S. Antoniazza, S. Wechsler, et al. 2018. "Swiss Breeding Bird Atlas 2013–2016. Distribution and Population Trends of Birds in Switzerland and Liechtenstein." Swiss Ornithological Institute.
- Knutti, R., and J. Sedlacek. 2013. "Robustness and Uncertainties in the New CMIP5 Climate Model Projections." *Nature Climate Change* 3: 369–373.
- Kramer-Schadt, S., J. Niedballa, J. D. Pilgrim, et al. 2013. "The Importance of Correcting for Sampling Bias in MaxEnt Species Distribution Models." *Diversity and Distributions* 19: 1366–1379.
- Külling, N., A. Adde, A. Lambiel, et al. 2024. "Nature's Contributions to People and Biodiversity Mapping in Switzerland: Spatial Patterns and Environmental Drivers." *Ecological Indicators* 163: 112079.
- Lamboley, Q., and Y. Fourcade. 2024. "No Optimal Spatial Filtering Distance for Mitigating Sampling Bias in Ecological Niche Models." *Journal of Biogeography* 51: 1783–1794.
- Lavergne, S., N. Mouquet, W. Thuiller, and O. Ronce. 2010. "Biodiversity and Climate Change: Integrating Evolutionary and Ecological Responses of Species and Communities." *Annual Review of Ecology, Evolution, and Systematics* 41: 321–350.
- Lawler, J. J., S. L. Shafer, D. White, et al. 2009. "Projected Climate-Induced Faunal Change in the Western Hemisphere." *Ecology* 90: 588–597.
- Lawler, J. J., J. E. M. Watson, and E. T. Game. 2015. "Conservation in the Face of Climate Change: Recent Developments." *F1000Research* 4.
- Lenoir, J., R. Bertrand, L. Comte, et al. 2020. "Species Better Track Climate Warming in the Oceans Than on Land." *Nature Ecology & Evolution* 4: 1044.

- Lenoir, J., and J. C. Svenning. 2015. "Climate-Related Range Shifts—a Global Multidimensional Synthesis and New Research Directions." *Ecography* 38: 15–28.
- Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. "The Velocity of Climate Change." *Nature* 462: 1052–1055.
- Lomba, A., L. Pellissier, C. Randin, et al. 2010. "Overcoming the Rare Species Modelling Paradox: A Novel Hierarchical Framework Applied to an Iberian Endemic Plant." *Biological Conservation* 143: 2647–2657.
- Mateo, R. G., M. J. Aroca-Fernández, A. Gastón, V. Gómez-Rubio, S. Saura, and J. I. García-Viñas. 2019. "Looking for an Optimal Hierarchical Approach for Ecologically Meaningful Niche Modelling." *Ecological Modelling* 409: 108735.
- Maxwell, S. L., R. A. Fuller, T. M. Brooks, and J. E. Watson. 2016. "Biodiversity: The Ravages of Guns, Nets and Bulldozers." *Nature* 536: 143.
- McCullagh, P., and J. A. Nelder. 1989. *Generalized Linear Models*. 2nd ed. London: Chapman and Hall.
- Mi, C., L. Ma, M. Yang, et al. 2023. "Global Protected Areas as Refuges for Amphibians and Reptiles Under Climate Change." *Nature Communications* 14: 1389.
- Midgley, G. F., L. Hannah, D. Millar, M. C. Rutherford, and L. W. Powrie. 2002. "Assessing the Vulnerability of Species Richness to Anthropogenic Climate Change in a Biodiversity Hotspot." *Global Ecology and Biogeography* 11: 445–451.
- Newbold, T. 2018. "Future Effects of Climate and Land-Use Change on Terrestrial Vertebrate Community Diversity Under Different Scenarios." *Proceedings of the Royal Society B: Biological Sciences* 285: 20180792.
- Nogués-Bravo, D., F. Rodríguez-Sánchez, L. Orsini, et al. 2018. "Cracking the Code of Biodiversity Responses to Past Climate Change." *Trends in Ecology & Evolution* 33: 765–776.
- Oliver, R. Y., C. Meyer, A. Ranipeta, K. Winner, and W. Jetz. 2021. "Global and National Trends, Gaps, and Opportunities in Documenting and Monitoring Species Distributions." *PLoS Biology* 19: e3001336.
- Owens, H. L., L. P. Campbell, L. L. Dornak, et al. 2013. "Constraints on Interpretation of Ecological Niche Models by Limited Environmental Ranges on Calibration Areas." *Ecological Modelling* 263: 10–18.
