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Refined gap analysis for biodiversity conservation under climate change

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ABSTRACT

In concert with climate change, our planet faces unprecedented biodiversity loss, with half of all species at risk of extinction. Despite global conservation efforts, the biodiversity crisis continues to outpace these actions. The Global Biodiversity Framework seeks to halt this trend by expanding protected areas (PAs) to cover 30 % of terrestrial and aquatic environments by 2030. Conservation gap analysis, based on species distribution models (SDMs), is vital for assessing the effectiveness of PAs under future climate scenarios. However, traditional gap analysis often relies on binary predictions, leading to critical information loss and failing to target multiple species groups simultaneously or address dynamic species distributions. To overcome these limitations, we propose a refined gap analysis method using a fuzzy approach with machine learning models. Our method incorporates multiple species groups, dispersal scenarios, and uncertainty assessments, offering improved conservation planning. We applied this approach to amphibians—a taxon highly vulnerable to climate change—and evaluated PA effectiveness and potential refugia under various future scenarios. Our findings show that while approximately 60 % of amphibians currently protected by PAs may continue to find refuge, their average habitat suitability is expected to decline significantly under future conditions, indicating potential losses in PA effectiveness. Our refined fuzzy gap analysis captures a continuous spectrum of habitat suitability, facilitates species comparability, and integrates multiple conservation targets. This approach provides a robust tool to guide biodiversity strategies, ensuring that conservation efforts are more adaptive, resilient, and precise in the face of climate change uncertainties.

1. Introduction

The global biodiversity loss is one of the most pressing environmental issue of our time (Dornelas et al., 2023; Kolbert, 2014) with the potential loss of up to half the species on Earth (Hughes, 2023). Despite international accords (Tittensor et al., 2014), biodiversity trajectories remain negative (Mace et al., 2018) and are likely accelerating due to anthropogenic activities in concert with climate change (Butchart et al., 2010). To stop and reverse biodiversity declines, the Kunming-Montreal

Global Biodiversity Framework (KM-GBF), was recently adopted with a set of ambitious goals and targets for 2030 and 2050 (Mace et al., 2018).

Protected areas (PAs) are the cornerstone of biodiversity conservation (Le Saout et al., 2013; Naughton-Treves et al., 2005; Watson et al., 2014). KM-GBF agreed to expand PAs coverage to 30 % of terrestrial and marine environments until 2030 by emphasizing areas of particular importance for biodiversity and ecosystem function and services which are ecologically representative and well-connected (Bongaarts, 2019; Joly, 2022). However, mere expansion is insufficient without ensuring

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the long-term effectiveness of these PAs in conserving species' populations (Zeng et al., 2023). A critical challenge lies in making decisions about where to locate these PAs. The effectiveness of PAs is often hindered by a myriad of factors, including suboptimal location choices in sites with low probabilities of persistence (Araújo and Williams, 2000, 2001), inadequate sizes that do not support viable species populations (Newmark, 1996), and the lack of ecological representativeness that cannot ensure the conservation of biodiversity in its entirety (Gaston et al., 2008; Lennon et al., 2004).

Climate change introduces an additional layer of complexity to biodiversity conservation by profoundly altering ecological systems. It drives shifts in species distributions and interactions, as many species relocate to track suitable climatic conditions (González-Trujillo et al., 2024; Sales et al., 2021; Parmesan, 2006). These shifts often result in habitat mismatches that threaten species survival and destabilize existing PAs, whose current locations may no longer align with the future habitats of the species they aim to protect. To address these challenges, conservation strategies must integrate adaptive, forward-looking approaches that account for the dynamic nature of climate change. Gap analysis is a tool to measure the degree to which PAs meet predefined conservation targets while identifying additional areas required to fulfil unmet targets (Araújo et al., 2007; Rodrigues et al., 2004; Scott et al., 2001). Although gap analysis has often been used with species occurrence data as the basic unit of analysis (e.g., Araújo et al., 2007; Csuti et al., 1997; Goettsch et al., 2019; Jennings, 2000; Rodrigues et al., 2004; Scott et al., 2001), when such data are limited it can utilise predictions of species occurrences from species distribution models (SDMs) (Guisan and Thuiller, 2005). By comparing predictions of species distributions with the geographical layout of PAs, conservation planners can identify 'gaps' where important species or ecosystems lack sufficient legal or physical protection measures (Gorenflo and Brandon, 2006). In addition, developing SDMs is crucial to project the impact of future climate change on the distribution of species which can then be used to evaluate whether PAs still remain effective in response to future climate change scenarios (Araújo et al., 2011; Lemes et al., 2014). This approach stands as a fundamental process in spatial planning for PA expansions which is essential for meeting the KM-GBF targets and addressing the challenges posed by global biodiversity declines.

Traditional gap analysis methods often rely solely on species composition, inherently assuming that if a species is adequately represented, it is also expected to persist (Araújo and Williams, 2000). However, this singular metric may not effectively address the conservation requirements of all target groups, potentially leading to suboptimal protection efforts (Howard et al., 2020). Notably, this approach may overlook specific needs of vulnerable groups, such as threatened or endemic species, which could lead to inefficient conservation outcomes (Belote et al., 2021; Brooks et al., 2006; Myers et al., 2000; Venter et al., 2014). Many old and new PAs do not target places with high concentrations of threatened species, often biased towards low-cost lands due to a lack of technical capacity to strategically identify critical areas (Venter et al., 2018). Alternatively, some studies focus exclusively on a particular species group as a conservation target, such as vulnerable species (Jung et al., 2021; Venter et al., 2014), or specific regions such as key biodiversity areas (Eken et al., 2004), often lying in transition zones with high concentrations of species at the edge of their ranges (Araújo, 2002; Araújo and Williams, 2001). Moreover, the static nature of many conservation strategies fails to account for the dynamic changes in species distributions driven by climate change and habitat shifts (Dobrowski et al., 2021; Ferro et al., 2014; Hoffmann et al., 2019; Mi et al., 2023), hence, the extent to which the existing PAs can be effective under the increasing threat of climate change remains unassessed in many studies (Ebrahimi et al., 2022; Kafash et al., 2018; Mi et al., 2023). To encapsulate the full breadth of biodiversity conservation, it is vital to methodologically advance conservation planning to a forward-looking approach (Hannah et al., 2020) which simultaneously integrates multiple conservation targets to evaluate the effectiveness of PAs and

identify biodiversity hotspots in the face of climate change.

Despite the widespread use of gap analysis in conservation planning, there are important uncertainties associated with the use SDMs, particularly in the context of climate change (Kujala et al., 2013). A significant source of uncertainty stems from the inherent unpredictability of future climate scenarios and their impact on species ranges, complicating efforts to identify areas of conservation priority. Another pressing issue is the widely used conversion of SDM outputs into binary presence-absence values to standardise results across species and studies. While this conversion facilitates comparability of SDM predictions, it leads to significant information loss by ignoring gradients of habitat suitability (Alagador et al., 2011). Additionally, the integration of species' dispersal capacities into SDMs for gap analysis and expansion of PAs (Williams et al., 2005) is vital yet often neglected in studies (Koo and Park, 2022; Bateman et al., 2013). Dispersal abilities are essential for assessing species' potential to adapt to new environmental conditions, but their omission can lead to a skewed understanding of an area's conservation needs (Engler et al., 2009; Keshkar and Voigt, 2016; Lemes et al., 2022; Miller and McGill, 2018; Thuiller et al., 2008), contributing to further uncertainty in the biodiversity conservation planning outcomes. Despite these and other possible sources of uncertainty embedded in gap analysis and prioritisation approaches, biodiversity conservation planning often ignores uncertainty (Kujala et al., 2013; Moilanen et al., 2006). Therefore, for gap analysis to effectively contribute to conservation efforts in the context of climate change, it must address some of these layers of uncertainty.

