



Loss of habitat suitability and distribution range of the endangered Japanese giant salamander under climate change

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Abstract

Giant salamanders are the world's largest amphibians and keystone predators in riverine ecosystems where they face global declines. Identifying environmental variables influencing their distribution is, therefore, an essential step for their conservation. This study aims to assess the current habitat suitability and distribution of the Japanese giant salamander (*Andrias japonicus*) and to predict changes under future climate scenarios. We used species distribution models (SDMs) over a 282,916 km² area, including 477 high-resolution occurrence data of giant salamanders and seven remote-sensing environmental predictors (climatic, topographic and land use). We projected the prediction maps, identified the most contributing variables and calculated the shifts of suitable areas for three periods (2050, 2070 and 2090) under projected climatic conditions. Climatic variables highly contributed to the distribution of giant salamanders (76% of the total), with preferences for areas with moderate precipitations during cold and wet seasons and mild summer temperatures. A moderately steep surrounding environment was favourable for salamanders, whereas the land-use variables had less influence. Future climate predictions indicate a major decrease of suitable areas. Altogether, our results highlight the habitat preferences of giant salamanders at a broad scale and the negative impact of climate change on future suitable areas. These findings provide important steps for upcoming conservation actions for this threatened species in delineating favourable distribution ranges and priority areas that should be directly affected by climate

change. Finally, they emphasise the need for new research at a fine scale on disturbances to the aquatic habitat to enhance the conservation of giant salamanders.

Highlights

- We used a species distribution model (MaxEnt), high-resolution occurrence data and remote sensing data (climatic, topographic and land use) to identify suitable habitats for the Japanese giant salamander in Japan.
- The most suitable environments for the Japanese giant salamander are located both within and beyond its current distribution range, with the 'Japanese Alps' forming an impassable natural barrier.
- Among the variables studied, precipitation of the warmest quarter, precipitation of the coldest quarter, mean temperature of the warmest quarter and mean temperature of the wettest quarter were the most important environmental predictors of the species' distribution.
- Climate change is expected to severely reduce the potential suitable geographical areas for the Japanese giant salamander in the future.
- The present work calls for new surveys based on the projected maps to improve the mapping of salamander distribution and to focus on ecological features and threats at the aquatic habitat level to understand the risks to their populations.

Keywords

Amphibian decline, *Andrias japonicus*, climate change, ecology, giant salamanders, habitat suitability, MaxEnt, projected distribution maps, species distribution models

Introduction

In recent decades, an increasing number of species have faced multiple threats to their survival, leading to a drastic biodiversity decline. Climate change is one of the main global environmental concerns, posing miscellaneous issues such as habitat modifications, alterations of species interactions (Parmesan 2006; Bellard et al. 2012) as well as shifts in species phenology and distribution ranges (Thomas et al. 2001; Chen et al. 2011; Zhu et al. 2012; Rödder et al. 2021). Ultimately, climate change can lead to extinction processes at local and/or global scales. Anticipating the impacts of climate change on the future distribution of species is one of the key goals of biodiversity conservation (Dawson et al. 2011; Muluneh 2021). In this perspective, species distribution models (SDMs) have proven to be efficient tools available for ecologists to achieve this goal (Zellmer et al. 2020; Seaborn et al. 2021).

SDMs have become one of the most widely used tools in macroecology in recent years (Zurell et al. 2020). They have been used to highlight relationships between species distributions and environmental variables and have been shown to perform well in determining the natural distributions of species and identifying their environmental predictors (Elith and Leathwick 2009). Different types of key environmental determinants can be identified through SDMs, such as climate, topography, geology and land use (Hirzel et al. 2006). Furthermore, SDMs can be projected to multiple scenarios in time and space (Werkowska et al. 2017; Yates et al. 2018). Therefore, SDMs have been widely used for species conservation and management (Franklin 2010; Guisan et al. 2013). More specifically, they provide insights into the habitat suitability and ecological requirements of species (Guisan et al. 2017), allowing predictions of potential spatial distributions, but also to delineate conservation areas (Esselman and Allan 2011; Denoël and Ficetola 2015; Chen et al. 2017) and to predict range shifts, such as those caused by climate change (Hijmans and Graham 2006; Zhang et al. 2020; Mi et al. 2023).

Amphibians are the most threatened vertebrates, with 40.7% of species globally threatened (Luedtke et al. 2023), and climate change is a dominant driver of conservation status deterioration (Araújo et al. 2006; Ceballos et al. 2017). The effects of climate change on amphibians are multifaceted, including eco-physiological shifts, changes in biogeographical characteristics and distribution range shifts (Li et al. 2013). Key amphibian responses to climate change, such as shifts in phenology, altitudinal distributions, and interactions with parasites, are relatively well understood, but

there is still a lack of knowledge on how their distribution may shift with climate change to address efficient conservation planning (Li et al. 2013). These conclusions have encouraged conservation biologists to study more precisely the impact of climate change on the distribution of a variety of amphibian species and the implications for their conservation (Schivo et al. 2019; Mi et al. 2022; Souza et al. 2023).

Giant salamanders (family Cryptobranchidae) are “living fossils” with a suite of unique traits, particularly their huge size (up to 1.8 m long), but also their retention of some larval traits at the adult stage (i.e. paedomorphosis), aquatic lifestyle, external fertilisation, parental care and walking mode of locomotion (Kawamichi and Ueda 1998; Okada et al. 2008, 2015; Bonett et al. 2022). They are facing severe declines, with the largest species now extinct or critically endangered in the wild (China), mainly due to overharvesting (Pan et al. 2016; Pitt et al. 2017; Turvey et al. 2018; Marr et al. 2024). The Japanese giant salamander (*Andrias japonicus*) is endemic to Japan, distributed from the southwest of Honshu Island to Gifu Prefecture in the centre of the island and the ‘Japanese Alps’ in the east. The species is absent from the northern part of Japan (north of the ‘Japanese Alps’ in Honshu Island). It is also present in Kyushu Island (Oita Prefecture) and possibly on Shikoku Island (IUCN SSC Amphibian Specialist Group 2022) (Fig. 1). This species is facing many anthropogenic threats, such as habitat destruction and fragmentation, but is still likely to persist as the species has been protected under Japanese law as a “special natural monument” since 1952 (Tochimoto et al. 2007; Taguchi and Natuhara 2009). The main conservation challenge for the Japanese giant salamander is the lack of information on its ecology in the wild, of global analyses across its range and the implementation of management measures (Okada et al. 2008; Bjordahl et al. 2020). Japanese giant salamanders are known to prefer relatively cold mountainous streams with high levels of dissolved oxygen that likely promotes breathing through their skin (Kawamichi and Ueda 1998; Okada et al. 2008; G. Da Silva Neto et al. 2023), implying potential negative impacts of climate change on its habitat suitability. It is therefore likely that their distribution is dependent on climate drivers such as shown in other giant salamanders (Zhang et al. 2020; Sutton et al. 2023). On another hand, as in the case of the North American giant salamander, also known as the hellbender (*Cryptobranchus alleganiensis*) (Bodinof Jachowski et al. 2016; Pugh et al. 2016), agricultural areas may negatively affect the species, but little is known concerning land use surrounding rivers used by Japanese giant salamanders.

The major objectives of this study were to determine the potential habitat suitability of the Japanese giant salamander both within and beyond the known range of the species, to identify priority areas and to highlight the environmental drivers of its distribution. The limits of the distribution due to the ‘Japanese Alps’ and possibly to unfavourable climatic conditions will be investigated to understand the absence of the giant salamanders beyond this geographical barrier. The second main purpose of this

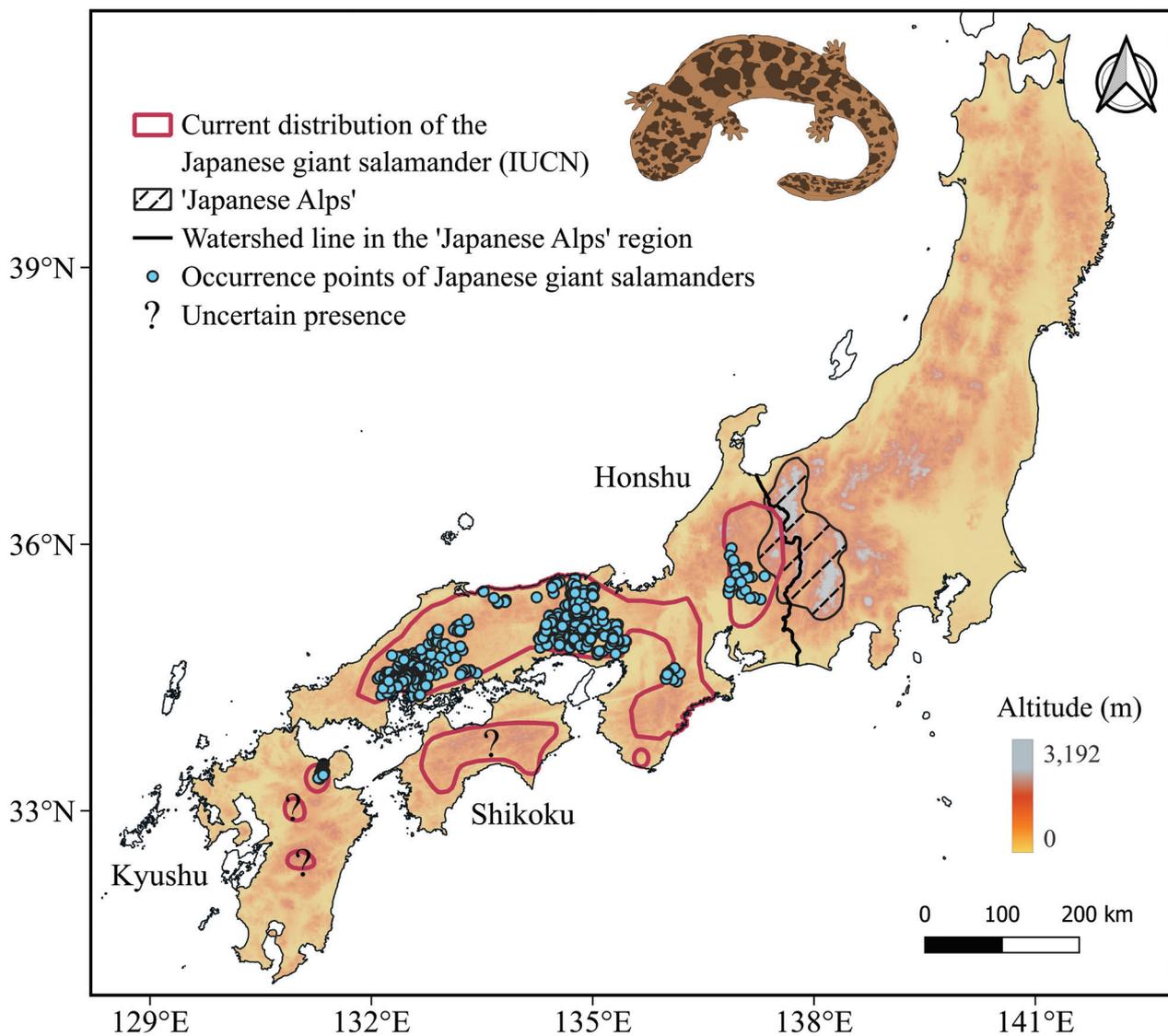


Figure 1. Distribution map of the Japanese giant salamander in Japan (Honshu, Shikoku and Kyushu Islands) provided by the IUCN SSC Amphibian Specialist Group in 2022 (modified) with the occurrence points used in the study (blue dots). The map background represents the mean altitudes (1×1 km grid, Ministry of Land, Infrastructure, Transport and Tourism of Japan).

