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Original Research Article

Effects of climate change on habitat and connectivity for populations of a vulnerable, endemic salamander in Iran

Mohammad Reza Ashrafzadeh [a], [*], Ali Asghar Naghipour [a],
Maryam Haidarian [b], Szilvia Kusza [c], David S. Pilliod [d]

[a] *Faculty of Natural Resources and Earth Sciences, Shahrekord University, 8818634141, Shahrekord, Iran*
[b] *Faculty of Natural Resources, Sari Agricultural Sciences and Natural Resources University, Sari, Iran*
[c] *Institute of Animal Science, Biotechnology and Nature Conservation, University of Debrecen, 4032, Debrecen, Hungary*
[d] *U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 970 Lusk Street, Boise, ID, 83706, USA*

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ABSTRACT

Habitat loss and fragmentation are among the biggest threats to amphibian populations and anthropogenic climate change may exacerbate these. The response of Iran's amphibians to climate change is uncertain and yet making an accurate prediction of how the species will respond is critical for conservation. We assessed how expected future climate scenarios before the years 2050 and 2070 might influence the geographic distribution and habitat connectivity of the Lorestan Mountain Newt (*Neurergus kaiseri*). We examined presence data (2010–2018) of the species according to environmental and anthropogenic factors, and created an ensemble model of habitat suitability based on eight species distribution models (SDMs). Then, we used the concept of circuit theory to estimate potential linkages between the habitat patches. We applied the ensemble calibrated models and quantified spatial connectivity to assess the influence of climate change on the species range for the years 2050 and 2070 under four representative concentration pathways (RCPs) of three general circulation models (GCMs). Models using current climate predicted that 6.8% of the 267,609 km^2 study area has suitable conditions for the species, but only about 7% of these climatically suitable landscapes are covered by conservation areas. Temperature and precipitation-related climatic variables made the largest contribution to the distribution model. Under projected climate conditions, we found a decline of 56–98% of the suitable habitat and predicted a potential for distributional shifts towards higher elevations by 2050 and 2070. Although there is relatively good connectivity between many habitat patches today, models predict that suitable areas available to the newt will become increasingly fragmented under projected climate change scenarios. Our findings support the hypothesis that projected climatic shifts will negatively influence suitable habitats of amphibians and likely cause upward shifts in elevation in range of some species. Identifying potentially suitable habitats and important linkages between habitat patches under different climate scenarios are crucial steps in conservation planning for the Lorestan Mountain Newt.

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[*] Corresponding author.
E-mail address: mrashrafzadeh@sku.ac.ir (M.R. Ashrafzadeh).

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1. Introduction

Climate and landscape characteristics strongly affect species distributions as well as connectivity among populations (Velo-Antón et al., 2013; Early and Sax, 2014; Kusza et al., 2019; Archis et al., 2018). Climate change is recognized one of the largest threats to biodiversity and is expected to result in shifting species distributions and increasing extinction risk of populations that are unable to adapt or relocate to suitable habitats (Bellard et al., 2012; Devictor et al., 2012; Sutton et al., 2015; Sugden, 2017; Ashrafzadeh et al., 2019). For example, significant range shifts have been documented for different species, such as a 6.1 km per decade on average shift towards poles (Parmesan and Yohe, 2003). Seasonal and annual patterns of temperature and precipitation, as the two most important factors in the climate, will influence vital processes of amphibian populations (Dervo et al., 2016), as well as performance of individuals (Clusella-Trullas et al., 2011; Archis et al., 2018). Habitat specialists, particularly those with sensitivity to environmental changes and lower dispersal ability, are particularly vulnerable to the synergistic effects of climate and landscape change (e.g., fragmentation, urbanization) (Mestre, 2017). Habitat fragmentation is considered one of the main causes of terrestrial diversity decline (Ochoa-Ochoa et al., 2012). Therefore, forecasting how a species will respond additionally to predicted climate changes requires an understanding of species-specific vulnerabilities, such as the ecological constraints on dispersal (Velo-Antón et al., 2013).

The geographic distribution of amphibian taxa is strongly influenced by climate and there is particular concern about how future climates may increase the risk of extinction for species with narrow climate niches (Carvalho et al., 2010; Milanovich et al., 2010; Clusella-Trullas et al., 2011; Pilliod et al., 2015; Archis et al., 2018). Amphibian populations are currently experiencing drastic declines in many parts of the world (Stuart et al., 2004; Grant et al., 2016; Greenberg et al., 2018) and nearly one-third of all amphibians' species are globally threatened or extinct (Sutton et al., 2015). Salamanders may be particularly vulnerable to climate change because of their limited dispersal abilities (Parra-Olea et al., 2005; Velo-Antón et al., 2013; Sutton et al., 2015; Tok et al., 2016; Van Riemsdijk et al., 2017). This vulnerability may also serve as an early indicator of the potential future effects of global climate change on other amphibian species (Welsh and Hodgson, 2013; Sutton et al., 2015).