In response to these challenges, this study aims to propose a sophisticated workflow to advance gap analysis by employing a fuzzy approach and a large ensemble of various machine learning models. Our new approach explicitly quantifies the importance of areas for biodiversity conservation for multiple species' target groups and improves the efficiency of gap analysis. In addition, we quantify the effect of multiple sources of uncertainty on gap analysis and measure the relative contribution of each uncertainty factor at the pixel level. Our new framework can quantify protection gaps given both the current and future climate suitability where future range shifts of species in response to various future climate scenarios and for different species dispersal assumptions are considered for multiple years of 2030, 2050, 2070, and 2090. Although our framework can be applied for any or multiple taxonomic groups, for the purpose of demonstration, we chose amphibians as a key taxon to test our proposed approach as they have a higher proportion of threatened species, considered the most vulnerable terrestrial vertebrates in the face of climate change (Alroy, 2015; Barnosky et al., 2011). Despite these concerns, recent studies have shown that, unlike many other taxa (Ebrahimi et al., 2021; Tang et al., 2022), amphibians remain unaltered in PAs in response to climate change (Chen et al., 2017; Mi et al., 2023). Thus, we tested whether our modified gap analysis approach yields a different conclusion for this specific taxonomic group.

2. Materials and methods

2.1. Study area and species occurrence data

We selected Southwest Asia as the case study area, known as an important biodiversity transition zone which intersects three biomes and exhibits rich biodiversity influenced by its topography, climate, and biogeographic history (Holt et al., 2013).

To compile a robust dataset of amphibian occurrences, we obtained and integrated data from multiple sources including HerpNet and Global Biodiversity Information Facility (GBIF), supplemented by records from our field studies, covering a temporal range between 1970 and 2023. To conduct pre-processing and cleaning of data, we first cross-referenced occurrence records with species range maps obtained from the International Union for Conservation of Nature (IUCN) and the Map of Life (MOL) to verify the accuracy of locations and exclude records falling outside of confirmed species ranges. Further, data cleaning was

conducted using the *CoordinateCleaner* (Zizka et al., 2019) and the *usdm* (Naimi et al., 2011; Naimi, 2015a) R packages to remove outliers, duplicates, and records with high locational uncertainty or with unreliable basis of records. Spatial thinning was applied at 1×1 km grid level to minimize over-representation within single grid cells (Aiello-Lammens et al., 2015). Only species with at least 30 reliable presence records were retained for analysis, resulting in a final database of 2781 occurrence records across 45 species (List of species in Table S1).

2.2. Climate data

Climate variables were obtained from the WorldClim global database, covering the standard 19 bioclimatic variables for the baseline period of 1970–2000 (Global Climate Data Version 2.1; Fick and Hijmans, 2017). For future projections, we obtained data from eight different global climate models (GCMs) to take future data uncertainty into account under four Shared Socio-economic Pathways (SSPs) to capture a range of potential future climate scenarios (e.g., Mohammadi et al., 2019; Naimi et al., 2022). The scenarios include SSP1–2.6 (Low forced scenario), SSP2–4.5 (Medium forced scenario), SSP3–7.0 (Medium-high forced scenario), and SSP5–8.5 (High forced scenario) for four time periods including 2021–2040 (2030), 2041–2060 (2050), 2061–2080 (2070), and 2081–2100 (2090). A collinearity check was performed using the Variance Inflation Factor (VIF) and a stepwise procedure implemented in the *usdm* R package (Naimi, 2015b). Each bioclimatic variable with a maximum value of VIF, if exceeding the threshold (10), was excluded at each step and the stepwise procedure was repeated until all variables with the sign of collinearity were excluded (Naimi et al., 2014).

2.3. Biodiversity modelling

We developed SDMs for each individual species using 10 commonly applied machine learning methods, implemented in the *sdm* R package (Naimi and Araújo, 2016). The methods included Generalized Linear Models (GLM; McCullagh, 1989), Generalized Additive Models (GAM; Hastie, 1992), Boosted Regression Trees (BRT; Elith et al., 2008), Multiple Adaptive Regression Splines (MARS; Friedman, 1991), Classification and Regression Trees (CART; Breiman et al., 1984), Random Forest (RF; Breiman, 2001), Maximum Entropy (Maxent; Phillips et al., 2006), Flexible Discriminant Analysis (FDA; Hastie et al., 1994), Maximum Likelihood estimation for presence-only (Maxlike; Fitzpatrick et al., 2013), and Bioclimatic Envelope Modelling (Bioclimate; Booth et al., 2014).

We generated 1000 background points randomly across the geographic space of the study area, used as pseudo-absence records to train SDMs along with the species presence records. To evaluate the performance of the models for their accuracy, we applied the bootstrapping resampling method with 10 replications to generate training and test datasets. This involved random sampling with replacement to maintain the original dataset size for training, while non-selected records were used to evaluate the models (Naimi et al., 2022). The receiver operating characteristic (ROC) analysis and the area under the curve (AUC) of ROC along with the true skill statistic (TSS) were used as the evaluation metrics to measure the performance of the models. AUC ranges from 0 to 1, and TSS ranges from -1 to 1, with higher values indicating better performance. A TSS of 0 and an AUC of 0.5 implies random predictive discrimination, while lower values indicate worse-than-chance discrimination (Allouche et al., 2006; Fielding and Bell, 1997).

The outputs from 100 individual SDMs (10 methods * 10 replications) for each species were combined into an ensemble prediction (Araújo and New, 2007; Naimi and Araújo, 2016; Ebrahimi et al., 2023), weighting individual model contributions by their AUC values. This ensemble approach not only offers improved predictions of the species distributions but also accounts for modelling uncertainty (Araújo and

Naimi, 2020). It has demonstrated effectiveness in predicting species richness patterns (Parviainen et al., 2009) and diversity (Mateo et al., 2012), as well as species range shifts when using temporally independent datasets (Araújo et al., 2005a; Mateo et al., 2012). We applied the ensemble approach for four distinct future time periods and four SSP scenarios using eight GCMs (BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, MRI-ESM2-0). To project species distributions in the future times, we applied three different dispersal scenarios: (1) Full-dispersal: assumes no dispersal restrictions, allowing species to reach all suitable areas regardless of geographical constraints and species' dispersal capacity. (2) No-dispersal: assumes no dispersal capacity for species, restricting their future suitable habitat projections to the current distribution extents, thus, newly suitable sites remain unoccupied. (3) Dispersal: accounts for species-specific dispersal abilities by considering average yearly potential dispersal capacities for three distinct groups of amphibians, including salamanders (0.5 km/year), frogs (2 km/year), and toads (3 km/year) (Alex Smith and M. Green, 2005).