study was to make projections of the future distribution of Japanese giant salamanders according to climate change scenarios. Our SDM approach took the benefit of combining a large number of precise locations of salamander occurrences across the distribution range with a multiple set of fine-scaled environmental variables, including climatic, topographic and land-use variables. We hypothesised that climatic variables should have a very large contribution to the distribution model and that cold and wet conditions in hilly areas should favour this species, whereas land use should less affect this species due to its fully aquatic lifestyle. We presume that areas with excessive precipitation are likely unsuitable for the species, due to excessive risk of flooding. We hypothesised that the future climate will globally result in the contraction of suitable habitats for the Japanese giant salamander within its current range. Given the climate differences between the northern and southern parts of Honshu Island, we hypothesised that climate change may make areas in the northern part of

Japan, i.e. beyond the current range of the species, more suitable for Japanese giant salamanders in the future than within the current range.

Materials and methods

Study area

To investigate the distribution of suitable habitats for the Japanese giant salamander, we defined the study area, based on the actual range of the species provided by the IUCN (IUCN SSC Amphibian Specialist Group 2022), covering the western part of Japan (western Honshu Island, Kyushu and Shikoku) (Fig. 1). The eastern limit of the actual extent of the species corresponds to the 'Japanese Alps', a series of mountain ranges bisecting Honshu Island and supposed to represent a natural barrier to the distribution of the species. To investigate the potential suitable areas

in Japan and to verify if the natural barrier could prevent the species from reaching favourable areas to the north of Japan, we included the entirety of the Honshu, Shikoku and Kyushu islands in the study, which extend eastwards from 129.34°E to 142.06°E and northwards from 30.99°N to 41.54°N, covering a total area of 282,916 km².

Species occurrence data

The occurrence data of Japanese giant salamanders were obtained from our field surveys as well as from previously published studies in Hyogo, Hiroshima, Gifu, Mie, Nara, Oita, Osaka, and Tottori Prefectures (Kuwabara et al. 2005; Tochimoto et al. 2007; Okada et al. 2008; Taguchi and Natuhara 2009; Bjordahl et al. 2020). In total, we gathered 1,228 presence records of Japanese giant salamanders. These data were collected between 1970 and 2024 (primarily after 1995) and align with the data range of the environmental predictors used in the study. Only high-resolution occurrence data (mainly GPS points) were used in this study, which fall within the grid cells used for environmental data. To avoid spatial autocorrelation issues (i.e. overfitting bias) in establishing the SDMs (Dormann et al. 2007, 2013), the data were filtered using the “spThin” package in R (Aiello-Lammens et al. 2015). Spatial filtering of the data is considered to be a robust correction method for SDMs (Kramer-Schadt et al. 2013; Boria et al. 2014; Fourcade et al. 2014). We randomly selected occurrence data localities that were at least 1 km apart from each other. We selected this distance because this study was conducted at a 1 km² grid scale and because the mean potential migratory distance of Japanese giant salamanders lies typically within this spatial scale (Taguchi 2009). After the thinning procedure, we obtained and used 477 presence data to run the models (Fig. 1).

Environmental predictors

To assess the distribution of the Japanese giant salamander, we used the presence data and their corresponding environmental characteristics, considering climatic, topographic and land-use predictors at a 1 km² resolution. As it is recommended to avoid too many predictors in the same models and to focus on variables likely to influence the distribution of the species (Ficetola et al. 2014; Fourcade et al. 2018), we used a limited set of environmental variables to perform the models, selected according to the Japanese giant salamander’s ecology (Okada et al. 2008; Harris et al. 2013; Bjordahl et al. 2020; Soley-Guardia et al. 2024). Four climatic variables were selected among the 19 bioclimatic variables of WorldClim version 2 climate dataset (Fick and Hijmans 2017) at a high (1 km²) spatial resolution: mean temperature of the wettest quarter (Bio8), mean temperature of the warmest quarter (Bio10), precipitation of the warmest quarter (Bio18) and precipitation of the coldest quarter (Bio19). Bio8 and Bio10 were selected because high temperature may be a critical condition

for the survival of the Japanese giant salamander. An increase in air temperature is indeed expected to raise water temperature as well as reduce dissolved oxygen concentration, which is a major parameter for salamander respiration. Bio18 and Bio19 were included because the Japanese giant salamander is entirely aquatic and lives in stream ecosystems; precipitation is, therefore, a critical parameter for survival. The mean slope of each 1 km² grid cell was selected over mean altitude as a topographical predictor because mean altitude was highly correlated with temperature predictors and to focus on the specific aspects of slopes (e.g. on water flow). Agricultural (including all types of agricultural activities) and urban areas (i.e. considering all kinds of man-made artificial areas) were included in the model processing as land-use variables. Japanese giant salamander populations can be found in various types of environments, such as agricultural areas and they are also occasionally found in densely built urban areas (Okada et al. 2008). We also made sure to use uncorrelated predictors. The Pearson correlation coefficient was used to assess multicollinearity between selected variables (all selected variables with $R < 0.558$; Suppl. material 1: table S1; Suppl. material 2: table S2 for details on each data sources) (Elith et al. 2006; Fourcade et al. 2018).

Species distribution modelling

SDMs for the Japanese giant salamander were developed using MaxEnt 3.4.1 (Phillips et al. 2006). This is a presence – background method comparing the relationship between environmental conditions of species-specific locations to the conditions along the entire background (Phillips and Dudík 2008). MaxEnt has the advantage of balancing goodness-of-fit with model complexity and being relatively easy to calibrate (Muscarella et al. 2014). To carry out distribution modelling, we followed recommendations to avoid violation of key assumptions in SDMs (Sillero and Barbosa 2021; Sillero et al. 2021; Soley-Guardia et al. 2024). To ensure that the model captures the environmental conditions specific to the current distribution of the Japanese giant salamander, we used only the known range of the species and restricted the background to this area during the model training phase. Once the model was developed, we projected it on to a broader area, including the northern part of Honshu Island, to explore potential habitat suitability beyond the current range. The selection of background (or pseudo-absence) data localities for SDMs is an important consideration. SDMs such as MaxEnt require data of species presence and also of the available environmental conditions (background) in the area (Barbet-Massin et al. 2012). The choice of the spatial extent from which background data are taken can seriously affect model performances and variable importance (VanDerWal et al. 2009; Elith et al. 2010; Fourcade et al. 2014). As there was a sampling bias concerning our occurrence data, we used a bias file implemented in the MaxEnt models to also apply a bias correction on the selection of the background. We created a

bias grid by delineating a Minimum Convex Polygon (MCP) around occurrence localities buffered by 50 km to also more broadly consider the watersheds in which the points of occurrence bordering the MCP are located (Peterson et al. 2011). In total, 10,000 background points were then randomly sampled from the selected background extent.

Data partition

We considered ‘masked geographically structured rules’ (Radosavljevic and Anderson 2014) to partition occurrence data and the environmental predictors into training and validation data subsets. We chose to use the spatial partitioning ‘block’ method that increases model transferability across space and time. This is a method that fits our study objectives on projecting our SDM into a novel spatial extent (north of Japan) and estimating the impact of future climate change on species distribution and habitat suitability (Muscarella et al. 2014). Species occurrence data were partitioned in four parts (i.e. through a 4-fold spatial partition) by the latitude and longitude and both occurrence and background data were then attributed to a spatial group depending on their location. This method reduces spatial autocorrelation between training and validation data (Roberts et al. 2017).

Model calibration

Model tuning and selection were performed using the R package ENMeval 2.0 (Kass et al. 2021). Two main settings were used to adjust model fitting: features classes (FC), which regulate the format of the marginal response curves and the relationship between environmental and background data and regularisation multipliers (RM), representing a penalty of including variables in the model. For example, models with complex FC associations and lower RM values result in more complex model predictions (Elith et al. 2011; Phillips et al. 2017).

We tested different combinations of simple and complex feature classes – L, LQ, H and LHQ (L = linear, Q = quadratic, H = hinge). We excluded the “product” and “threshold” feature classes as their omission results in easier to interpret models (Kass et al. 2020). For each feature class combination, we tested nine regularisation multipliers (1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5). This parameter control model complexity, with small values leading to overly complex models and high values to more simple models (Radosavljevic and Anderson 2014). The different RM values combined with the feature classes resulted in a total of 36 parameter combinations. Model selection was performed using the corrected Akaike Information Criteria (AICc) (Akaike 1974). Top models with $\Delta\text{AICc} < 2$ were selected (Burnham and Anderson 2002). If several models were selected, we chose the models with the highest AUC ratio for the partial ROC performance metric (Peterson et al. 2011). To highlight the relationship between habitat suitability and environmental predictors for the Japanese

giant salamander, we constructed species response curves for each environmental variable.

As SDMs selected by minimising AICc may not perform well on withheld data (Galante et al. 2018), we determined the confidence and effect sizes of the performance metrics of the tuned model by comparing them to those calculated with null models. If the performance metrics of the empirical model did not differ from metrics calculated with the null models, the confidence in the evaluation metrics was considered as low (Raes and ter Steege 2007). We built null models using the same occurrence data, with the same spatial partitioning parameters (4-fold partition) as the empirical model and using 100 iterations to create different null models. For each iteration, n localities across the training folds were selected, where n is equal to the total number of real occurrence localities in these folds and then evaluated the model on the real Japanese giant salamander occurrences in the withheld fold (also using the same background values). We used a L (linear) feature class and a regularisation multiplier of 5 to create the null models, which correspond to simple models. Null models were generated using the R package ENMeval 2.0 (Kass et al. 2021).