The genus *Neurergus* in the family salamandridae has a relatively wide distribution from southwestern Iran (Zagros Mountains) to Iraq and southern Turkey (Baloutch and Kami, 1995; Vaissi et al., 2012), but the Lorestan Mountain Newt (*N. kaiseri*, Schmidt 1952) is a rare species (Mobaraki et al., 2013; IUCN SSC Amphibian Specialist Group, 2016) found only in southwestern Iran and restricted to Lorestan and Khuzestan provinces (Mobaraki et al., 2013; Farasat and Sharifi, 2016) (Fig. 1, Fig. S1). *Neurergus kaiseri* has been assessed as a vulnerable species (IUCN SSC Amphibian Specialist Group, 2016) and is included in Appendix I of the Convention to the International Trade to Endangered Species (CITES). The species range is reported at about 9398 km^2, where it has been found between 385−1500 m asl (IUCN SSC Amphibian Specialist Group, 2016). *Neurergus kaiseri* is found in springs, streams, water troughs and waterfalls within oak-pistachio open woodlands. As with many other salamanders (Dervo et al., 2016), migration between spring and autumn habitats for breeding and hibernation is one of the most critical activities of the species' life cycle. Shifts in this migration period caused by changing climatic conditions, particularly warming, could have negative consequences for population persistence. *Neurergus kaiseri* is also currently faced with the decline of local populations due to overharvesting for pet trade, deforestation, water resource mismanagement, predation by cyprinid fish (*Barbus* sp.), pollution, drought, livestock grazing, agriculture and ecotourism (Sharifi et al., 2008; Vaissi et al., 2012; Mobaraki et al., 2013; IUCN SSC Amphibian Specialist Group, 2016). Although some authors have documented *N. kaiseri* distribution (Sharifi et al., 2008, 2013; Torki, 2012; Mobaraki et al., 2013; Barabanov and Litvinchuk, 2015), habitat suitability (Zangene et al., 2016; Farasat et al., 2016) and phylogeny (Farasat et al., 2016), no study to date has evaluated the potential climate change consequences on the species in Iran. The fate of the species likely depends on its ability to adapt or adjust to climate change. Thus, it becomes one of the most important priorities to project how the species may respond to forthcoming climates throughout its contemporary range in southwestern Iran.

Scientific evidence for climate change effects on amphibians, such as recent climate-related shifts in species distributions, indicates that using future climate change scenarios is a useful tool in current management and conservation decisions (Parmesan and Yohe, 2003; Barrett et al., 2014; Kafash et al., 2018). Furthermore, the synergistic effects of climate change and habitat disturbance emphasize the importance of first detecting climate refugia (i.e., landscapes with relatively suitable local temperature and humidity conditions in the face of climate change; Sutton et al., 2015) and assessing habitat connectivity among refugia under changing climate for conservation of populations. Identifying suitable habitats and assessing connectivity are critical to maintain key landscapes for small isolated, threatened populations (Habibzadeh and Ashrafzadeh, 2018). Species distribution models (SDMs) have been widely used to detect current suitable habitats and to forecast potential impacts of climate change on the species such as predicting future range shifts (Elith et al., 2006; Beaumont et al., 2007; Milanovich et al., 2010; Hole et al., 2011; Ashrafzadeh et al., 2019; Archis et al., 2018).

In this study, we used species distribution modeling to identify the current suitable habitats of *N. kaiseri* and predict whether its range is likely to expand or contract under projected climate change scenarios. We hypothesize that the drier and warmer climates in the near future will reduce the amount and connectivity of suitable habitats. We suspect that these habitat changes will increase extinction risk of many populations and shift the distribution of the species to higher elevations. The study area is southwestern Iran, which covers the whole range of the species (Mobaraki et al., 2013; IUCN SSC Amphibian Specialist Group, 2016; Farasat et al., 2016). We search for answers to the following questions: (i) Which areas are predicted currently as suitable habitats for *N. kaiseri* in southwestern Iran? (ii) Will the distribution of the species likely expand or contract under various climate change scenarios by 2050 and 2070? (iii) To what extent will suitable habitat be covered by