2.4. Gap analysis

To evaluate the effectiveness of PAs, we adopted the conventional gap analysis approach that traditionally relies on binarised predictions from SDMs (i.e., predicted presence-absences) to quantify their overlaps with PAs. The binarising process, which converts probability of occurrence to presence-absence, often results in significant information loss as it treats all pixels above a certain threshold as uniform presences, despite variation in suitability levels (Blüthgen et al., 2006; Calabrese et al., 2014; Guillera-Aroita et al., 2015).

In this study, we used a linear fuzzy membership function (Eastman, 1999; Abbaspour et al., 2011) to transform probabilities of occurrence within suitable areas into continuous fuzzy suitability scores ranging from 0 to 1, where higher scores indicate greater suitability. For each SDM, the parameters of the fuzzy membership function (Eq. (1)) were derived from the predicted probabilities for the baseline (current) time period. Initially, we identified a threshold for each model using a widely used threshold selection method that maximizes the sum of sensitivity and specificity evaluation metrics ($\max[\text{sensitivity} + \text{specificity}]$; Nenzén and Araújo, 2011). This procedure, commonly employed to binarise SDM predictions, involves calculating sensitivity and specificity for all possible thresholds and identifying the threshold that yields the highest combined value as the optimal cutoff. However, instead of converting probabilities above this threshold to binary presence-absence values, we used the identified threshold as the lower bound (P_{min}) for the fuzzy suitability transformation. The upper bound (P_{max}) was set to the maximum predicted probability for the baseline period. Using this membership function (Eq. (1)), predicted probabilities for both the baseline and future time periods were then transformed into continuous fuzzy suitability values. Thus, unlike the binary map with the same value for all pixels within suitable areas, the degree of suitability in this approach is assigned to each pixel, allowing its comparability across various species and among global change scenarios. We used this method to quantify the mean degree of suitability within PAs for each species across different time periods (baseline and future) and under various future climate change and dispersal scenarios.

$$f(x) = \begin{cases} 0, & P < P_{min} \\ \frac{P - P_{min}}{P_{max} - P_{min}}, & P_{min} \leq P \leq P_{max} \\ 1, & P > P_{max} \end{cases} \quad (1)$$

where P is the predicted probability by SDM at a pixel, P_{min} is the selected threshold representing the minimum probability of suitable areas, and P_{max} is the maximum probability in the current time period (baseline).

Determining what portion of a species' suitable range is located

within PAs is a common approach in gap analysis to understand whether a species is adequately protected. This percentage can vary based on conservation goals or species conservation status. A frequently used threshold ranges between 10 % and 30 % of a species range (Rodrigues et al., 2004) while this threshold for particularly vulnerable or endangered species is at least 50 %.

For our new gap analysis approach, we overlaid the fuzzy maps with PA spatial polygons to identify pixels with a fuzzy suitability value greater than 0. We then calculated the portion of species' geographical range covered by PAs by counting the number of these pixels within and outside PAs. Additionally, we calculated the mean fuzzy suitability values within the entire suitable areas, as well as for subsets of pixels located inside and outside of PAs, to provide insights into the effectiveness of PAs at the species level.

We employed a non-parametric Wilcoxon test to determine whether the degree of suitability within PAs is significantly decreased in future scenarios compared to the baseline. Further, we examined whether the effectiveness of PAs varied among threatened and endangered species as categorized by the IUCN red list.

For species richness calculations in our gap analysis, we diverged from traditional approaches by incorporating multiple groups of species simultaneously. We considered two groups: the first included all species, while the second focused solely on IUCN Red List species labeled as endangered, threatened, or vulnerable. For each group, we stacked the fuzzy-transformed SDM predictions and calculated the sum of fuzzy values at each pixel, subsequently determining species richness for each group. By normalizing these values against the maximum fuzzy value across the study area, we derived the relative species richness for each target group. We then performed a fuzzy union operation on the relative species richness values of these two groups to generate the final species richness map. This approach enabled us to compare richness values inside and outside PAs and to assess trends in average richness across time within PAs for each future climate scenario. In addition, we quantified the changes in richness between future scenarios and the baseline.

2.5. Uncertainty analysis

Uncertainty in gap analysis can arise from various sources, including the choice of modelling methods to develop SDMs and inherent unpredictability of future climate scenarios (GCMs and SSPs), which leads to variability in projected species ranges. In addition, assumptions of species dispersal capacity influence future projections of species distributions. To assess magnitudes and spatial patterns of uncertainty in our species richness predictions, we conducted a three-way Analysis of Variance (ANOVA) to decompose the variation across 3200 model projections. These projections were derived from 10 different modelling methods (SDMs), each with 10 replications across four future scenarios (SSPs) and 8 GCMs (100 SDMs \times 8 GCMs \times 4 SSPs) for each future time period analysed. In our analysis, we performed a three-way ANOVA without replication (Legendre and Legendre, 2012; Pike et al., 1982) for each pixel, treating species richness as the response variable and species distribution models (SDM), global climate models (GCM), and future scenarios (SSP) as the factors. This analysis allowed us to quantify and compare the variation attributable to the models themselves with the variation associated with projected changes in species richness due to different climate scenarios.

From the ANOVA, we extracted the sums of squares attributed to each main effect (SDM, GCM, SSP) and their interactions (SDM \times GCM, SDM \times SSP, GCM \times SSP, SDM \times GCM \times SSP). Since the interaction terms were not significant, they were excluded from further analysis. We then calculated the variance components as the proportions of the total sum of squares for each source of variation, providing a nuanced understanding of how much each factor contributes to the overall uncertainty in species richness predictions (Diniz-Filho et al., 2009). These analyses were performed for each pixel, and we mapped each variance component separately to visually represent the spatial distribution of

uncertainty across the study area.

Additionally, we applied the same variance decomposition approach using an ensemble of SDM predictions—combining 100 predictions from 10 methods—to analyse the variation in species richness resulting from different GCMs, SSPs, and dispersal scenarios (DISP). This ensemble approach provides a more robust representation of predicted outcomes, and a solution to effectively address model-based uncertainty. With the model-based uncertainty addressed through incorporating the ensemble procedure, our further analyses focused on decomposing uncertainty arising from GCMs, SSPs, and DISP sources to assess the contributions of these factors to overall uncertainty in species richness. We also quantified the standard deviation of probabilities at each pixel to assess the total variability of all SDMs, as an indicator of the total uncertainty at the pixel-level (Fig. 1). The R scripts, including functions and codes used to conduct our analysis, are available in a GitHub repository at spatialecology/FuzzyGap.

3. Results

3.1. Species distribution models and richness pattern

To minimize the effect of collinearity on SDMs, we selected 10 bioclimatic variables with VIF values below 10. These variables included mean diurnal range (bio2), temperature annual range (bio7), mean temperature of wettest quarter (bio8), mean temperature of driest quarter (bio9), mean temperature of warmest quarter (bio10), precipitation of wettest month (bio13), precipitation of driest month (bio14), precipitation seasonality (bio15), precipitation of warmest quarter (bio18) and precipitation of coldest quarter (bio19).

The individual SDMs and their ensembles demonstrated high accuracy, as evidenced by AUC and TSS values. For individual SDMs, the mean AUC and TSS were 0.855 and 0.695, respectively. Among the various modelling methods, RF performed the best, with a mean AUC of 0.911 and a mean TSS of 0.773. In contrast, MaxLike was the poorest-performing method, with a mean AUC and a mean TSS of 0.708 and 0.508, respectively (Fig. S1).

The assessment of relative variable importance showed that the most influential variables varied among species; however, bio19, bio14 and bio8 consistently contributed the most across models.