Future habitat suitability projections

We generated future projections of the Japanese giant salamander distribution for three periods: 2050 (average for 2041–2060), 2070 (average for 2061–2080) and 2090 (average for 2081–2100). We considered two shared socioeconomic pathways (SSPs) scenarios (i.e. climatic scenarios), based on the representative concentration pathways (RCPs): SSP126, a remake of the RCP2.6, equal to the optimistic scenario (i.e. with a reduction of carbon dioxide emissions in the future) and SSP370, a scenario between RCP6.0 and RCP8.5, which represents the pessimistic scenario (i.e. with a continuous increase of carbon dioxide emissions in the future) in our study. We averaged the climate data among four global circulation models (GCMs) – CMCC-ESM2, MIROC6, IPSL-CM6A-LR and MRI-ESM2-0 – to reduce the uncertainties among the models in order to produce the maps of future habitat suitability of the Japanese giant salamander. Future climate projections for all models were retrieved from WorldClim version 2 (Fick and Hijmans 2017). In addition, we ran multivariate environmental similarity surface analysis (MESS) to evaluate and identify potential high extrapolation risk when projecting the model to new areas and new periods (Elith et al. 2010). MESS measures the similarity between the climatic conditions at a point in time and the reference layer. Thus, we ran a MESS analysis to compare the climatic variables of the reference layer (corresponding to the extent of the bias grid created to sample the background) that we used to develop the model and the climatic variables of the projection layer (all Honshu, Shikoku and Kyushu Islands) and we also ran six MESS to compare the present climatic conditions of all Japan and the future conditions (six different future conditions). All the MESS

analysis highlighted small areas of extrapolation, meaning a high environmental similarity for each condition tested and, therefore, a low extrapolation risk when projecting the model. One example of MESS results is presented in the supplementary materials (Suppl. material 3: fig. S1).

The selected model for current habitat suitability and the projections were mapped on to the study area using a log-log ('cloglog') approximation of the probability of presence of the species (Phillips et al. 2017). In order to calculate the surface areas of areas favourable to the species, probability values (ranging from 0 to 1) were classified into four categories using the Jenks natural breaks classification method (Jenks 1963): unsuitable (0–0.11), low suitability (0.11–0.37), moderate suitability (0.37–0.72) and high suitability (> 0.72). Classification and map rendering were performed using ArcMap 10.8.1 (ESRI) and QGIS 3.34.6.

Results

The optimal MaxEnt model included all LQH feature classes and a small value of regularisation multiplier ($rm = 1$), suggesting a complex relationship between the Japanese giant salamander distribution and the environmental predictors. The training AUC with this model was 0.87, the average validation AUC was 0.71 ± 0.11 . The partial ROC AUC ratio was 1.43. The model performed convincingly when its metrics were compared to those of the null models (Suppl. material 4: fig. S2).

Habitat suitability and environmental predictors importance

The selected MaxEnt model was mainly influenced by climatic predictors with a total contribution of 76.21%, which was split into 36.73% for the precipitation of the warmest quarter (Bio18), 13.77% for the precipitation of the coldest quarter (Bio19), 13.54% for the mean temperature of the warmest quarter (Bio10) and 12.17% for the mean temperature of the wettest quarter (Bio8). Precipitation and temperature variables contributed to 50.5% and 25.71% of the model, respectively. The contribution of the mean slope was of 11.62%. Land-use predictors (urban and agricultural) contributed to 9.36% and 2.81%, respectively. All contribution values are based on the permutation importance of each variable.

According to the response curves of the five most contributing environmental predictors, the probability of presence of Japanese giant salamanders was the highest in areas with an average air temperature around 20–24°C, whereas all areas between freezing average temperature and 20° air temperature, as well as those warmer than 24°C, were less favourable. The probability of presence of the Japanese giant salamanders is high at relatively low average precipitation, with increase of precipitations favourable in the coldest quarter (around 100–300 mm)

and unfavourable in the wettest quarter, with a sharp decrease of suitability above 500 mm precipitation. Beside climatic variables, the probability of presence increased with the mean slopes of the surrounding lands up to 17% but decreasing for steeper areas (Fig. 2). The two land-use variables (agricultural and urban areas) were the two least contributing variables (Suppl. material 5: fig. S3).

The current habitat suitability map for the Japanese giant salamander (Fig. 3) highlights the presence of highly suitable areas for the species both within and beyond the current range of the species. Focusing on the current distribution area of the species (59,193 km² in total), 30% were identified as unsuitable (17,712 km²), 37% with low suitability (21,853 km²), 22% with moderate suitability (13,166 km²) and 11% with high suitability (6,462 km²). In the area beyond the range of the species (223,723 km²), unsuitable areas represent 36% (81,276 km²), low suitability 30% (66,073 km²), moderate suitability 15% (33,866 km²) and high suitability 19% (42,508 km²).

Future Japanese giant salamander range

The results of the projections of future changes in habitat suitability (Fig. 4) indicate that climate change is expected to lead to a restriction of the current distribution ranges. Decreases in habitat suitability and range expansion are predicted both within and beyond the currently occupied areas (Fig. 4). Considering the extent of the current distribution of the Japanese giant salamander, there will be a loss of habitat suitability in more than 50% of the geographic area at any time in the future (2050–2090) and this, for both future climate scenarios (Fig. 5). The loss of suitable habitats is more important when considering the pessimistic scenario for all time periods, with the most important loss (in 64.5% of the area) predicted in 2090. In 2050, the proportion of areas gaining in suitability is higher in the pessimistic scenario (13.6%) than in the optimistic scenario (11.1%). The largest increase in suitability is observed in 2070 and 2090 with the optimistic scenario, with an increase in 14.5% and 14.3% of the area, respectively. It is slightly lower for the pessimistic scenario for the same periods (10.7% and 9.1%, respectively).

Discussion

Our SDM approach allowed us to delineate suitable areas, determine environmental drivers of distributions and predict changes in the geographic range of the emblematic and threatened Japanese giant salamander. It supports globally our hypotheses, particularly highlighting the role of climatic drivers in explaining distribution patterns. These findings provide new key information on the role of climate change in causing a loss of favourable habitats for this original freshwater megafauna species. Altogether, these global threats add to the risks associated with habitat fragmentation and destruction (He et al. 2017).

Environmental predictors and present potential distribution

Of the seven tested environmental predictors, six had a contribution to the distribution of the species greater than 10% (Fig. 2) and the four most contributing variables are climatic. They show that precipitation and temperature are important drivers of the distribution of the species. More specifically, precipitation of the warmest and the coldest seasons are the most contributing variables. Precipitation is closely related to the living environment of giant salamanders. The amount and periodicity of precipitation affect water quantity and stream velocity (Allan et al. 2021), a critical factor for salamanders as cutaneous respiration is essential to their survival. An increase in water velocity and mixing facilitate the dissolution of oxygen in water

(Ultsch 2012). However, our results also indicate that excessive precipitation could be a detrimental factor for salamander presence, as strong currents or prolonged flooding are likely to negatively affect their populations. Such large excesses of water flows specifically occur during the warmest months. Studies investigating the effects of flooding on salamander populations, including the hellbender, highlight that flood events particularly affect larval stages, leading to a decline in adult recruitment (Nickerson et al. 2007; Walls et al. 2013). This may also interfere with nesting – a key element in the life of giant salamanders where the male guards the eggs in a submerged cavity, which can be particularly affected in the case of flooding (Okada et al. 2015; Takahashi et al. 2017).

Another important parameter for water velocity and dissolved oxygen is the slope. This parameter also appears to be very important for the distribution of salamanders.

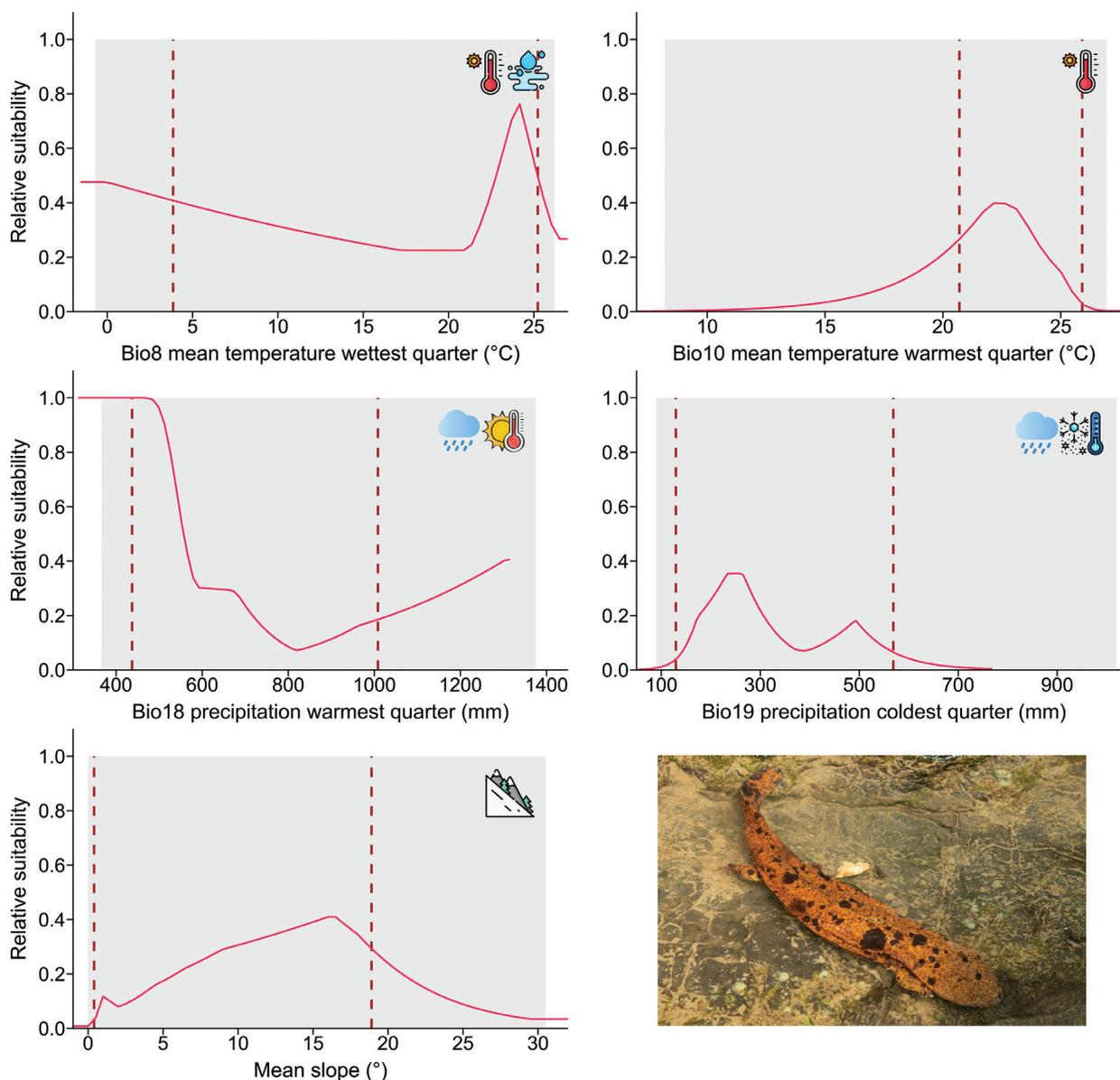


Figure 2. Response curves from the MaxEnt model of the five predictor variables contributing the most to the habitat suitability of the Japanese giant salamander. For each response curve, the grey area represents the range of values observed in Japan and the dotted brown vertical lines delineate the minimum and maximum values of the occurrence data. Photo of Japanese giant salamander by M. Denoël.