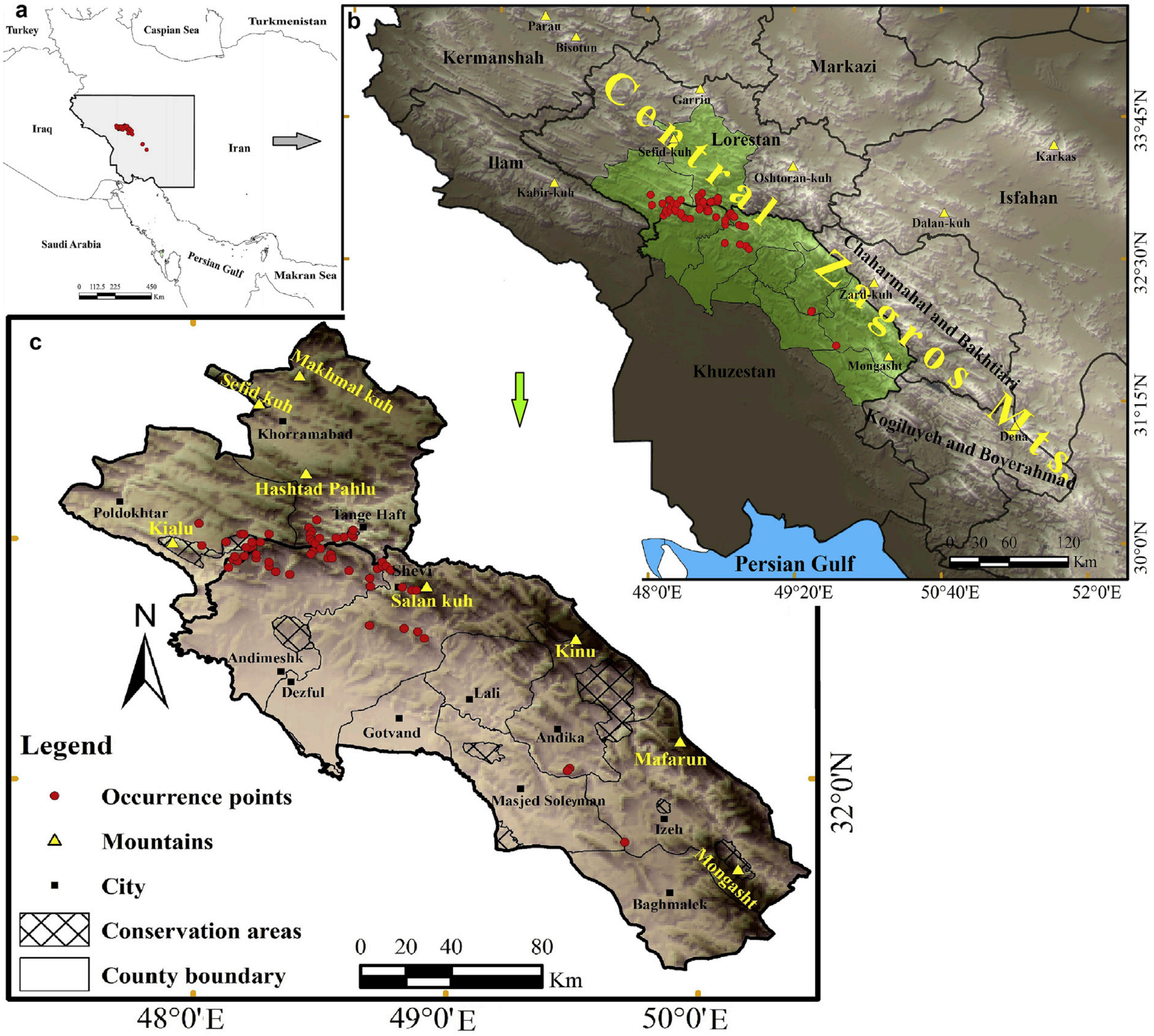

Fig. 1. Map of the study area in Southwestern Iran (a and b). The approximate (known) range of the species (c, the same extent as the green shade in b) is adopted from Mobaraki et al. (2013), Farasat et al. (2016) and IUCN SSC Amphibian Specialist Group (2016). First, the models were fitted in the known range of the species (c) and then projected to the study area (the larger extent or b). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

existing conservation areas in the future? (iv) What are potential consequences of changing climate on permeability of landscapes to the newt's movements?

2. Material and methods

2.1. Study area

Our study area includes a geographic range about 267,609 km^2 in southwestern Iran (Fig. 1b). The Zagros Mountains form the major mountain system of western Iran with long linear valleys separated by high ridges. The elevation of the mountain range is from 200 to 4500 m whereas the elevation of the study area ranges from sea level to 4223 m. The Zagros Mountains have a semi-arid temperate climate with average annual temperatures from 9 to 25 °C and annual precipitation from 250 to 800 mm (Sagheb-Talebi et al., 2014). The climax vegetation in the Zagros Mountains is an open xerophytic cold-resistant deciduous oak forest, which dominates at elevations from 1000 to 2000 m (Sagheb-Talebi et al., 2014). The unique climate and landscape of Zagros Mountains support a high level of biological endemism, including *N. kaiseri*.

2.2. Data collection

We compiled 106 records of occurrence from two sources: our field surveys (51 occurrence points) carried out in different parts of the study area (2015–2018) and distribution records (55 occurrence points) compiled by Iranian Department of the Environment (DoE) (2010–2018). We personally visited many sites across the study area to find reliable records and used only occurrence locations that were validated by our team and DoE's experts. We were not able to validate 12 occurrence points, which were excluded from our dataset. After excluding unverified occurrences, 94 records remained (51 and 43 points from the first and second sources, respectively). We excluded all multiple records of sites within a minimum distance of 2 km to reduce impacts of repetitive occurrences made at specific sites. This selection process reduced our occurrence records to 75 data points that were used for the distribution modeling approach.