3.2. Relative fuzzy richness

The species richness patterns under different dispersal scenarios for the baseline and future climate scenarios indicate that the highest richness in the period of 2081–2100 under SSP585 scenario (Fig. 2) is mainly located in the north-west of the study area across the entire border strip of Turkey, parts of Georgia, western Russia, eastern Iraq, northern and western Iran, and western Syria and Lebanon. From the current time to 2090, a decline in species richness was observed in the western parts of Turkey, Lebanon, Syria, and Iran, with the most pronounced contractions occurring in northern Iran and the western of Turkey. The main areas of species richness became increasingly confined within the crescent formed by Georgia and Russia, extending towards the northern fringe of Turkey. Future climate scenarios also highlighted new patches of richness in eastern Afghanistan and Pakistan. Although the visual distinctions between the full dispersal, dispersal, and no dispersal maps are subtle, quantitative analyses reveal marked differences in the extent of species richness. Under the full dispersal scenario, species richness is distributed across a broader area while incorporating species dispersal limitations affects the patterns of richness in the future times. Specifically, the areas with species richness greater than 0 for the full dispersal scenario covers an area of 11,183,494 km², while the area for the dispersal and no dispersal scenarios are 9,131,515 and 5,040,825 km², respectively—representing 19 % and 55 % less than the full dispersal scenario, respectively. The overarching patterns across various scenarios and time periods remain largely consistent, as detailed

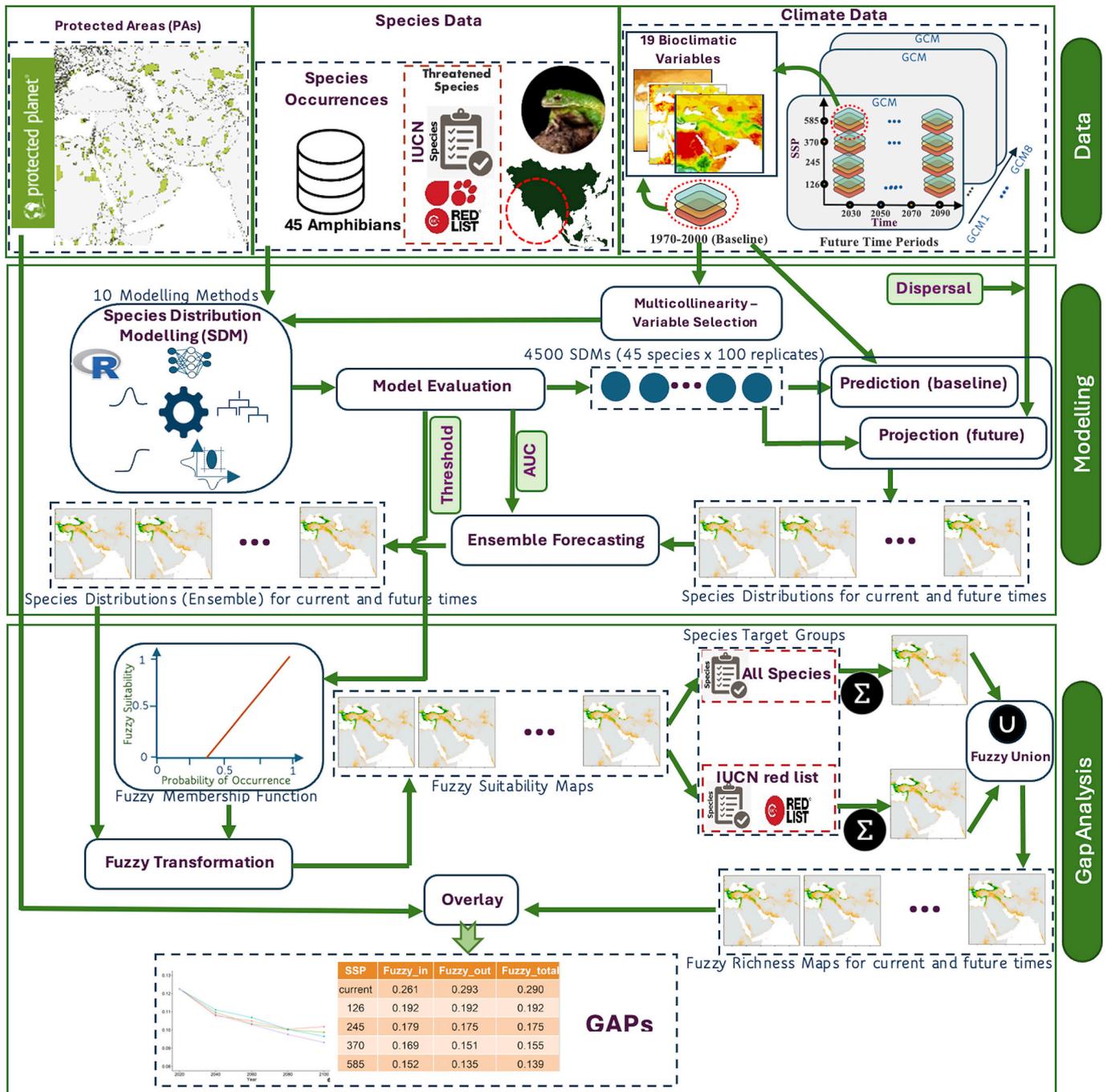


Fig. 1. A schematic diagram representing the workflow of fuzzy gap analysis for biodiversity conservation under climate change.

in Figs. S2, S3, S4 and S5.

3.3. Changes in species richness

The spatial distribution of gains and losses in species richness in response to climate change at the pixel level (Figs. 3 and S6) illustrated that moderate changes are predicted across the study area by 2050 based on the SSP126 scenario. Noticeable losses are evident in specific regions, such as the western parts of Iran and northern Iraq, indicated by yellow and red colors. However, some areas, particularly the northern strip of Turkey and parts of Georgia and western Russia, Iran, eastern Afghanistan and Pakistan exhibit slight gains in richness, indicated by the green color. Although the distributions of pixels with gain and loss are mostly consistent between scenarios, from the best case (SSP126) to

the worst case (SSP585) scenarios, their magnitudes on both gain and loss sides are increased in the SSP585. By 2090 the SSP126 scenario indicates a more pronounced reduction in species richness. The losses become more widespread and intense, especially in the western parts of Iran and northern Iraq and west and south of Turkey. In contrast, the extent and intensity of species richness loss under the SSP585 scenario increase dramatically. Border line of Iran and Iraq, the western border line of Syria, west and south of Turkey exhibit substantial losses. Conversely, regions in northern Turkey, Georgia, and western Russia show persistent and slightly expanded areas of increased species richness and describe that east Pakistan and Afghanistan and north of Azerbaijan and the central part of Georgia will be a new potential habitat for species richness. The trend of changes across various future scenarios and timeframes reveals the most pronounced losing trend for