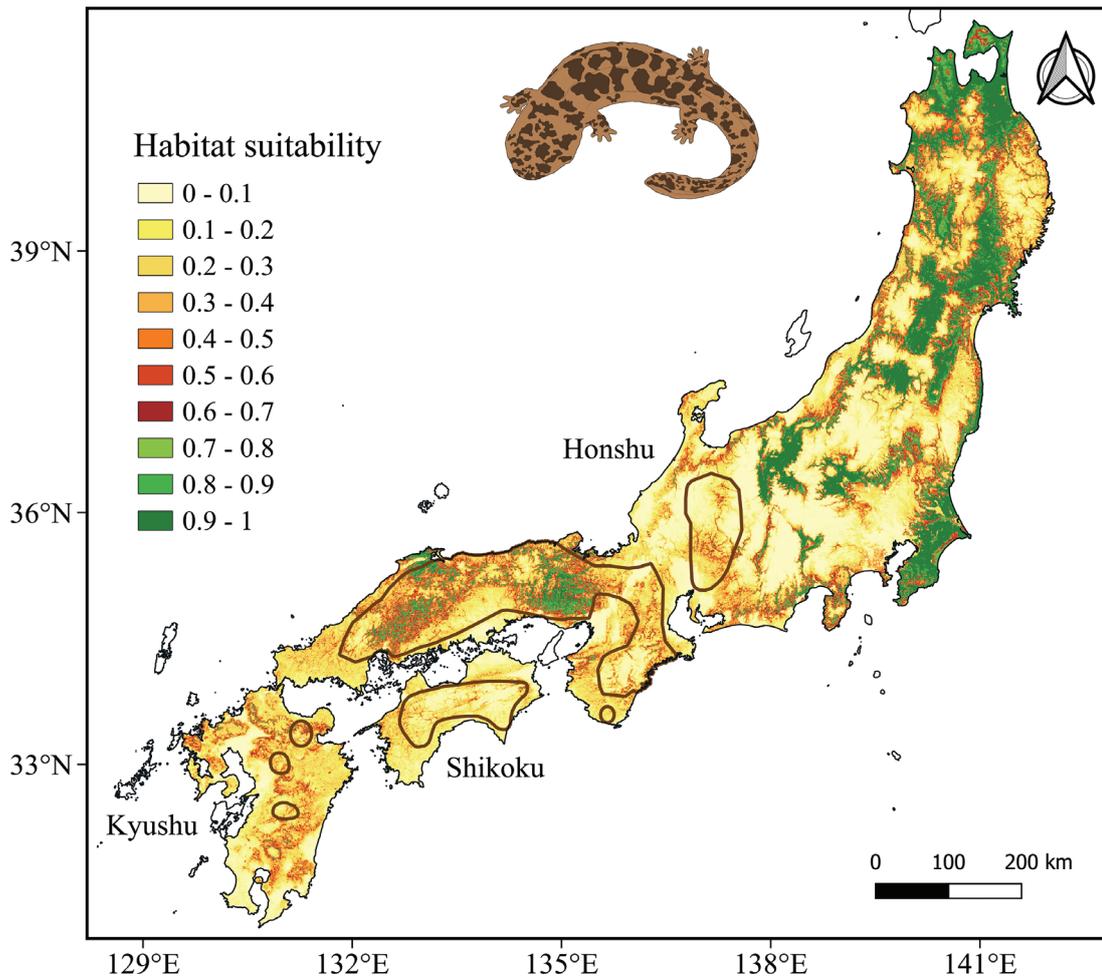


Figure 3. Habitat suitability prediction map of the Japanese giant salamander according to the optimal selected MaxEnt model. Brown thick contour lines represent the current distribution of the Japanese giant salamander according to the IUCN.

The higher the mean slope of the surrounding environment, the higher the probability of the presence of salamanders becomes. However, there is an upper slope limit beyond 17%, where suitability decreases. Steeper slopes result in higher water velocities and, in mountainous areas, streams tend to be smaller as the slope increases, which may not be ideal for giant salamanders. However, the mean slope of the terrain does not necessarily reflect the slope of the rivers. Our results are comparable to those on habitat preferences of the Chinese giant salamander (*Andrias davidianus*), where slope, temperature and precipitations strongly influence habitat suitability for this species (Zhang et al. 2020). The land-use variables tested here (i.e. agricultural areas and urban areas) had only a small contribution to the distribution of the species. These results corroborate the known local data on the habitat preferences of Japanese giant salamanders (Okada et al. 2008). This contrasts with the situation of the Chinese giant salamanders, which are harvested for food and, therefore, less likely to persist near urban areas (Turvey et al. 2018). Nests and larvae of Japanese giant salamanders are often found in small headwaters (Bjordahl et al. 2020). These streams are often surrounded by broadleaf

forests, tree plantations or agricultural areas. Our models suggest that an increase of urbanisation may increase the probability of finding the Japanese giant salamanders. This is, in fact, caused by the urbanisation and associated agriculture which takes place more along the main river network than outside, which means that it often follows the habitat of the salamanders. The long-term persistence of these populations in such areas may, therefore, be uncertain as also shown by the low abundance of the species or the absence of breeding sites (pers. obs.). This is particularly reinforced by the fact that giant salamanders have a long life expectancy (Klein et al. 2024) and may then subsist, but not breed in some habitats for many years following disturbance. Therefore, the long-term viability of salamander populations in urban areas is precarious, due to the artificialisation of streams and rivers (e.g. concrete banks and dams), decreasing catchments and breeding sites availability, as well as impeding connectivity (Tochimoto et al. 2007; Okada et al. 2008; Taguchi and Natuhara 2009; Bjordahl et al. 2020; pers. obs.).

The projection of the current potential distribution (Fig. 3) highlights that, within the current distribution range of the species, many areas present a moderate

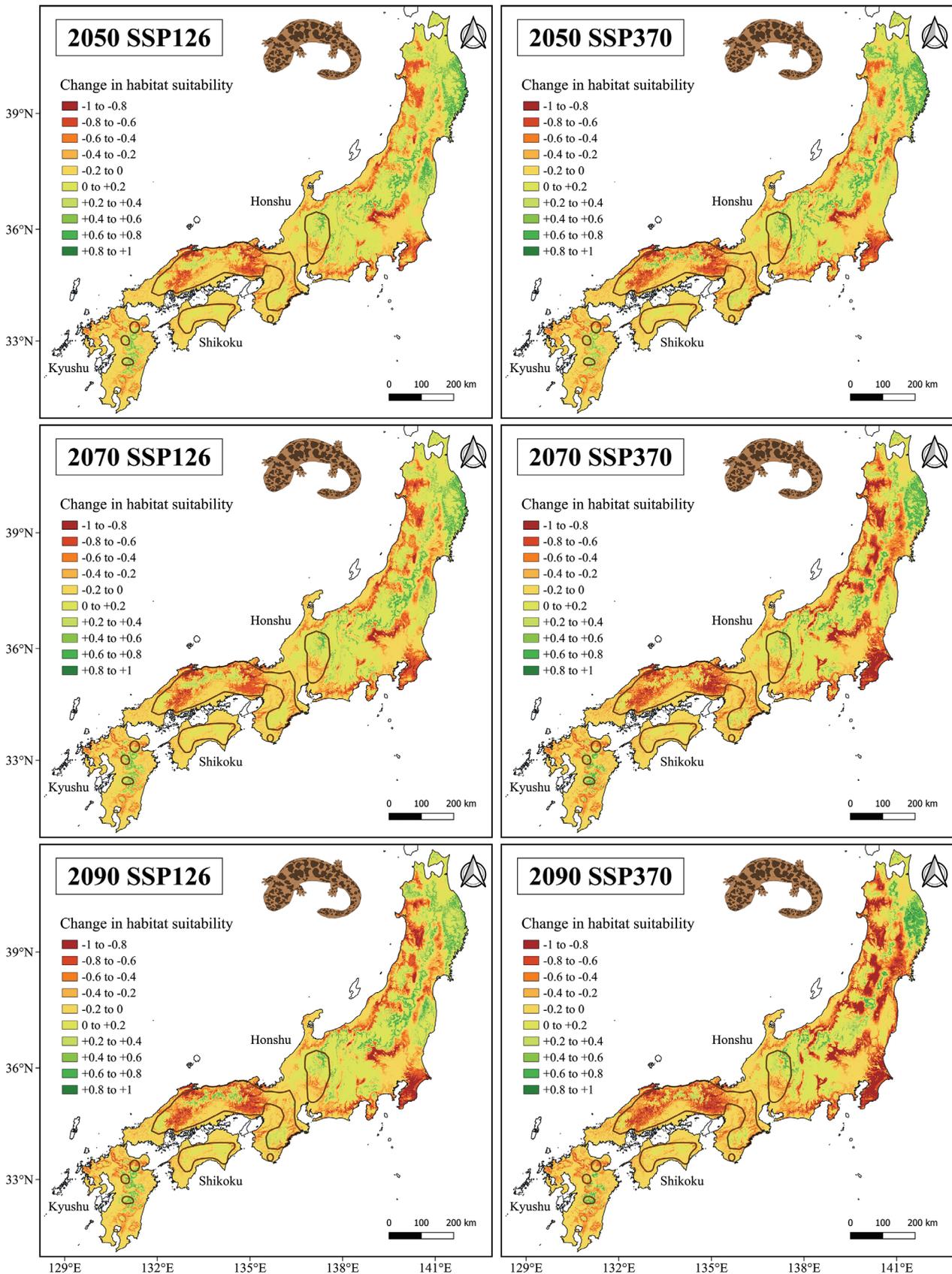


Figure 4. Projection maps of changes in habitat suitability of the Japanese giant salamander for three time periods considering an optimistic (SSP126) and a pessimistic scenario (SSP370) for future climate change. Brown lines represent the current distribution of the Japanese giant salamander according to the IUCN. Change in habitat suitability was determined by subtracting the current habitat suitability (Fig. 1) from the predicted future habitat suitability raster at 1×1 km resolution (Suppl. material 6: fig. S4).