- Pearman, P. B., A. Guisan, and N. E. Zimmermann. 2011. "Impacts of Climate Change on Swiss Biodiversity: An Indicator Taxa Approach." *Biological Conservation* 144: 866–875.
- Pecl, G. T., M. B. Araujo, J. D. Bell, et al. 2017. "Biodiversity Redistribution Under Climate Change: Impacts on Ecosystems and Human Well-Being." *Science* 355: eaai9214.
- Pereira, H. M., L. M. Navarro, and I. S. Martins. 2012. "Global Biodiversity Change: The Bad, the Good, and the Unknown." *Annual Review of Environment and Resources* 37: 25–50.
- Peterson, A. T., J. Soberón, R. G. Pearson, et al. 2011. *Ecological Niches and Geographic Distributions*. Princeton: Princeton University Press.
- Petitpierre, B., K. McDougall, T. Seipel, O. Broennimann, A. Guisan, and C. Kueffer. 2016. "Will Climate Change Increase the Risk of Plant Invasions Into Mountains?" *Ecological Applications* 26: 530–544.
- Phillips, S. J., R. P. Anderson, M. Dudik, R. E. Schapire, and M. E. Blair. 2017. "Opening the Black Box: An Open-Source Release of Maxent." *Ecography* 40: 887–893.
- Pocock, M. J., J. C. Tweddle, J. Savage, L. D. Robinson, and H. E. Roy. 2017. "The Diversity and Evolution of Ecological and Environmental Citizen Science." *PLoS One* 12: e0172579.
- Pompe, S., J. Hanspach, F. Badeck, S. Klotz, W. Thuiller, and I. Kuhn. 2008. "Climate and Land Use Change Impacts on Plant Distributions in Germany." *Biology Letters* 4: 564–567.
- Qian, H., C. Badgley, and D. L. Fox. 2009. "The Latitudinal Gradient of Beta Diversity in Relation to Climate and Topography for Mammals in North America." *Global Ecology and Biogeography* 18: 111–122.
- Rahbek, C., M. K. Borregaard, R. K. Colwell, et al. 2019. "Humboldt's Enigma: What Causes Global Patterns of Mountain Biodiversity?" *Science* 365: 1108–1113.
- Randin, C. F., R. Engler, P. B. Pearman, P. Vittoz, and A. Guisan. 2010. "Using Georeferenced Databases to Assess the Effect of Climate Change on Alpine Plant Species and Diversity." In *Data Mining for Global Trends in Mountain Biodiversity*, 149–163. Boca Raton, USA: Press, C.
- Reside, A. E., N. Butt, and V. M. Adams. 2017. "Adapting Systematic Conservation Planning for Climate Change." *Biodiversity and Conservation* 27: 1–29.
- Roth, T., M. Plattner, and V. Amrhein. 2014. "Plants, Birds and Butterflies: Short-Term Responses of Species Communities to Climate Warming Vary by Taxon and With Altitude." *PLoS One* 9: e82490.
- Sanchez-Fernandez, D., J. M. Lobo, and O. L. Hernandez-Manrique. 2011. "Species Distribution Models That Do Not Incorporate Global Data Misrepresent Potential Distributions: A Case Study Using Iberian Diving Beetles." *Diversity and Distributions* 17: 163–171.
- Santangeli, A., T. Toivonen, F. M. Pouzols, et al. 2016. "Global Change Synergies and Trade-Offs Between Renewable Energy and Biodiversity." *GCB Bioenergy* 8: 941–951.
- Scherrer, D., M. Esperon-Rodriguez, L. J. Beaumont, V. L. Barradas, and A. Guisan. 2021. "National Assessments of Species Vulnerability to Climate Change Strongly Depend on Selected Data Sources." *Diversity and Distributions* 27: 1367–1382.
- Seekell, D. A., and M. L. Pace. 2011. "Climate Change Drives Warming in the Hudson River Estuary, New York (USA)." *Journal of Environmental Monitoring* 13: 2321–2327.
- Shrestha, U. B., and B. B. Shrestha. 2019. "Climate Change Amplifies Plant Invasion Hotspots in Nepal." *Diversity and Distributions* 25: 1599–1612.
- Soberon, J., and T. Peterson. 2005. "Interpretation of Models of Fundamental Ecological Niches and species' Distributional Areas." *Biodiversity Informatics* 2: 1–10.
- Somers, R. H. 1962. "A New Asymmetric Measure of Association for Ordinal Variables." *American Sociological Review* 27: 799–811.
- Steen, V. A., M. W. Tingley, P. W. C. Paton, and C. S. Elphick. 2020. "Spatial Thinning and Class Balancing: Key Choices Lead to Variation in the Performance of Species Distribution Models With Citizen Science Data." *Methods in Ecology and Evolution* 12: 216–226.