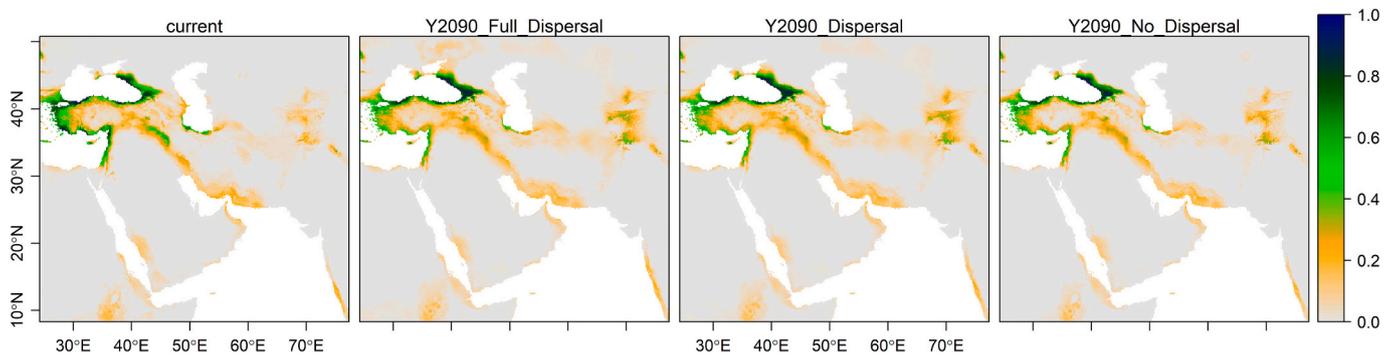


Fig. 2. Fuzzy species richness maps for the baseline (current time) and future (2081–2100) time for the climate scenario of SSP585 and three dispersal scenarios including: full dispersal (no dispersal limitation), dispersal (assuming a geographical distance-based dispersal capacity for each species), and no dispersal (assuming no dispersal capacity for species).

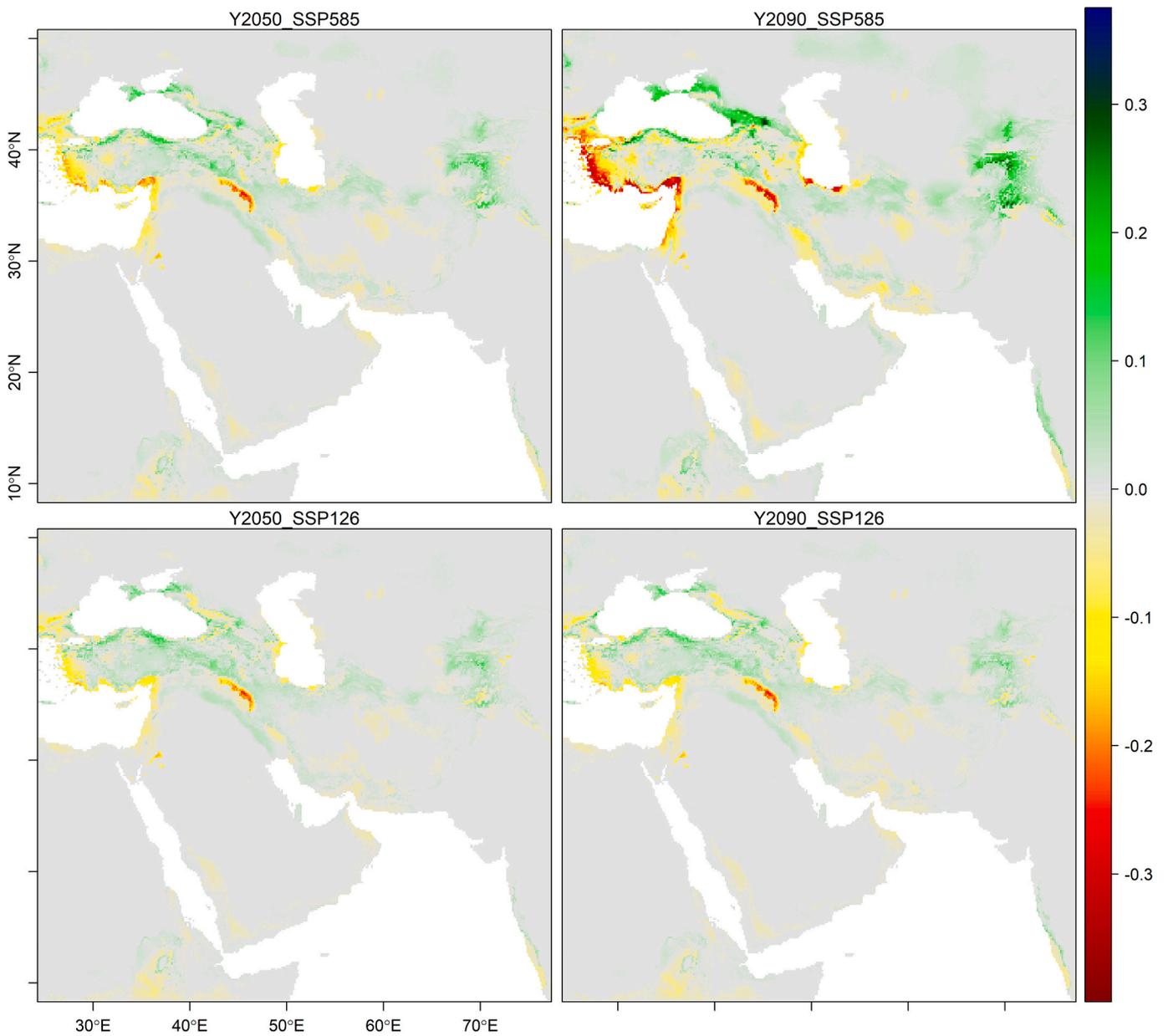


Fig. 3. Changes in richness due to climate change between baseline and future times for the years 2050 (2041–2060) and 2090 (2081–2100) under two climate scenarios of SSP126 and SSP585; Negative values represents loss in richness while positive values represent gain in richness in response to climate change.

SSP585 in the years 2070 and 2090, followed by SSP370 in the same years, as depicted in Fig. S6.

3.4. Gap analysis

The analysis of species' suitable ranges within PAs showed that, using a threshold of 10 %, 29 out of 45 species are adequately protected in the baseline, dropping to 27 species by 2100 across all scenarios. For a threshold of 20 %, only 7 species are protected in both the baseline and future times, with no species meeting the threshold of 30 %. Among the 13 IUCN Red List species in our study area, 8 have at least 10 % of their range within PAs, but only 4 species exceed the 20 % threshold in current and future times.

Fuzzy suitability and richness values at the pixel level indicate significant declines in both metrics within PAs under various future climate scenarios. Specifically, the mean fuzzy richness values suggest that many PAs will lose their effectiveness in preserving biodiversity over time, as evidenced by decreasing richness and suitability trends across all SSPs (Fig. 4a). The analysis shows that suitability values for the majority of pixels within PAs range from 0.1 to 0.4 in the baseline, but decline significantly across all future climate scenarios, whether full-dispersal (Fig. S7) or realistic species-specific dispersal capacities are considered (Fig. 4a). Although all scenarios exhibit a decreasing trend in habitat suitability, the decline becomes more pronounced under more pessimistic scenarios.

Furthermore, density plots (Fig. 4b) demonstrate an increasing frequency of pixels within PAs with lower suitability values over time. The peak density of mean fuzzy suitability values within PAs shifts from 0.35 in the baseline to 0.25 under SSP126 and 0.1 under SSP585, highlighting a substantial decline in habitat suitability under more pessimistic scenarios. Fig. 4b shows that, despite the declining trends, mean fuzzy suitability values within PAs remain consistently higher than those outside PAs and across the total study area for all SSP scenarios. The patterns observed in the full dispersal scenario are similar to those in the limited dispersal scenario, but both differ from the no dispersal scenario,

where the peak of mean fuzzy suitability within PAs remains around 0.3. The decline in suitability values is less pronounced in the full and no dispersal scenarios compared to the limited dispersal scenario (Fig. S8).