2.3. Environmental variables

Topographic, landcover, anthropogenic and bioclimatic variables were used for *N. kaiseri* distribution models according to their relevance with the distribution of the species (Sharifi et al., 2008, 2013; Mobaraki et al., 2013; Zangene et al., 2016). We used a Digital Elevation Model (DEM, http://www.worldclim.org) to generate topographic variables. We used landcover data extracted from a map developed by the Iranian Forests, Ranges and Watershed Management Organization (IFRWMO, 2014). We used a human footprint model (Sanderson et al., 2002) to evaluate the anthropogenic effects on the newt's habitat, including land transformation, population density, human access and presence of infrastructures. We extracted the bioclimatic variables (bio1-bio19) from a 30 arc-seconds (~1 km) resolution dataset in WorldClim-Global Climate data (http://www.worldclim.org). All layers were projected onto the UTM grid, with WGS84 datum. We tested for multicollinearity among predictors by calculating Pearson correlation coefficients and used an $r < 0.7$ criteria to select which variables ($n = 11$) to include in the distribution models (Table 1). Because the aim of the study was to figure out the consequences of climate variable selection on distribution forecasts, we changed only the climate data when projecting to various time periods, while keeping the values of all other variables constant over time (current and future time periods).

2.4. Model construction

We employed a consensus model (i.e., “ensemble” model) approach to model *N. kaiseri* distribution (Thuiller et al., 2009) using R v. 3.1.2 (R Development Core Team, 2014) with the biomod2 package (Thuiller et al., 2016). The ensemble forecasting approach can generate a more robust model and overcome the uncertainties resulting from interpretation of results from individual models (Araújo and New, 2007; Hao et al., 2019). Our ensemble model used to predict *N. kaiseri* distribution across the study area included the generalized linear model (GLM), generalized boosted model (GBM), classification tree analysis (CTA), artificial neural network (ANN), surface range envelope (SRE), flexible discriminant analysis (FDA), random forest (RF), and maximum entropy (MaxEnt). There are unconfirmed reports for *N. kaiseri* in other provinces of western Iran besides Lorestan and Khuzestan. Thus, we first fitted the models in the known range of the species (the areas where we have presence points for the species) and then projected to the larger extent (the study area) (Václavík and Meentemeyer, 2012; Simpson and Prots, 2013) to provide more accurate predictions of the potential area of future suitable habitat (Archis et al., 2018). Most of the algorithms used require simulated pseudo-absence data for model fitting and evaluation. Since a larger proportion of pseudo-absence points against presences has been found to affect model performance positively or negatively (Barbet-Massin et al., 2012; Senay et al., 2013), we selected the number of pseudo-absences equal to the presence points (Senay et al., 2013; Iturbide et al., 2015; Hamid et al., 2018) with ten replicates per each model. Random pseudo-absences were selected only within the species' known range, with a minimum distance of 1 km (corresponds to grain size) between pseudo-absences (Arenas-Castro et al., 2018). By limiting the study area, large ranges where the species is not present

Table 1
Uncorrelated predictors and mean of their contributions (%) in eight *N. kaiseri* distribution models in southwestern Iran.

Variables	Relative importance (%)	SD
Bio7 (temperature annual range, maximum temperature of the warmest month-minimum temperature of the coldest month)	33.68	8.07
Bio17 (precipitation of driest quarter)	21.80	6.71
Bio13 (precipitation of wettest month)	14.22	5.48
Bio1 (annual mean temperature)	8.95	4.32
Slope	6.89	4.59
Bio4 (temperature seasonality, standard deviation*100)	5.91	3.56
Landcover	4.80	2.27
Bio3 (isothermality, [mean diurnal range/temperature annual range] [*100])	2.16	1.68
Bio14 (precipitation of driest month)	0.84	0.79
Aspect	0.39	0.44
Human footprint	0.35	0.42

were excluded in further analyses to avoid over-predicting the distribution extent of the species (Bobrowski et al., 2017). More, an exclusion buffer of 1 km around the occurrences was set to avoid cells covering both presence and pseudo-absence points (Chefaoui and Lobo, 2008). The set of pseudo-absence points was produced following Barbet-Massin et al. (2012) and Senay et al. (2013) in the Create Random Point tool in ArcGIS 10.3.

We used 75% of the occurrence points as training data for model calibration and the remaining 25% to evaluate the model's predictive performance. We used the variable importance criterion to estimate changes in modeling by accumulating the reduction in model statistics with the addition of each variable to the model (Kuhn, 2008). The consensus probabilistic map, indicating suitable habitats for *N. kaiseri* in response to current environmental conditions, was created by averaging the projections made by the various algorithms (Marmion et al., 2009). Model performance was evaluated using the area under the receiver operating curve (AUC) and the true skill statistic (TSS) because both criteria are independent of prevalence in the species data (Allouche et al., 2006; Zipkin et al., 2012). These two evaluation metrics are indicators of discrimination capacity, which quantifies how well the model can distinguish presences from absences (or presences from background samples, when absences are unavailable). In Hao et al. (2019) ensemble procedures often assess predictive accuracy using one or more measures of discrimination derived from a confusion matrix (e.g., 168 studies using AUC and 116 studies using TSS). Although evaluation and interpretation of the species distribution's projections are complex (Yackulic et al., 2013), TSS is recommended as a more realistic and practical criterion than AUC, Sensitivity and Specificity (Shabani et al., 2018).