- Svenning, J. C., and F. Skov. 2007. "Could the Tree Diversity Pattern in Europe Be Generated by Postglacial Dispersal Limitation?" *Ecology Letters* 10: 453–460.
- Telwala, Y., B. W. Brook, K. Manish, and M. K. Pandit. 2013. "Climate-Induced Elevational Range Shifts and Increase in Plant Species Richness in a Himalayan Biodiversity Epicentre." *PLoS One* 8: e57103.
- Theodoridis, S., T. S. Patsiou, C. Randin, and E. Conti. 2018. "Forecasting Range Shifts of a Cold-Adapted Species Under Climate Change: Are Genomic and Ecological Diversity Within Species Crucial for Future Resilience?" *Ecography* 41: 1357–1369.
- Thomas, C. D., A. Cameron, R. E. Green, et al. 2004. "Extinction Risk From Climate Change." *Nature* 427: 145–148.
- Thuiller, W., S. Lavorel, M. B. Araujo, M. T. Sykes, and I. C. Prentice. 2005. "Climate Change Threats to Plant Diversity in Europe." *Proceedings of the National Academy of Sciences of the United States of America* 102: 8245–8250.
- Titeux, N., D. Maes, T. Van Daele, et al. 2017. "The Need for Large-Scale Distribution Data to Estimate Regional Changes in Species

- Richness Under Future Climate Change.” *Diversity and Distributions* 23: 1393–1407.
- Trull, N., M. Böhm, and J. Carr. 2018. “Patterns and Biases of Climate Change Threats in the IUCN Red List.” *Conservation Biology* 32: 135–147.
- Urban, M. C., G. Bocedi, A. P. Hendry, et al. 2016. “Improving the Forecast for Biodiversity Under Climate Change.” *Science* 353: 1113.
- van Vuuren, D. P., J. Edmonds, M. Kainuma, et al. 2011. “The Representative Concentration Pathways: An Overview.” *Climatic Change* 109: 5–31.
- Velásquez-Tibatá, J., P. Salaman, and C. H. Graham. 2013. “Effects of Climate Change on Species Distribution, Community Structure, and Conservation of Birds in Protected Areas in Colombia.” *Regional Environmental Change* 13: 235–248.
- Venables, W. N., and B. D. Ripley. 2002. *Modern Applied Statistics With S-Plus*. 4th ed. New York, NY: Springer.
- Vihervaara, P., A.-P. Auvinen, L. Mononen, et al. 2017. “How Essential Biodiversity Variables and Remote Sensing Can Help National Biodiversity Monitoring.” *Global Ecology and Conservation* 10: 43–59.
- Vincent, C., R. F. Fernandes, A. R. Cardoso, et al. 2019. “Climate and Land-Use Changes Reshuffle Politically-Weighted Priority Areas of Mountain Biodiversity.” *Global Ecology and Conservation* 17: e00589.
- Vitasse, Y., S. Ursenbacher, G. Klein, et al. 2021. “Phenological and Elevational Shifts of Plants, Animals and Fungi Under Climate Change in the European Alps.” *Biological Reviews* 96: 1816–1835.
- Vittoz, P., D. Cherix, Y. Gonseth, et al. 2013. “Climate Change Impacts on Biodiversity in Switzerland: A Review.” *Journal for Nature Conservation* 21: 154–162.
- Vollering, J., R. Halvorsen, I. Auestad, and K. Rydgren. 2019. “Bunching Up the Background Better Bias in Species Distribution Models.” *Ecography* 42: 1717–1727.
- Wiens, J. J., and J. Zelinka. 2024. “How Many Species Will Earth Lose to Climate Change?” *Global Change Biology* 30: e17125.
- WMO. 2017. *WMO Guidelines on the Calculation of Climate Normals*. Switzerland: World Meteorological Organization Geneva.
- Zhang, Z., S. Ma, Á. Bede-Fazekas, et al. 2024. “Considering Biotic Interactions Exacerbates the Predicted Impacts of Climate Change on Coral-Dwelling Species.” *Journal of Biogeography* 51: 769–782.
- Zizka, A., D. Silvestro, T. Andermann, et al. 2019. “CoordinateCleaner: Standardized Cleaning of Occurrence Records From Biological Collection Databases.” *Methods in Ecology and Evolution* 10: 744–751.
- Zurell, D., J. Franklin, C. König, et al. 2020. “A Standard Protocol for Reporting Species Distribution Models.” *Ecography* 43: 1–17.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.