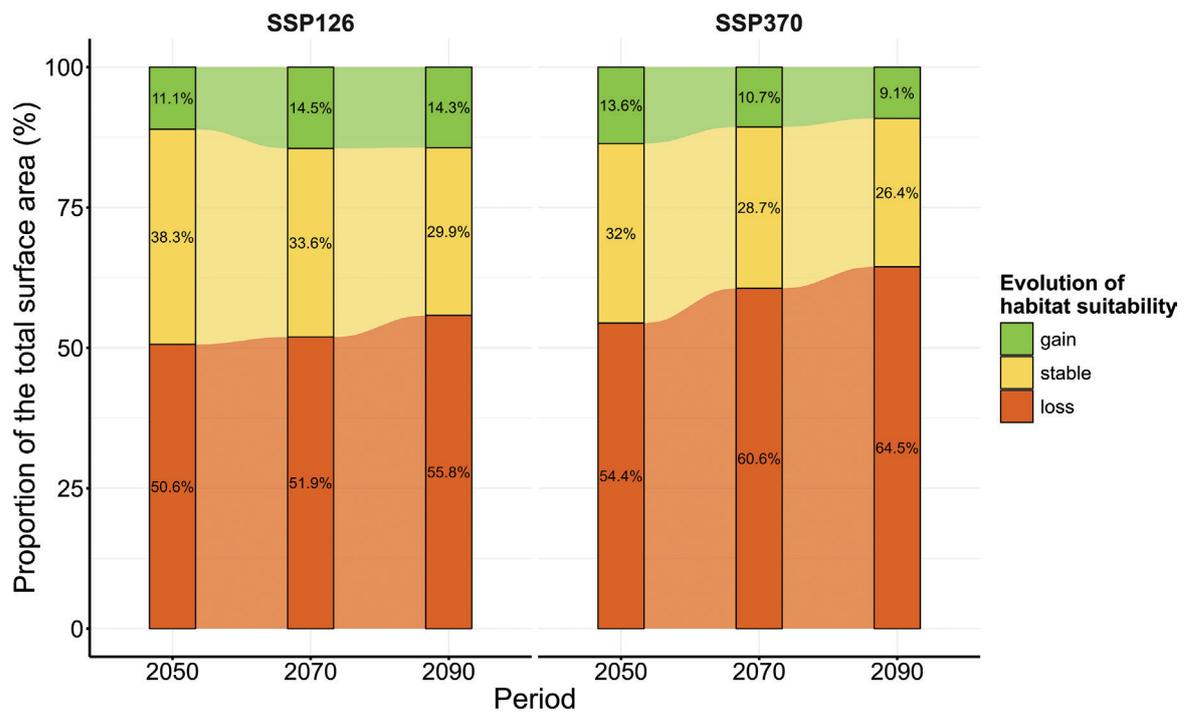


Figure 5. Sankey diagrams of the predicted evolution of habitat suitability within the current distribution range of the Japanese giant salamander for each time period (2050, 2070 and 2090) and climate change scenario (SSP126: optimistic scenario; SSP370: pessimistic scenario). A gain of habitat suitability was considered when the change in habitat suitability was > 0.1 , a loss was identified when the change was < -0.1 and stability when the change was between -0.1 and 0.1 .

(red colour) and high suitability (green colour). However, several regions of the distribution of the species provided by the IUCN (IUCN SSC Amphibian Specialist Group 2022) include unsuitable habitats projected by our model, especially throughout Shikoku Island. Few detailed data about the distribution in Shikoku Island are available in literature and, therefore, our study provides a foundation for future mapping efforts, focusing on areas of medium to high suitability and under-sampled regions, as it has been done with the hellbender (Freake and DePerno 2017). More specifically, there is a particular need for more surveys on the large islands of Shikoku and Kyushu. Although palaeontological evidence of the species presence from the Ehime Prefecture in Shikoku was reported by Shikama and Hasegawa (1962), Ikoma (1963) mentioned the discovery of only two individuals on the island without providing a map. Kobara (1985) reported scattered occurrences across the island (included in unfavourable areas according to our models) and Matsui (2008) pinpointed a single locality in Shikoku Island, from Tokushima Prefecture (these occurrence references were not included in the occurrence data of the present study as the precise location were not available). Similarly, the presence of the species in Kyushu Island was only clearly mapped in the Oita Prefecture. In Honshu Island, the distribution is split into two main areas, with most locality data coming from the western part. Although some mountain barriers may be responsible for this separation, which also explains the genetic difference between these two groups of populations (Matsui et al. 2008), some of the areas appeared as

suitable and would deserve future surveys. Moreover, within their distribution range, giant salamanders were found in some areas classed as moderately suitable according to our models suggesting either conservation issues (i.e. possible future declines) or the need for complementary samplings to fine tune the models. In this perspective, the use of eDNA surveys could give promising data to be followed up by visual surveys of positive sites (Bjordahl et al. 2020; Neto et al. 2020; Hidaka et al. 2024). In the northern part of Japan, numerous habitats have been identified as potentially highly suitable for Japanese giant salamanders. This finding aligns with our initial hypotheses, suggesting that the climatic differences between the northern and southern regions of Japan do not account for the current absence of the species in the north. Instead, the biogeography of the Japanese giant salamander and the natural barrier formed by the Japanese Alps in the centre of Honshu Island appears to be the primary factor preventing the species from establishing a wider distribution.

Potential future distribution and influence of climate change

Our projections of the distribution of the Japanese giant salamander in the upcoming decades using SDMs suggest that suitable areas for the species will severely decrease both within and beyond the current distribution range of the species. The decrease of highly suitable areas will be more moderate beyond the current distribution

range of the species (Fig. 4), especially if we consider the optimistic scenario. These results suggest that climate change may have direct negative effects on Japanese giant salamander populations. It is in accordance with previous studies of the Chinese giant salamander (Zhang et al. 2020) and the North American giant salamander (Sutton et al. 2023) as for these other species, the predictions made revealed that future distributions may be severely reduced under climate change. The maps of habitat suitability changes (Fig. 4) and future habitat suitability (Suppl. material 6: fig. S4) show that, within the current distribution range, the most suitable areas will be mainly restricted to inland regions of Honshu and Kyushu Islands in the future, while on the island of Shikoku, highly suitable areas seem to be absent by 2050. Future climatic projections suggest that the intensity of precipitations and temperature will increase (but with local variations) in all regions of Japan (Takabatake and Inatsu 2022). One main issue of the increase of heavy and sustained rainfalls is that it increases the frequency of flooding events (Shakti et al. 2020; Hatsu-zuka et al. 2021), a noticeable disturbance for the species, suggesting a potential negative influence on Japanese giant salamander survival. On the other hand, the life habits of giant salamanders, especially their fully aquatic life and benthic mode of locomotion, may turn out to be a protection from climate extremes (Brooks and Kindsvater 2022). This lifestyle and habitat may have supported the survival of giant salamanders as a fully aquatic clade for millions of years. However, data are currently lacking to investigate how water temperature would be locally affected by increasing global temperatures and, therefore, long-term monitoring on rivers is needed to assess such changes more precisely. A study conducted on the North American giant salamander (*Cryptobranchus alleganiensis*) showed that a 2°C increase in temperature decreased the immune function and growth rate and increased physiological stress of the individuals (Terrell et al. 2013).

Potential habitat suitability in the north and dispersal limitations

Our findings suggest that the northern part of the Honshu Island may be able to hold large areas of suitable habitats for the Japanese giant salamander in the present and the future (Figs 3, 4, Suppl. material 6: fig. S4). However, access to these potential areas is limited as the main barrier to salamanders' expansion to the north is represented by the 'Japanese Alps', a mountain chain bisecting Honshu Island (Fig. 1) and, therefore, fully preventing the direct cross and dispersal of this species, which could not climb terrestrial environments outside of riverine areas. Ultimately, natural dispersal to the north is, therefore, unrealistic. Considering that habitat suitability within the current distribution range of giant salamanders will severely decrease in the future (Fig. 4), increased habitat fragmentation could exacerbate dispersal limitations in this area. This may increase the vulnerability of the species to climate change

by preventing access to potentially suitable habitats (Cappat et al. 2016). This very specific condition allows us to keep in mind that distinction must be made between the potential distribution (all the suitable habitats) and the actual distribution (also called realised distribution) of a species (De Kort et al. 2020). In our study, we predicted the potential distribution of the Japanese giant salamander without accounting for dispersal constraints, specifically to illustrate how the 'Japanese Alps' restrict its distribution primarily to the south-western regions of Japan. Another major obstacle to dispersal is the low habitat connectivity caused by dams, which can reduce or block movements of this species along the inhabited watercourses (Tochimoto 1995; Taguchi and Natuhara 2009; Takahashi et al. 2016).

Conservation and management implications

In addition to highlighting that the Japanese giant salamander populations would be threatened by future climate change, it is necessary to keep in mind the current endangered status of this species. The conservation status rank of the species was changed from Near Threatened to Vulnerable in the 2022 IUCN Red List (IUCN SSC Amphibian Specialist Group 2022), but is likely to be reassessed as many populations are, in fact, declining. Moreover, due to the long life expectancy of this species, the real status of the populations is difficult to assess. This species is facing many other threats and one of the most disturbing is habitat degradation and fragmentation (Takahashi et al. 2016). Habitat fragmentation is particularly due to dam construction for agriculture and flood control to protect human settlements (Taguchi and Natuhara 2009; Borzée et al. 2024). These facilities deeply affect the habitat connectivity within and between waterways, as well as the suitability of breeding microhabitats. Thus, we have identified potential future suitable habitats for *A. japonicus* within the current distribution range, but without connectivity between habitats, they would be inaccessible to the giant salamanders. The study of habitat connectivity is fundamental to biodiversity conservation (Correa Ayram et al. 2016), but such data are not yet available for modelling at the country scale. As a fully aquatic species, Japanese giant salamanders have limited migration abilities when facing barriers in the rivers and long-distance migration is unrealistic. These findings suggest that the highest conservation priority for Japanese giant salamanders is to characterise their ecology at a local scale, such as habitat preferences and implement the most effective conservation actions possible to preserve populations and improve habitat connectivity (Bjordahl et al. 2020). Moreover, the decreasing trend of the human population in Japan, especially in rural areas, could benefit Japanese giant salamander populations by reducing human pressure on giant salamander habitats. For example, an increasing number of small agricultural dams are no longer maintained and eventually burst (pers. obs.), restoring habitat connectivity. However, the

construction of facilities to control floods and damages due to erosion is increasing in Japan (Itsukushima 2023), threatening many habitats of the Japanese giant salamander and it is directly linked to climate change.

Conclusions

By using SDMs, we determined environmental predictors influencing the distribution of the Japanese giant salamander (*Andrias japonicus*) and mapped their suitable habitats under current and future climate scenarios. These results can be used as conservation tools for future decisions for the species. Climatic variables are very important in determining suitable areas for the Japanese giant salamander and future climate may have a negative impact in decreasing the quantity of highly suitable habitat areas. Due to their large geographical distribution and their ecological role as top predators in structuring communities, protecting their habitat may also benefit other aquatic species relying on the same habitats (“umbrella effect”) (Sergio et al. 2006, 2008).

Suitable habitat characteristics identified in this study can be considered for future monitoring and conservation surveys for the Japanese giant salamander. Many locations in Japan have not been surveyed and the discovery of new populations may be possible. Similar to efforts in other regions of the world, centralising distribution data of giant salamanders across the different prefectures will allow us to produce distribution maps and analyse changes across time (Denoël et al. 2023). Future investigations are also highly needed to accurately identify the microhabitat preferences of giant salamanders and to enhance distribution models with detailed data on abundance and breeding evidence. This will enable refinement of conservation decisions for habitat protection at both local and global scales.