General circulation models (GCMs), which use different representative concentration pathways (RCPs), provide credible quantitative estimates of future climate. RCPs are the four independent pathways of greenhouse gas concentration scenarios (IPCC, 2014). Projections from climate distribution modeling depend on the chosen GCM and assumptions on future atmospheric CO2 levels (Milanovich et al., 2010). Whereas no consensus exists as to what makes the most accurate GCM, integrating the different GCMs and RCPs to reinforce accuracy of the projections is strongly recommended (Sutton et al., 2015). We used the ensemble calibrated models of current conditions for projecting the future potential distributions of *N. kaiseri* for the years 2050 and 2070 under four RCPs of the GCMs of MRI-CGCM3 (Meteorological Research Institute, Japan), CCSM4 (National Center for Atmospheric Research, USA) and BCC-CSM1-1 (Beijing Climate Center, China Meteorological Administration). We chose the three GCMs for the following reasons: MRI-CGCM3 is suggested as one of the best models for regional climate change projections in Iran (Abbasian et al., 2019) and both MRI-CGCM3 and CCSM4-1 have shown more accuracy than other GCMs from simulations of climatic data across Iran (Masoompour Samakosh et al., 2018). Also, BCC-CSM1-1 was among the best in the distribution models for other species in Iran (e.g., Ashrafzadeh et al., 2019).

The ensemble prediction was also carried out by applying a proportional weighted average of each model's projections based on the AUCs. To investigate the impact of climate change on the geographic distribution of *N. kaiseri*, we identified a spatially explicit habitat threshold for each predictor that split habitat suitability into two classes that we designated as suitable and unsuitable. This habitat threshold was determined on the basis of a receiver operating curve (ROC) criteria (Ashrafzadeh et al., 2019) and used for generating habitat suitability maps. We detected the habitat loss and gain by years 2050 and 2070 under four RCPs in all GCMs using the habitat suitability maps. We calculated the elevation and range size of potential occurrences. We then compared the mean value of elevation between the current time, 2050 and 2070, as well as the predicted shifts in total range size for future time periods (2050 and 2070). All projections were implemented using ArcGIS 10.3 (http://www.esri.com).

We overlaid the ensemble suitability map with the designated conservation areas (CAs) in the study area. This enabled us to evaluate whether existing CAs effectively protect *N. kaiseri* habitats and provided information to help guide future development plans for new CAs. We applied circuit theory approach (McRae et al., 2008) in Circuitscape v5 (www.circuitscape.org) to explore potential connectivity of the newt's suitable habitats under various climate scenarios in the study area. This method depends on an underlying resistance map, where each cell in the landscape is coded according to its resistance (or its relative unsuitability) reflecting how permeable each cell is to the movement for the target species. In the other words, more suitable landscapes are assigned a lower resistance value and vice versa. The resistance map can also be considered the inverse of a suitable habitat map, but with a focus on the movement of individuals across a certain cell (McRae et al., 2008). The circuit approach uses the resistance map to measure the probability of animal movements (i.e., using an electrical current analogue) between pairs of nodes (i.e., habitat patches) that make up the source and destination locations for flow of individuals across the study area (McRae et al., 2008; Grafius et al., 2017). In this research, the probability of movement between all pairs of habitat patches was evaluated to generate a cumulative map of potential connectivity among all possible pairs. We also used the map to identify critical areas for maintaining connectivity across the entire network of habitat patches in the study area (Dickson et al., 2013). We used habitat patches as source patches and the ensemble distribution map as an index of conductance (i.e., conductance of each raster point for movement).

3. Results

3.1. Modeled current distribution

All models had high predictive capacity, with an AUC range of 0.90–0.97 and TSS range of 0.78–0.88, but MaxEnt performed best (Table 2). Our models predicted that about 6.8% (18,159 km^2) of the study area is currently (1970–2000) suitable habitat for *N. kaiseri* (Fig. 2). As expected, the southern areas of the Lorestan province and northern and northwestern areas of Khuzestan province were mostly suitable, providing the largest habitat area for the species. Our models also projected that

Table 2
Evaluation of eight applied models predicting *N. kaiseri* distribution in southwestern Iran using area under the ROC curve (AUC) and true skill statistic (TSS).

	RF	SRE	GBM	GLM	FDA	CTA	ANN	MaxEnt
AUC	0.95	0.90	0.93	0.90	0.92	0.92	0.96	0.97
TSS	0.81	0.78	0.86	0.79	0.80	0.78	0.84	0.88