3.5. The trend of mean fuzzy richness within PAs

In the most realistic scenario, the dispersal scenario, there is a noticeable declining trend in mean fuzzy richness within PAs from 2020 to 2100. All SSP scenarios maintain a downward trend, except for SSP126, which shows a slight increase towards the end of the century. This same trend is observed in the full dispersal scenario (Fig. 5). However, in the no dispersal scenario, the trend is reversed, showing an increase in mean fuzzy richness over this period (Fig. S9).

3.6. Uncertainty in species richness predictions

The standard deviation of richness values at the pixel level across all SDM replications reflects variability or uncertainty resulted from GCMs, SSPs, and SDM methods (Fig. 6a). The data reveal a maximum standard deviation of 0.20, identifying areas with significant uncertainty, with most pixels showing values above 0.15, indicating widespread uncertainty across the landscape. Decomposing this total uncertainty (Fig. 6b) shows that SDMs contribute the most, followed by GCMs, particularly in mountainous regions, and SSPs, which exhibit a relatively uniform uncertainty distribution. This pattern is consistent across other time periods (Fig. S10).

When SDMs are combined through the ensemble procedure, the standard deviation of richness values decreased, with a maximum of 0.05 (Fig. 7a). Most regions show minimal uncertainty, but mountainous and coastal areas have higher uncertainty levels. Decomposing the total uncertainty attributed to the sources of GCMs, SSPs, and dispersal scenarios (Fig. 7b) reveals that GCMs contribute the most, especially in complex climatic regions, followed by SSPs, which are more uniformly distributed, and dispersal scenarios, which significantly influence areas with high species richness. This pattern also holds across other time

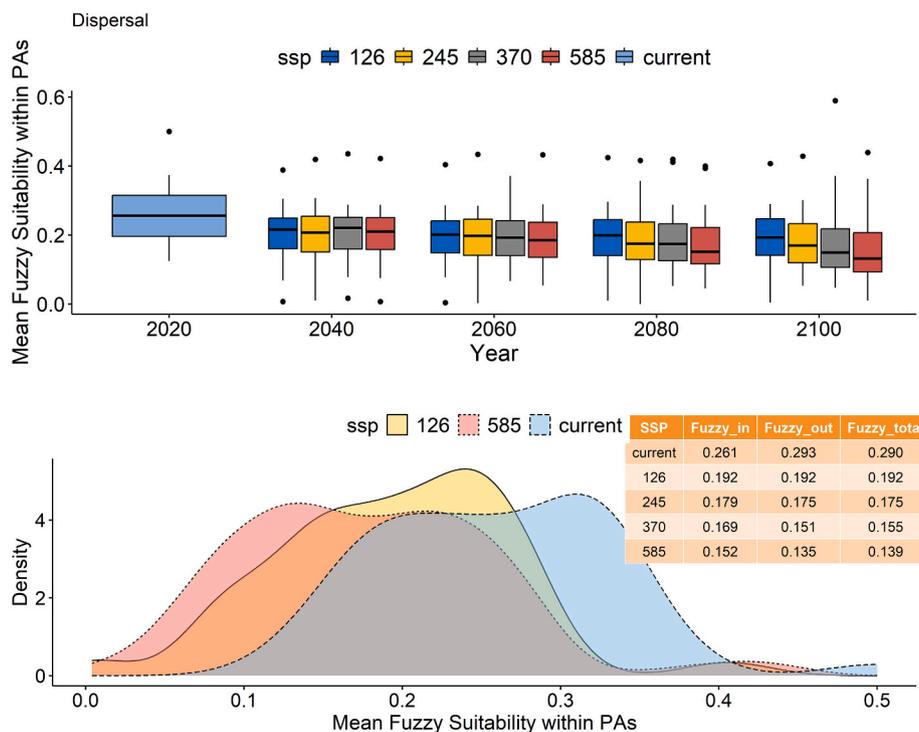


Fig. 4. (a) Variation in the degree of fuzzy habitat suitability values within PAs in the current and future times based on four climate change scenarios (SSPs); (b) comparison between distributions of the mean fuzzy suitabilities within PAs between the current time and the year 2090 based on two future scenarios of SSP126 and SSP585.

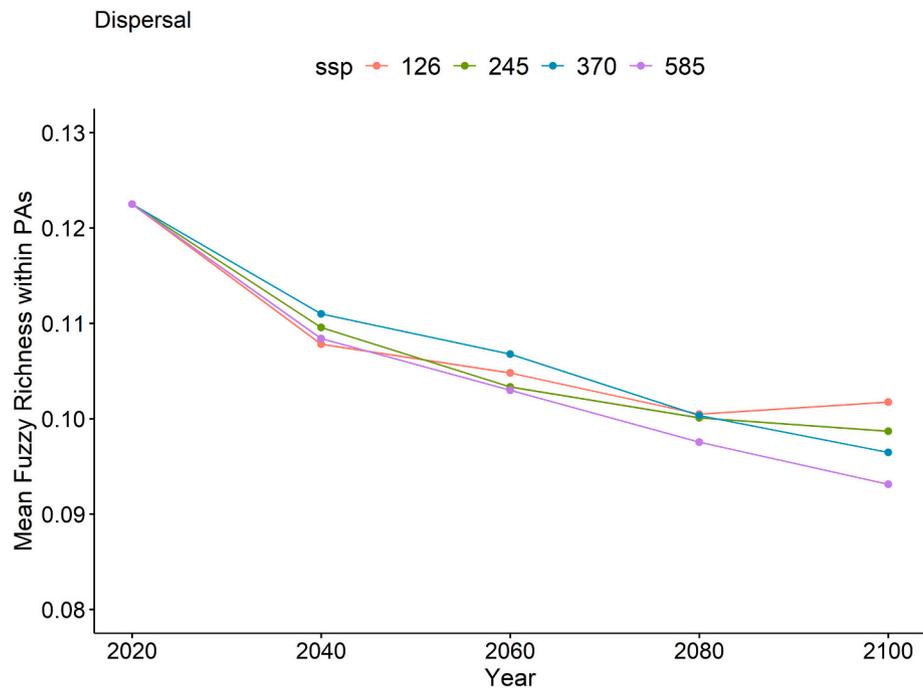


Fig. 5. The trend of mean fuzzy richness within PAs across different SSP scenarios from 2020 to 2100.