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Author contributions

C.D. and M.D. conceived the research. All authors contributed to data acquisition. C.D., A.H. and M.D. developed the methodology. C.D. conducted the statistical analyses. M.D. supervised the research. M.D., S.O., O.K., Y.T. and M.K.T. provided resources. C.D. wrote the initial manuscript draft, M.D. revised the different drafts and all authors commented on the manuscript.

Data accessibility statement

Datasets generated during the current study are available from the corresponding author on reasonable request.

References

- Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* 38: 541–545. <https://doi.org/10.1111/ecog.01132>
- Akaike H (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19: 716–723. <https://doi.org/10.1109/TAC.1974.1100705>
- Allan JD, Castillo MM, Capps KA (2021) Stream ecology: structure and function of running waters. Springer, Dordrecht, 494 pp. <https://doi.org/10.1007/978-3-030-61286-3>
- Araújo MB, Thuiller W, Pearson RG (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* 33: 1712–1728. <https://doi.org/10.1111/j.1365-2699.2006.01482.x>
- Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution* 3: 327–338. <https://doi.org/10.1111/j.2041-210X.2011.00172.x>
- Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters* 15: 365–377. <https://doi.org/10.1111/j.1461-0248.2011.01736.x>
- Bjordahl B, Okada S, Takahashi MK (2020) Assessment of small tributaries as possible habitats for larvae and juveniles of Japanese giant salamanders, *Andrias japonicus*, by coupling environmental DNA with traditional field surveys. *Salamandra* 56: 148–158.
- Bodinof Jachowski CM, Millspaugh JJ, Hopkins WA (2016) Current land use is a poor predictor of hellbender occurrence: why assumptions matter when predicting distributions of data-deficient species. *Diversity and Distributions* 22: 865–880. <https://doi.org/10.1111/ddi.12446>
- Bonett RM, Ledbetter NM, Hess AJ, Herrboldt MA, Denoël M (2022) Repeated ecological and life cycle transitions make salamanders an ideal model for evolution and development. *Developmental Dynamics* 251: 957–972. <https://doi.org/10.1002/dvdy.373>
- Boria RA, Olson LE, Goodman SM, Anderson RP (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling* 275: 73–77. <https://doi.org/10.1016/j.ecolmodel.2013.12.012>
- Borzée A, Angulo A, Meredith H, Taguchi Y, Groffen J, Kohler DB, Abernethy JPD, Othman SN, Messenger K, Heo K, Wan L, Um TE, Zhang

- X, Shin Y, Bae Y, Wang Z, Qiu Z, Pearce R (2024) Protecting Japanese giant salamanders (*Andrias japonicus*) in the Nawa River Basin, Japan: policy recommendations addressing water pollution and waterway disruption. *Frontiers in Amphibian and Reptile Science* 2: 1348251. <https://doi.org/10.3389/famrs.2024.1348251>
- Brooks GC, Kindsvater HK (2022) Early development drives variation in amphibian vulnerability to global change. *Frontiers in Ecology and Evolution* 10: 813414. <https://doi.org/10.3389/fevo.2022.813414>
- Burnham KP, Anderson DR (2002) Model selection and multimodal inference: a practical information-theoretic approach. 2nd Edition. Springer-Verlag, New York, 488 pp.
- Caplat P, Edelaar P, Dudaniec RY, Green AJ, Okamura B, Cote J, Krooko J, Jonsson PR, Löndahl J, Tesson SV, Petit EJ (2016) Looking beyond the mountain: dispersal barriers in a changing world. *Frontiers in Ecology and the Environment* 14: 261–268. <https://doi.org/10.1002/fee.1280>
- Ceballos G, Ehrlich PR, Dirzo R (2017) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences* 114: E6089–E6096. <https://doi.org/10.1073/pnas.1704949114>
- Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* 333: 1024–1026. <https://doi.org/10.1126/science.1206432>
- Chen Y, Zhang J, Jiang J, Nielsen SE, He F (2017) Assessing the effectiveness of China's protected areas to conserve current and future amphibian diversity. *Diversity and Distributions* 23: 146–157. <https://doi.org/10.1111/ddi.12508>
- Correa Ayram CA, Mendoza ME, Etter A, Salicrup DRP (2016) Habitat connectivity in biodiversity conservation: A review of recent studies and applications. *Progress in Physical Geography: Earth and Environment* 40: 7–37. <https://doi.org/10.1177/0309133315598713>
- Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM (2011) Beyond predictions: biodiversity conservation in a changing climate. *Science* 332: 53–58. <https://doi.org/10.1126/science.1200303>
- De Kort H, Baguette M, Lenoir J, Stevens VM (2020) Toward reliable habitat suitability and accessibility models in an era of multiple environmental stressors. *Ecology and Evolution* 10: 10937–10952. <https://doi.org/10.1002/ece3.6753>
- Denoël M, Ficetola GF (2015) Using kernels and ecological niche modeling to delineate conservation areas in an endangered patch-breeding phenotype. *Ecological Applications* 25: 1922–1931. <https://doi.org/10.1890/14-1041.1>
- Denoël M, Schmidt BR, Fonters R, Hansbauer G, Johanet A, Kühnis J, Pobljsaj K, Schweiger S, Sillero N (2023) Quantifying rarity of intraspecific diversity at multiple spatial scales by combining fine-grain citizen-based data across national boundaries. *Biological Conservation* 280: 109937. <https://doi.org/10.1016/j.biocon.2023.109937>
- Dormann CF, McPherson J, B. Araújo M, Bivand R, Bolliger J, Carl G, Davies R, Hirzel A, Jetz W, Daniel Kissling W, Kühn I, Ohlemüller R, Peres-Neto P, Reineking B, Schröder B, M. Schurr F, Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30: 609–628. <https://doi.org/10.1111/j.2007.0906-7590.05171.x>
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36: 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40: 677–697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>
- Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. *Methods in Ecology and Evolution* 1: 330–342. <https://doi.org/10.1111/j.2041-210X.2010.00036.x>
- Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17: 43–57. <https://doi.org/10.1111/j.1472-4642.2010.00725.x>
- Elith J, H. Graham C, P. Anderson R, Dudík M, Ferrier S, Guisan A, J. Hijmans R, Huettmann F, R. Leathwick J, Lehmann A, Li J, G. Lohmann L, A. Loiselle B, Manion G, Moritz C, Nakamura M, Nakazawa Y, McC. M. Overton J, Townsend Peterson A, J. Phillips S, Richardson K, Scachetti-Pereira R, E. Schapire R, Soberón J, Williams S, S. Wisz M, E. Zimmermann N (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- Esselman PC, Allan JD (2011) Application of species distribution models and conservation planning software to the design of a reserve network for the riverine fishes of northeastern Mesoamerica. *Freshwater Biology* 56: 71–88. <https://doi.org/10.1111/j.1365-2427.2010.02417.x>
- Ficetola GF, Bonardi A, Múcher CA, Gilissen NLM, Padoa-Schioppa E (2014) How many predictors in species distribution models at the landscape scale? Land use versus LiDAR-derived canopy height. *International Journal of Geographical Information Science* 28: 1723–1739. <https://doi.org/10.1080/13658816.2014.891222>
- Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37: 4302–4315. <https://doi.org/10.1002/joc.5086>
- Fourcade Y, Besnard AG, Secondi J (2018) Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Global Ecology and Biogeography* 27: 245–256. <https://doi.org/10.1111/geb.12684>
- Fourcade Y, Engler JO, Rödder D, Secondi J (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: e97122. <https://doi.org/10.1371/journal.pone.0097122>
- Franklin J (2010) Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge, 338 pp. <https://doi.org/10.1017/CBO9780511810602>
- Freake MJ, DePerno CS (2017) Importance of demographic surveys and public lands for the conservation of eastern hellbenders *Cryptobranchus alleganiensis alleganiensis* in southeast USA. *PLOS ONE* 12: e0179153. <https://doi.org/10.1371/journal.pone.0179153>
- G. Da Silva Neto J, Williams LA, Lawson CR, Groves JD, Byl TD, Gibson CM, Perkins CR, Sutton WB (2023) Land-use and water-quality threats to current and historical *Cryptobranchus alleganiensis* streams across multiple ecoregions. *Freshwater Science* 42: 347–362. <https://doi.org/10.1086/727800>