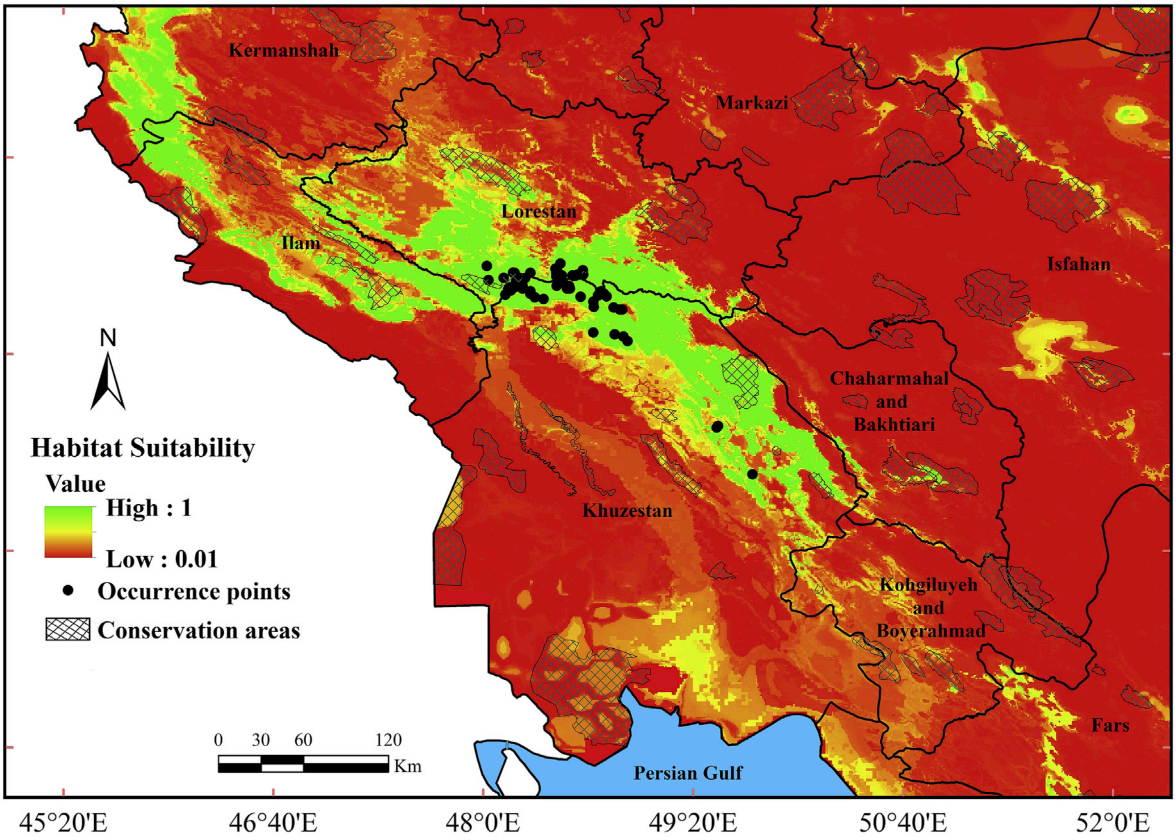

Fig. 2. Projected current habitat suitability for *Neurergus kaiseri* modeled based on consensus model.

there are other areas of potentially suitable habitat in southwestern Iran, especially parts of Kermanshah and Ilam provinces, but the species has not been detected there (Fig. 2). Small portions of Chaharmahal-Bakhtiari and Kohgiluye-Boyerahmad provinces also have moderate to high suitability under the current climate model. The current climate model also showed very small, isolated areas of low to moderate suitability in Fars and Isfahan provinces that are far away from known locations for the species.

Temperature annual range (33.7%), precipitation of driest quarter (21.8%), precipitation of wettest month (14.2%) and annual mean temperature (8.9%) made the greatest contribution to model performance, respectively (Table 1). The response curves indicated that *N. kaiseri* had the highest modeled suitable habitats in areas with annual mean temperature between 10.7 and 24.0 °C. The models also predicted higher habitat suitability in slightly moister areas, where precipitation of driest quarter is 1–4 mm and precipitation of wettest month of 25–130 mm. The average elevation of currently suitable habitat for *N. kaiseri* was estimated at 1156 m, but ranged from 274 to 2360 m. Only 7.1% (1288.43 km^2) of currently suitable habitats was projected to be represented within conservation areas (Fig. 2).

3.2. Modeled future distribution

The suitable habitat for *N. kaiseri* was projected to decline 55.8% (RCP4.5, MRI-CGCM3) to 98.1% (RCP8.5, BCC-CSM1-1) by 2050 and 2070 (Table 3). Under all climate scenarios, suitable habitat will decline over time across most the species range, but particularly at lower elevation areas (Fig. 3, Fig. 4). Parts of the newt's geographic range are projected to remain stable (Fig. 3, Fig. 4). Depending on the GCM and RCP combination, the ensemble models projected that by 2050 and 2070 new suitable habitat (i.e., previous unsuitable) will increase by 2.3% (412 km^2) (RCP6, BCC-CSM1-1, 2050) to 45.9% (8339 km^2) (RCP6, MRI-CGCM3, 2070), especially at higher elevations (Table 3, Table S1). All climate change scenarios implied an upward shift in

Table 3
Changes in current suitable habitats (loss/gain) of *N. kaiseri* by 2050 and 2070 under four RCP scenarios within the three general circulation models (MRI-CGCM3, CCSM4 and BCC-CSM1-1) in southwestern Iran. For detailed information on areas (km^2) see Table S1.