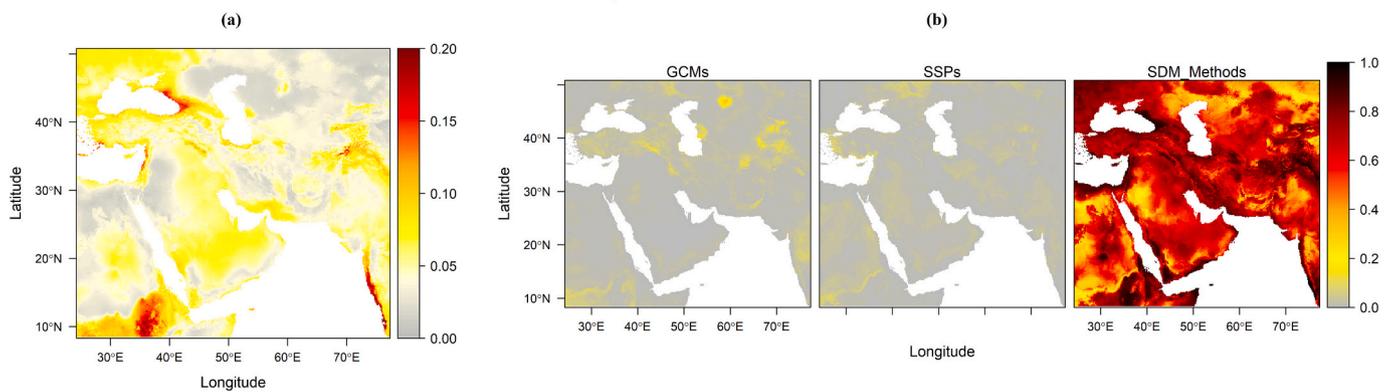


Fig. 6. (a) Standard deviation of Uncertainty in GCMs, SSPs, and SDMs; (b) Decomposing Sources of Uncertainty in GCMs, SSPs, and SDMs.

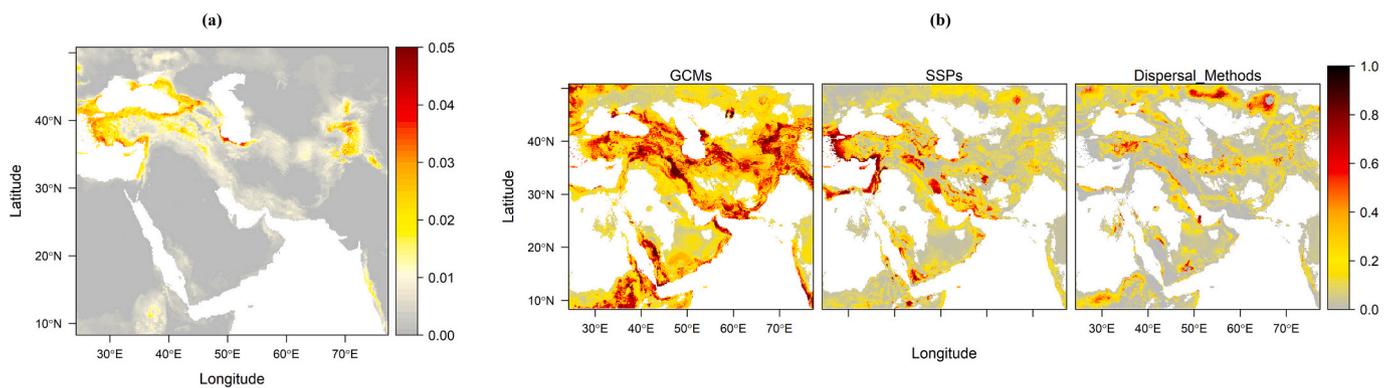


Fig. 7. (a) Standard deviation of Uncertainty in GCMs, SSPs, and Dispersal Methods; (b) Decomposing Sources of Uncertainty in GCMs, SSPs, and Dispersal Methods.

periods (Fig. S11).

4. Discussion

This study presents a refined gap analysis method for biodiversity conservation by employing a fuzzy approach, offering distinct

advantages over traditional methods. Firstly, this approach allows us to assess suitabilities in a continuous form as an indicator of a species' habitat quality, and track changes in suitability over time, making the assessment more flexible while avoiding information loss typically associated with binarising SDMs. Secondly, our method enables the simultaneous consideration of multiple target groups of species, a critical improvement for conservation planning. In this study, we demonstrated this capability by analysing gaps in conservations and assessing effectiveness of PAs by simultaneously considering two widely used groups: all species and vulnerable species. Traditional gap analysis often focuses on total species richness, considering all species, to address general conservation needs and ensure comprehensive biodiversity protection. In contrast, some studies conducted gap analysis by considering only vulnerable species (Jung et al., 2021; Venter et al., 2014) to align with global conservation goals that prioritise the protection of threatened biodiversity unlike traditional approaches, our fuzzy-based gap analysis can easily incorporate multiple target groups simultaneously, ensuring a broader representation of biodiversity within PAs. Additionally, relative fuzzy values at the pixel level, generated by our approach, provide a continuous measure of habitat importance for biodiversity conservation, serving as a crucial indicator for effective biodiversity prioritisation. This capability enhances the precision and relevance of conservation strategies to be both comprehensive and targeted, ensuring that critical habitats are identified and prioritised effectively.

Our novel fuzzy approach also enhances the identification of refugia, which are important for biodiversity conservation and prioritisation. Refugia are areas that remain consistently suitable both in the current and future times (Brambilla et al., 2022). Traditional gap analysis using binarised SDMs typically identifies these refugia by overlaying binary suitable habitats in both time periods. Our fuzzy approach allows for a more nuanced identification and separation of refugia. Specifically, we can distinguish between refugia that are gaining suitability in the future, indicating an increasing trend in habitat quality, and those that, while still suitable, show a decreasing trend in suitability. Sites that are gaining suitability are preferred in conservation prioritisation as they are likely to provide better long-term habitats for species under changing climate conditions. This differentiation is crucial, as it allows conservation efforts to focus on areas with the highest potential for maintaining and enhancing biodiversity, thereby ensuring more effective and resilient conservation strategies.

We selected amphibians as a model group to test our approach because they are highly vulnerable to climate change (Alroy, 2015; Barnosky et al., 2011). However, recent studies indicated that the conservation gaps of PAs for amphibians will increase under future climate conditions, suggesting that PAs might become more effective for this group in the future (Chen et al., 2017; Ebrahimi et al., 2022; Mi et al., 2023) which contrasts with many other groups (Ebrahimi et al., 2021; Tang et al., 2022). Consistent with these studies, our findings show that amphibians, that are currently protected by PAs, will remain protected in the future under various future scenarios. However, our approach revealed a decreasing trend in the average suitability of their habitats within PAs. These results highlight the importance of distinguishing sites with positive suitability trends from others in conservation prioritisation.

Amphibians may shift to higher altitudes to track suitable climatic conditions, with different range outcomes depending on habitat availability and connectivity (Chen et al., 2011; Colwell et al., 2008; Mi et al., 2023). Therefore, high-altitude PAs are essential for conserving amphibian biodiversity under climate change (Araújo et al., 2011; Dudley et al., 2013). We found that most of the future amphibian refuges are in the Taurus, Pontic, Lesser Caucasus, Elburz, and Greater Caucasus Mountains (e.g., Ahmadzadeh et al., 2020; Amiri et al., 2021; Figs. 3 and S6). This suggests that PAs situated in mountainous regions may act as important refuges for amphibians under climate change, providing a range of habitats and climatic conditions along elevation gradients (Luo

et al., 2021). In developing countries, PAs are often established in highland areas, as they are less attractive for human activities and therefore less costly to protect (UNEP-WCMC and IUCN, 2021). This may benefit amphibians in the future, as they may find suitable habitats and refuges within these high-elevation PAs (Mi et al., 2023). However, our results also show that Turkey, which hosts a large proportion of the amphibian richness in the region, has limited PAs that need to be expanded. Therefore, we recommend that conservation planning for amphibians should consider the potential effects of climate change on their elevational shifts and prioritise the establishment and expansion of PAs that can accommodate these shifts.