- Galante PJ, Alade B, Muscarella R, Jansa SA, Goodman SM, Anderson RP (2018) The challenge of modeling niches and distributions for data-poor species: a comprehensive approach to model complexity. *Ecography* 41: 726–736. <https://doi.org/10.1111/ecog.02909>
- Guisan A, Thuiller W, Zimmermann NE (2017) *Habitat suitability and distribution models: with applications in R*. Cambridge University Press, Cambridge, 513 pp. <https://doi.org/10.1017/9781139028271>
- Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AIT, Regan TJ, Brotons L, McDonald-Madden E, Mantyka-Pringle C, Martin TG, Rhodes JR, Maggini R, Setterfield SA, Elith J, Schwartz MW, Wintle BA, Broennimann O, Austin M, Ferrier S, Kearney MR, Possingham HP, Buckley YM (2013) Predicting species distributions for conservation decisions. *Ecology Letters* 16: 1424–1435. <https://doi.org/10.1111/ele.12189>
- Harris RMB, Porfirio LL, Hugh S, Lee G, Bindoff NL, Mackey B, Beeton NJ (2013) To be or not to be? Variable selection can change the projected fate of a threatened species under future climate. *Ecological Management & Restoration* 14: 230–234. <https://doi.org/10.1111/emr.12055>
- Hatsuzuka D, Sato T, Higuchi Y (2021) Sharp rises in large-scale, long-duration precipitation extremes with higher temperatures over Japan. *npj Climate and Atmospheric Science* 4: 4–29. <https://doi.org/10.1038/s41612-021-00184-9>
- He F, Zarfl C, Bremerich V, Henshaw A, Darwall W, Tockner K, Jähnig SC (2017) Disappearing giants: a review of threats to freshwater megafauna. *Wiley Interdisciplinary Reviews: Water* 4: e1208. <https://doi.org/10.1002/wat2.1208>
- Hidaka S, Jo TS, Yamamoto S, Katsuhara KR, Tomita S, Miya M, Ikegami M, Ushimaru A, Minamoto T (2024) Sensitive and efficient surveillance of Japanese giant salamander (*Andrias japonicus*) distribution in western Japan using multi-copy nuclear DNA marker. *Limnology* 25: 189–198. <https://doi.org/10.1007/s10201-023-00740-7>
- Hijmans RJ, Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* 12: 2272–2281. <https://doi.org/10.1111/j.1365-2486.2006.01256.x>
- Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* 199: 142–152. <https://doi.org/10.1016/j.ecolmodel.2006.05.017>
- Ikoma Y (1963) Notes on the giant salamander (*Megalobatrachus japonicus* (Temminck) Stejneger). *Bulletin of the Tsuyama Museum of Science Education* 1: 1–10.
- Itsukushima R (2023) Historical development and the present status of Japanese dams. *River Research and Applications* 39: 1136–1147. <https://doi.org/10.1002/rra.4129>
- IUCN SSC Amphibian Specialist Group (2022) *Andrias japonicus*. The IUCN Red List of Threatened Species 2022: e.T1273A177177761.
- Jenks GF (1963) Generalization in statistical mapping. *Annals of the Association of American Geographers* 53: 15–26. <https://doi.org/10.1111/j.1467-8306.1963.tb00429.x>
- Kass JM, Muscarella R, Galante PJ, Bohl CL, Pinilla-Buitrago GE, Boria RA, Soley-Guardia M, Anderson RP (2021) ENMeval 2.0: Redesign for customizable and reproducible modeling of species' niches and distributions. *Methods in Ecology and Evolution* 12: 1602–1608. <https://doi.org/10.1111/2041-210X.13628>
- Kass JM, Anderson RP, Espinosa-Lucas A, Juárez-Jaimes V, Martínez-Salas E, Botello F, Tavera G, Flores-Martínez JJ, Sánchez-Cordero V (2020) Biotic predictors with phenological information improve range estimates for migrating monarch butterflies in Mexico. *Ecography* 43: 341–352. <https://doi.org/10.1111/ecog.04886>
- Kawamichi T, Ueda H (1998) Spawning at nests of extra-large males in the giant salamander *Andrias japonicus*. *Journal of Herpetology* 32: 133–136. <https://doi.org/10.2307/1565495>
- Klein N, Konietzko-Meier D, Kalita S, Noda M, Ishikawa S, Taguchi Y, Anzai W, Hayashi S (2024) Unique bone histology of modern giant salamanders: a study on humeri and femora of *Andrias* spp. *Zoological Letters* 10: 18. <https://doi.org/10.1186/s40851-024-00240-1>
- Kobara J (1985) *O-sansyo-uo [The Japanese Giant Salamander]*. Dobutsu-sha, Tokyo, Japan [in Japanese].
- Kramer-Schadt S, Niedballa J, Pilgrim JD, Schröder B, Lindenborn J, Reinfelder V, Stillfried M, Heckmann I, Scharf AK, Augeri DM, Cheyne SM, Hearn AJ, Ross J, Macdonald DW, Mathai J, Eaton J, Marshall AJ, Semiadi G, Rustam R, Bernard H, Alfred R, Samejima H, Duckworth JW, Breitenmoser-Wuersten C, Belant JL, Hofer H, Wilting A (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions* 19: 1366–1379. <https://doi.org/10.1111/ddi.12096>
- Kuwabara K, Ashikaga K, Minamigata N, Nakanishi M, Shimada H, Kamada H, Fukumoto Y (2005) The breeding ecology and conservation of the Japanese giant salamander, *Andrias japonicus*, at Shijihara and Kamiishi in Toyohira-cho, Hiroshima Prefecture. *Natural History of Nishi-Chugoku Mountains* 10: 101–133.
- Li Y, Cohen JM, Rohr JR (2013) Review and synthesis of the effects of climate change on amphibians. *Integrative Zoology* 8: 145–161. <https://doi.org/10.1111/1749-4877.12001>
- Luedtke JA, Chanson J, Neam K, Hobin L, Maciel AO, Catenazzi A, Borzée A, Hamidy A, Aowphol A, Jean A, Sosa-Bartuano Á, Fong G. A, de Silva A, Fouquet A, Angulo A, Kidov AA, Muñoz Saravia A, Diesmos AC, Tominaga A, Shrestha B, Gratwicke B, Tjaturadi B, Martínez Rivera CC, Vásquez Almazán CR, Señaris C, Chandramouli SR, Strüssmann C, Cortez Fernández CF, Azat C, Hoskin CJ, Hilton-Taylor C, Whyte DL, Gower DJ, Olson DH, Cisneros-Heredia DF, Santana DJ, Nagombi E, Najafi-Majd E, Quah ESH, Bolaños F, Xie F, Brusquetti F, Álvarez FS, Andreone F, Glaw F, Castañeda FE, Kraus F, Parra-Olea G, Chaves G, Medina-Rangel GF, González-Durán G, Ortega-Andrade HM, Machado IF, Das I, Dias IR, Urbina-Cardona JN, Crnobrnja-Isailović J, Yang J-H, Jianping J, Wangyal JT, Rowley JLL, Measey J, Vasudevan K, Chan KO, Gururaja KV, Ovaska K, Warr LC, Canseco-Márquez L, Toledo LF, Díaz LM, Khan MMH, Meegaskumbura M, Acevedo ME, Napolitano MF, Ponce MA, Vaira M, Lampo M, Yáñez-Muñoz MH, Scherz MD, Rödel M-O, Matsui M, Fildor M, Kusri MD, Ahmed MF, Rais M, Kouamé NG, García N, Gonwouo NL, Burrowes PA, Imbun PY, Wagner P, Kok PJR, Joglar RL, Auguste RJ, Brandão RA, Ibáñez R, von May R, Hedges SB, Biju SD, Ganesh SR, Wren S, Das S, Flechas SV, Ashpole SL, Robleto-Hernández SJ, Loader SP, Incháustegui SJ, Garg S, Pimmachak S, Richards SJ, Slimani T, Osborne-Naikatini T, Abreu-Jardim TPF, Condez TH, De Carvalho TR, Cutajar TP, Pierson TW, Nguyen TQ, Kaya U, Yuan Z, Long B, Langhammer P, Stuart SN (2023) Ongoing declines for the world's amphibians in the face of emerging threats. *Nature* 622: 308–314. <https://doi.org/10.1038/s41586-023-06578-4>

- Marr MM, Hopkins K, Tapley B, Borzée A, Liang Z, Cunningham AA, Yan F, Wang J, Turvey ST (2024) What's in a name? Using species delimitation to inform conservation practice for Chinese giant salamanders (*Andrias* spp.). *Evolutionary Journal of the Linnean Society* 3: kzae007. <https://doi.org/10.1093/evolinnean/kzae007>
- Matsui M, Tominaga A, Liu W, Tanaka-Ueno T (2008) Reduced genetic variation in the Japanese giant salamander, *Andrias japonicus* (Amphibia: Caudata). *Molecular Phylogenetics and Evolution* 49: 318–326. <https://doi.org/10.1016/j.ympev.2008.07.020>
- Mi C, Huettmann F, Li X, Jiang Z, Du W, Sun B (2022) Effects of climate and human activity on the current distribution of amphibians in China. *Conservation Biology* 36: e13964. <https://doi.org/10.1111/cobi.13964>
- Mi C, Ma L, Yang M, Li X, Meiri S, Roll U, Oskyrko O, Pincheira-Donoso D, Harvey LP, Jablonski D, Safaei-Mahroo B, Ghaffari H, Smid J, Jarvie S, Kimani RM, Masroor R, Kazemi SM, Nneji LM, Fokoua AMT, Tasse Taboue GC, Bauer A, Nogueira C, Meirte D, Chapple DG, Das I, Grismer L, Avila LJ, Ribeiro Júnior MA, Tallowin OJS, Torres-Carvajal O, Wagner P, Ron SR, Wang Y, Itescu Y, Nagy ZT, Wilcove DS, Liu X, Du W (2023) Global protected areas as refuges for amphibians and reptiles under climate change. *Nature Communications* 14: 1389. <https://doi.org/10.1038/s41467-023-36987-y>
- Mulneh MG (2021) Impact of climate change on biodiversity and food security: a global perspective—a review article. *Agriculture & Food Security* 10: 1–25. <https://doi.org/10.1186/s40066-021-00318-5>
- Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, Anderson RP (2014) ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution* 5: 1198–1205. <https://doi.org/10.1111/2041-210X.12261>
- Neto JGDS, Sutton WB, Spear SF, Freake MJ, Kéry M, Schmidt BR (2020) Integrating species distribution and occupancy modeling to study hellbender (*Cryptobranchus alleganiensis*) occurrence based on eDNA surveys. *Biological Conservation* 251: 108787. <https://doi.org/10.1016/j.biocon.2020.108787>
- Nickerson MA, Amber LP, Michelle DP (2007) The effects of flooding on Hellbender salamander, *Cryptobranchus alleganiensis* Daudin, 1803, populations. *Salamandra* 43: 111–118.
- Okada S, Fukuda Y, Takahashi MK (2015) Paternal care behaviors of Japanese giant salamander *Andrias japonicus* in natural populations. *Journal of Ethology* 33: 1–7. <https://doi.org/10.1007/s10164-014-0413-5>
- Okada S, Utsunomiya T, Okada T, Felix ZI, Ito F (2008) Characteristics of Japanese giant salamander (*Andrias japonicus*) populations in two small tributary streams in Hiroshima prefecture, western Honshu, Japan. *Herpetological Conservation and Biology* 3: 192–202.
- Pan Y, Wei G, Cunningham AA, Li S, Chen S, Milner-Gulland EJ, Turvey ST (2016) Using local ecological knowledge to assess the status of the Critically Endangered Chinese giant salamander *Andrias davidianus* in Guizhou Province, China. *Oryx* 50: 257–264. <https://doi.org/10.1017/S0030605314000830>
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37: 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
- Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2011) *Ecological niches and geographic distributions*. Princeton University Press, 328 pp. <https://doi.org/10.1515/9781400840670>
- Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31: 161–175. <https://doi.org/10.1111/j.0906-7590.2008.5203.x>
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Phillips SJ, Anderson RP, Dudík M, Schapire RE, Blair ME (2017) Opening the black box: an open-source release of Maxent. *Ecography* 40: 887–893. <https://doi.org/10.1111/ecog.03049>
- Pitt AL, Shinskie JL, Tavano JJ, Hartzell SM, Delahunty T, Spear SF (2017) Decline of a giant salamander assessed with historical records, environmental DNA and multi-scale habitat data. *Freshwater Biology* 62: 967–976. <https://doi.org/10.1111/fwb.12917>
- Pugh MW, Hutchins M, Madritch M, Siefferman L, Gangloff MM (2016) Land-use and local physical and chemical habitat parameters predict site occupancy by hellbender salamanders. *Hydrobiologia* 770: 105–116. <https://doi.org/10.1007/s10750-015-2570-0>
- Radosavljevic A, Anderson RP (2014) Making better Maxent models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography* 41: 629–643. <https://doi.org/10.1111/jbi.12227>
- Raes N, ter Steege H (2007) A null-model for significance testing of presence-only species distribution models. *Ecography* 30: 727–736. <https://doi.org/10.1111/j.2007.0906-7590.05041.x>
- Roberts DR, Bahn V, Ciuti S, Boyce MS, Elith J, Guillera-Aroita G, Hauenstein S, Lahoz-Monfort JJ, Schröder B, Thuiller W, Warton DI, Wintle BA, Hartig F, Dormann CF (2017) Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography* 40: 913–929. <https://doi.org/10.1111/ecog.02881>
- Rödler D, Schmitt T, Gros P, Ulrich W, Habel JC (2021) Climate change drives mountain butterflies towards the summits. *Scientific Reports* 11: 14382. <https://doi.org/10.1038/s41598-021-93826-0>
- Schivo F, Bauni V, Krug P, Quintana RD (2019) Distribution and richness of amphibians under different climate change scenarios in a subtropical region of South America. *Applied Geography* 103: 70–89. <https://doi.org/10.1016/j.apgeog.2019.01.003>
- Seaborn T, Goldberg CS, Crespi EJ (2021) Drivers of distributions and niches of North American cold-adapted amphibians: evaluating both climate and land use. *Ecological Applications* 31: e2236. <https://doi.org/10.1002/eap.2236>
- Sergio F, Newton I, Marchesi L, Pedrini P (2006) Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology* 43: 1049–1055. <https://doi.org/10.1111/j.1365-2664.2006.01218.x>
- Sergio F, Caro T, Brown D, Clucas B, Hunter J, Ketchum J, McHugh K, Hiraldo F (2008) Top predators as conservation tools: ecological rationale, assumptions, and efficacy. *Annual Review of Ecology, Evolution, and Systematics* 39: 1–19. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173545>
- Shakti PC, Hirano K, Iizuka S (2020) Flood inundation mapping of the Hitachi region in the Kuji River Basin, Japan, during the October 11–13, 2019 extreme rain event. *Journal of Disaster Research* 15: 712–725. <https://doi.org/10.20965/jdr.2020.p0712>