Year/Scenario	Habitat loss (%)			Habitat gain (%)		
	MRI-CGCM3	CCSM4	BCC-CSM1-1	MRI-CGCM3	CCSM4	BCC-CSM1-1
2050						
RCP2.6	88.10	88.26	95.98	23.78	30.07	9.36
RCP4.5	55.84	62.43	88.10	30.13	37.50	7.42
RCP6	71.16	83.03	97.76	24.06	28.50	2.27
RCP8.5	85.14	85.12	98.04	21.69	13.16	7.43
2070						
RCP2.6	82.12	86.31	93.67	43.36	39.28	20.42
RCP4.5	74.93	64.07	87.39	39.44	40.02	16.23
RCP6	67.87	81.46	96.81	45.92	38.67	11.30
RCP8.5	94.32	87.52	98.13	16.84	17.56	8.34

mean elevation of suitable habitat conditions of about 73 m by 2050 and 138 m by 2070, from an average of 1156 m currently to 1229 m for the year 2050 and 1294 m for the year 2070. More, expected future elevational range of *N. kaiseri* by 2050 is from a minimum 281 m (RCP2.6, MRI-CGCM3) to 2595 m (RCP8.5, MRI-CGCM3). This range for the 2070 is from a minimum 303 m (RCP2.6, BCC-CSM1-1) to 2639 m (RCP8.5, MRI-CGCM3).

3.3. Current and predicted future connectivity

Circuit theory indicated relatively good connectivity among many detected habitat patches in the current ensemble model, particularly throughout the areas where *N. kaiseri* has been recorded (Fig. 5). Weak connectivity coincided with poor habitat quality and increasing concentration of human activities. Our maps of the cumulative current flow suggest that the connectivity among many of suitable habitats (stable and new habitats patches) may be reduced by 2050 and 2070 (Fig. 5).

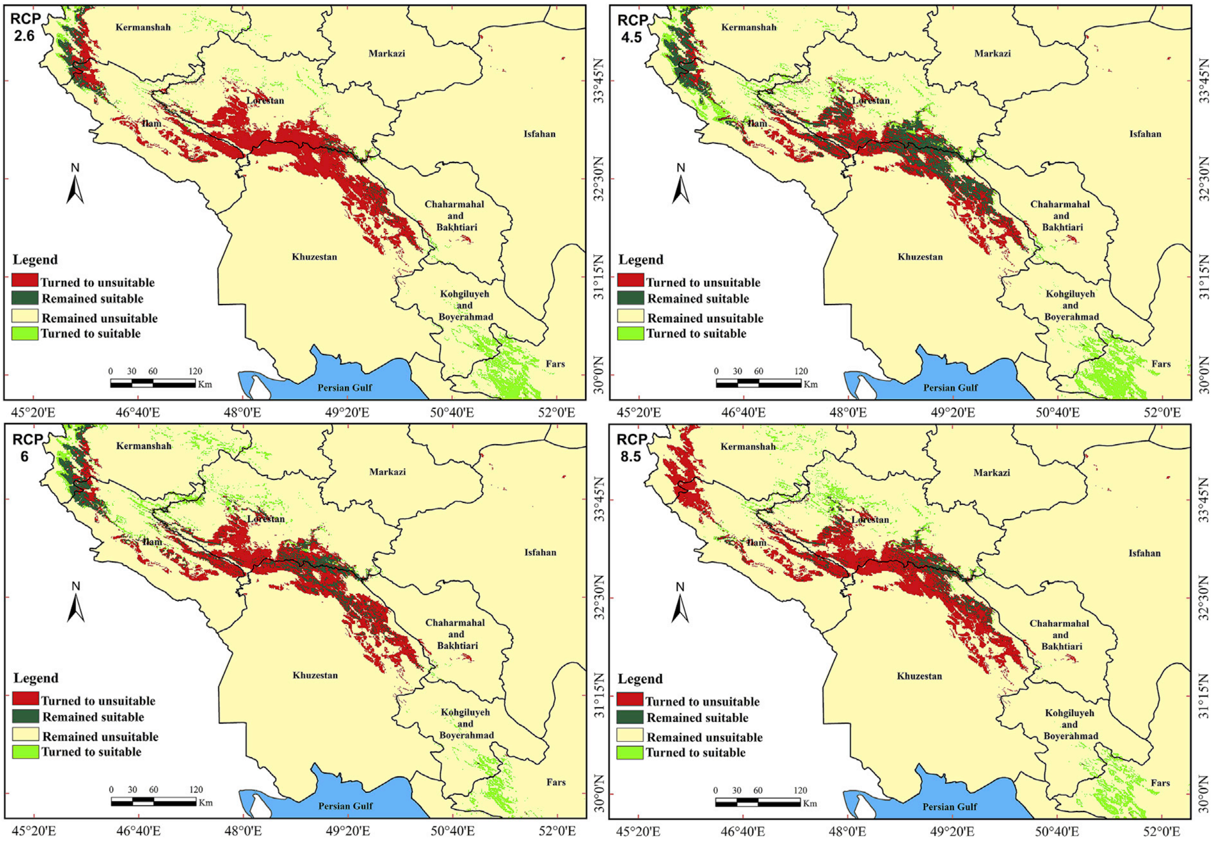

Fig. 3. Changes in suitable habitat of *Neurergus kaiseri* from current climatic conditions (1950–2000) to near future climatic conditions (year 2050) based on MRI-CGCM3 model with four RCP scenarios.