In our gap analysis, we followed the best-practice standards (Araújo et al., 2019) to implement a sophisticated workflow for species distribution modelling, utilising an ensemble of multiple machine learning methods to predict current species distributions and project their future distributions under various climate change scenarios and multiple GCMs. By incorporating dispersal capacity of species, our projections are made more realistic, accounting for how species might move across landscape. This comprehensive methodology not only enhances the robustness and accuracy of our predictions, but also allows for spatial uncertainty assessments. We argue that this advanced workflow can be applied beyond gap analysis, serving as a good practice for SDM applications in various ecological and conservation contexts, ultimately contributing to the development of more effective and resilient strategies and informed decision making.

Although widely used SDMs often generate probabilities of species occurrence to predict geographical distributions, their interpretation as actual occurrence probabilities can be problematic due to various factors, such as sampling biases, sample sizes, and differences in species detectability (Araújo and Guisan, 2006; Elith and Leathwick, 2009). Consequently, these probabilities are often interpreted as relative habitat suitability instead. However, an unresolved issue of these suitability values is their lack of comparability across different SDMs developed using various modelling methods or for different species. For example, a suitability score of 0.7 for one species may indicate a more favorable habitat compared to a score of 0.9 for another species, which complicates conservation planning and biodiversity assessment when multiple species are involved. To address this issue, binary conversion of SDMs is often applied to standardise outputs for comparability; however, this process leads to significant information loss by reducing continuous gradients of habitat suitability into a simple presence-absence format. In contrast, the fuzzy transformation of SDMs employed in our study maintains the continuous nature of SDM predictions, while standardising values to a comparable range between 0 and 1. This method ensures that habitat suitability gradients remain intact across species and models, providing a more interpretable representation of habitat quality. Thus, we recommend incorporating of the fuzzy transformation approach into standard SDM practices for applications beyond gap analysis. Additionally, we advocate for future methodological research to focus on developing and adopting traditional approaches that utilise continuous, standardised SDMs rather than binary data, to enhance the accuracy and consistency of habitat suitability assessments.

Despite using three different dispersal scenarios in this study, we emphasise that the “dispersal” scenario is likely the most realistic, as it considers the species' ability to move and adapt to changing conditions. The other two scenarios—full dispersal and no dispersal—serve as extremes for comparison, highlighting the role of dispersal in shaping future species distributions. Our findings demonstrate that dispersal capacity significantly affects the projected future range dynamics of species, emphasising the importance of incorporating realistic dispersal capacity of species in conservation planning (Lechner et al., 2015). We used a straightforward procedure to filter out pixels potentially suitable under future climate conditions but beyond species' dispersal reach. This could be refined further by incorporating barriers and connectivity to more precisely identify pixels out of species' reach.

To fully demonstrate the effects of different sources of uncertainty in the gap analysis of PAs, we employed a comprehensive modelling with 3200 replications of 10 machine learning algorithms for each species and dispersal scenario, totaling 432,000 replications. Our uncertainty assessments were conducted at two levels. First, we produced the richness maps for each modelling method separately, allowing us to assess the contribution of SDM algorithms, GCMs and SSPs. The results revealed that the choice of modelling method accounts for 80 to 90 % of the total uncertainty. These findings underscore the critical importance of using an ensemble approach as a robust solution to mitigate model-based uncertainty by combining outcomes from multiple methods into a consensus prediction (Araújo and New, 2007). This strategy was applied in our second uncertainty assessment, where we used ensemble predictions to quantify the contributions of GCMs, SSPs, and dispersal scenarios. A significant reduction in total variability across models—assessed through the standard deviation—demonstrates the robustness of the ensemble approach in enhancing confidence in spatial predictions of species richness, a conclusion also supported by previous studies (Araújo et al., 2005b; Marmion et al., 2009).

By quantifying and visualising these sources of uncertainty, our analysis provides valuable insights for conservation planning. Areas with high variability highlight regions where adaptive management strategies are essential to address uncertainty effectively, while regions with low uncertainty and high suitability emerge as strong candidates for immediate conservation action. Integrating these uncertainty metrics into decision-making frameworks strengthens spatial prioritisation and ensure conservation strategies remain resilient under diverse climate and socioeconomic scenarios (Kujala et al., 2013).

However, we acknowledge that models may also be affected by other sources of uncertainty not explicitly considered in this study. For instance, SDMs relying on presence-only data often fail to account for imperfect detection, where species remain undetected during surveys despite their presence (Yackulic et al., 2013). Imperfect detection can bias predictions of habitat suitability (Rocchini et al., 2023) and conservation gaps, particularly when occurrence records are opportunistically collected rather than systematically surveyed. Although we did not explicitly incorporate detection probabilities due to data limitations, this remains a key area for improvement in future studies. In addition, the accuracy of the fuzzy gap analysis relies on the quality and availability of species distribution data (Hortal et al., 2008; Xueyan et al., 2024), which remains a significant challenge in regions with sparse or incomplete occurrence records (Boakes et al., 2010). In data-deficient regions like Southwest Asia, SDM predictions may be less reliable, potentially affecting the precision of conservation assessments. However, the sensitivity of SDMs to such data issues varies among modelling methods (Wisz et al., 2008). Using the ensemble approach may partially address this limitation by combining different models to minimize biases and generate robust consensus predictions (Araújo and New, 2007). While this ensemble method cannot fully eliminate the impacts of incomplete data, it reduces the influence of individual model inaccuracies and enhances prediction reliability. Future efforts to improve the quality and completeness of occurrence records—through systematic surveys, targeted data collection, and citizen science platforms—are crucial to further strengthen SDM-based gap analyses, particularly in underrepresented regions (Theobald et al., 2015).

5. Conclusion

Our study presents a sophisticated fuzzy-based approach for gap analysis in biodiversity conservation, offering significant improvements over traditional methods. By maintaining continuous habitat suitability values and considering multiple target species groups, we enhance the accuracy and relevance of conservation assessments. The ability to distinguish between refugia with increasing and decreasing suitability trends provides valuable insights for prioritising conservation efforts. Our comprehensive modelling approach, incorporating species dispersal

and future climate scenarios, underscores the robustness of our method. Our uncertainty assessment, involving 432,000 modelling replications, revealed that the choice of modelling method accounts for 80 to 90 % of the total uncertainty, highlighting the importance of ensemble approaches.

Furthermore, we demonstrated that species richness alone may not accurately reflect the true vulnerability of natural communities and is not an efficient criterion for identifying conservation gaps. By considering the conservation status of species, our method allows for a more targeted and effective approach to conservation interventions. These advancements contribute to more effective and resilient conservation strategies, guiding policymakers and practitioners in safeguarding biodiversity amidst climate change. Future research should continue to refine these methods and expand their application across various ecological contexts.

CRedit authorship contribution statement

Elham Ebrahimi: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Faraham Ahmadzadeh:** Writing – review & editing, Writing – original draft, Supervision, Resources, Investigation, Funding acquisition, Conceptualization. **Asghar Abdoli:** Writing – review & editing, Writing – original draft, Supervision, Resources, Investigation. **Miguel B. Araújo:** Writing – review & editing, Supervision, Methodology. **Babak Naimi:** Writing – review & editing, Writing – original draft, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors have no conflict of interest to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111054>.

Data availability

Data will be made available on request.

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