- Shikama T, Hasegawa Y (1962) Discovery of the fossil giant salamander (*Megalobatrachus*) in Japan. *Transactions and Proceedings of the Palaeontological Society of Japan* 45: 197–200.
- Sillero N, Barbosa AM (2021) Common mistakes in ecological niche models. *International Journal of Geographical Information Science* 35: 213–226. <https://doi.org/10.1080/13658816.2020.1798968>
- Sillero N, Arenas-Castro S, Enriquez-Urzelai U, Vale CG, Sousa-Guedes D, Martínez-Freiría F, Real R, Barbosa AM (2021) Want to model a species niche? A step-by-step guideline on correlative ecological niche modelling. *Ecological Modelling* 456: 109671. <https://doi.org/10.1016/j.ecolmodel.2021.109671>
- Soley-Guardia M, Alvarado-Serrano DF, Anderson RP (2024) Top ten hazards to avoid when modeling species distributions: a didactic guide of assumptions, problems, and recommendations. *Ecography* 2024: e06852. <https://doi.org/10.1111/ecog.06852>
- Souza KS, Fortunato DS, Jardim L, Terribile LC, Lima-Ribeiro MS, Mariano CÁ, Pinto-Ledezma JN, Loyola R, Dobrovolski R, Rangel TF, Machado IF, Rocha T, Batista MG, Lorini ML, Vale MM, Navas CA, Maciel NM, Villalobos F, Olalla-Tarraga MÁ, Rodrigues JFM, Gouveia SF, Diniz-Filho JAF (2023) Evolutionary rescue and geographic range shifts under climate change for global amphibians. *Frontiers in Ecology and Evolution* 11: 1038018. <https://doi.org/10.3389/fevo.2023.1038018>
- Sutton WB, Grisnik M, Williams LA, Groves JD (2023) Climatic and landscape vulnerability of the eastern Hellbender salamander (*Cryptobranchus alleganiensis alleganiensis*). *Global Ecology and Conservation* 46: e02554. <https://doi.org/10.1016/j.gecco.2023.e02554>
- Taguchi Y (2009) Seasonal movements of the Japanese giant salamander (*Andrias japonicus*): Evidence for possible breeding migration by this stream-dwelling amphibian. *Japanese Journal of Ecology* 59: 117–128.
- Taguchi Y, Natuhara Y (2009) Requirements for small agricultural dams to allow the Japanese giant salamander (*Andrias japonicus*) to move upstream. *Japanese Journal of Conservation Ecology* 14: 165–172.
- Takabatake D, Inatsu M (2022) Summertime precipitation in Hokkaido and Kyushu, Japan in response to global warming. *Climate Dynamics* 58: 1671–1682. <https://doi.org/10.1007/s00382-021-05983-7>
- Takahashi MK, Okada S, Fukuda Y (2017) From embryos to larvae: seven-month-long paternal care by male Japanese giant salamander. *Journal of Zoology* 302: 24–31. <https://doi.org/10.1111/jzo.12433>
- Takahashi Y, Rashid MH, Sarkar A, Asaeda T, Isono M, Omura T, Koga K (2016) Use of ladderways in fragmented habitat to aid the movement of Japanese giant salamander (*Andrias japonicus*). *International Journal of River Basin Management* 14: 233–241. <https://doi.org/10.1080/15715124.2016.1159572>
- Terrell KA, Quintero RP, Murray S, Kleopfer JD, Murphy JB, Evans MJ, Nissen BD, Gratwicke B (2013) Cryptic impacts of temperature variability on amphibian immune function. *Journal of Experimental Biology* 216: 4204–4211. <https://doi.org/10.1242/jeb.089896>
- Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, Musciche M, Conradt L (2001) Ecological and evolutionary processes at expanding range margins. *Nature* 411: 577–581. <https://doi.org/10.1038/35079066>
- Tochimoto T (1995) Ecological studies on the Japanese giant salamander, *Andrias japonicus*, in the Ichi River in Hyogo Prefecture. 10. An attempt to rebuild spawning places along the river. *Journal of the Japanese Association of Zoos and Aquaria* 37: 13–17.
- Tochimoto T, Taguchi Y, Onuma H, Kawakami N, Shimizu K, Doi T, Kakinoki S, Natuhara Y, Mitsuhashi H (2007) Distribution of Japanese giant salamander in Hyogo Prefecture, western Japan. *Humans and Nature* 18: 51–65.
- Turvey ST, Chen S, Tapley B, Wei G, Xie F, Yan F, Yang J, Liang Z, Tian H, Wu M, Okada S, Wang J, Lü J, Zhou F, Papworth SK, Redbond J, Brown T, Che J, Cunningham AA (2018) Imminent extinction in the wild of the world's largest amphibian. *Current Biology* 28: R592–R594. <https://doi.org/10.1016/j.cub.2018.04.005>
- Ultsch GR (2012) Metabolism, gas exchange, and acid-base balance of giant salamanders. *Biological Reviews* 87: 583–601. <https://doi.org/10.1111/j.1469-185X.2011.00211.x>
- VanDerWal J, Shoo LP, Graham C, Williams SE (2009) Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecological Modelling* 220: 589–594. <https://doi.org/10.1016/j.ecolmodel.2008.11.010>
- Walls SC, Barichivich WJ, Brown ME (2013) Drought, deluge and declines: the impact of precipitation extremes on amphibians in a changing climate. *Biology* 2: 399–418. <https://doi.org/10.3390/biology2010399>
- Werkowska W, Márquez AL, Real R, Acevedo P (2017) A practical overview of transferability in species distribution modeling. *Environmental Reviews* 25: 127–133. <https://doi.org/10.1139/er-2016-0045>
- Yates KL, Bouchet PJ, Caley MJ, Mengersen K, Randin CF, Parnell S, Fielding AH, Bamford AJ, Ban S, Barbosa AM, Dormann CF, Elith J, Embling CB, Ervin GN, Fisher R, Gould S, Graf RF, Gregr EJ, Halpin PN, Heikkinen RK, Heinänen S, Jones AR, Krishnakumar PK, Lauria V, Lozano-Montes H, Mannocci L, Mellin C, Mesgaran MB, Moreno-Amat E, Mormede S, Novaczek E, Opper S, Ortuño Crespo G, Peterson AT, Rapacciuolo G, Roberts JJ, Ross RE, Scales KL, Schoeman D, Snelgrove P, Sundblad G, Thuiller W, Torres LG, Verbruggen H, Wang L, Wenger S, Whittingham MJ, Zharikov Y, Zurell D, Sequeira AMM (2018) Outstanding challenges in the transferability of ecological models. *Trends in Ecology & Evolution* 33: 790–802. <https://doi.org/10.1016/j.tree.2018.08.001>
- Zellmer AJ, Slezak P, Katz TS (2020) Clearing up the crystal ball: Understanding uncertainty in future climate suitability projections for amphibians. *Herpetologica* 76: 108–120. <https://doi.org/10.1655/0018-0831-76.2.108>
- Zhang Z, Mammola S, Liang Z, Capinha C, Wei Q, Wu Y, Zhou J, Wang C (2020) Future climate change will severely reduce habitat suitability of the Critically Endangered Chinese giant salamander. *Freshwater Biology* 65: 971–980. <https://doi.org/10.1111/fwb.13483>
- Zhu K, Woodall CW, Clark JS (2012) Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology* 18: 1042–1052. <https://doi.org/10.1111/j.1365-2486.2011.02571.x>
- Zurell D, Franklin J, König C, Bouchet PJ, Dormann CF, Elith J, Fandos G, Feng X, Guillera-Arroita G, Guisan A, Lahoz-Monfort JJ, Leitão PJ, Park DS, Peterson AT, Rapacciuolo G, Schmatz DR, Schröder B, Serra-Díaz JM, Thuiller W, Yates KL, Zimmermann NE, Merow C (2020) A standard protocol for reporting species distribution models. *Ecography* 43: 1261–1277. <https://doi.org/10.1111/ecog.04960>

Supplementary materials

Supplementary material 1

Correlation matrix of the environmental predictors used in the study (.pdf)

Link: <https://doi.org/10.21425/fob.18.133105.suppl1>

Supplementary material 2

Environmental variables used in the modelling procedure (1 km² grid cell resolution) (.pdf)

Link: <https://doi.org/10.21425/fob.18.133105.suppl2>

Supplementary material 3

Results of the MESS analysis comparing the reference climatic variables to the climatic variables of the projection layer (all Japan) (.pdf)

Link: <https://doi.org/10.21425/fob.18.133105.suppl3>

Supplementary material 4

Null models results (.pdf)

Link: <https://doi.org/10.21425/fob.18.133105.suppl4>

Supplementary material 5

Response curves of the two land use variables: agricultural and urban areas (.pdf)

Link: <https://doi.org/10.21425/fob.18.133105.suppl5>

Supplementary material 6

Japanese giant salamander habitat suitability projection maps generated for three time periods (2050, 2070 and 2090) considering an optimistic (SSP126) and a pessimistic scenario (SSP370) for future climate change (.pdf)

Link: <https://doi.org/10.21425/fob.18.133105.suppl6>