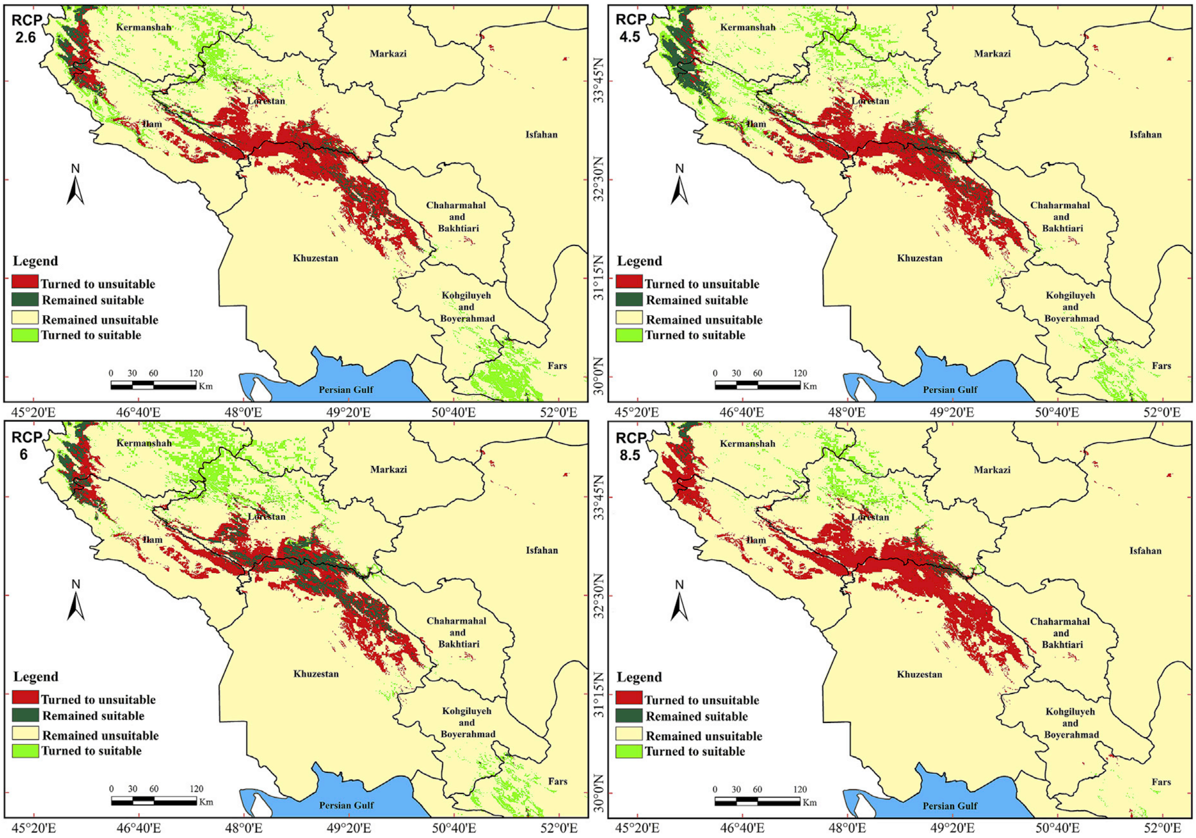

Fig. 4. Changes in suitable habitat of *Neurergus kaiseri* from current climatic conditions (1950–2000) to future climatic conditions (year 2070) based on MRI-CGCM3 model with four RCP scenarios.

4. Discussion

To date, the occurrence of *N. kaiseri* has been confirmed from Lorestan and Khuzestan provinces and, not surprisingly, our models predicted that the southern areas of Lorestan province and northern and northwestern areas of Khuzestan province contain the majority of suitable habitat for the species. However, current climate models also suggest that the newt's distribution may include more range in southwestern Iran, such as Chaharmahal- Bakhtiari, Kohgiluye-Boyerahmad, Ilam, and Kermanshah provinces. Further survey efforts in these areas are thus warranted.

N. kaiseri, like other salamanders, is highly influenced by the physical environment. Temperature and rainfall affect important processes such as habitat selection and migrations (Dervo et al., 2016). The life cycle of the newt is represented by seasonal migrations among aquatic (for breeding) and terrestrial (for foraging) habitats (Sharifi et al., 2013). In the current range of the species, a cold and wet highland climate infiltrates the warm and dry lowland climate of the Persian Gulf littoral (Vaissi et al., 2012). On the one hand, numerous first-order streams, originating from the southern highlands of the Iranian plateau, have sufficiently cool temperatures to maintain *N. kaiseri* populations (Vaissi et al., 2012). The dynamic interactions of the two climatic systems in the south and north create warmer temperatures with longer frost-free periods (Vaissi et al., 2012). In contrast to the recorded range of the species, the climatic conditions in higher areas of Central Zagros Mountain Range is characterized by long freezing periods.

Temperature annual range, precipitation of driest quarter, precipitation of wettest month and annual mean temperature were the most important predictive variables (in total, 78.7% contribution) in our study model. In accordance with our findings, Sutton et al. (2015) identified temperature annual range and annual mean temperature as the most important variables for predicting the climatic niche across numerous salamander taxa.

4.1. Climate change and habitat loss

Our model results support our hypothesis that projected climatic shifts will likely influence future habitat suitability of *N. kaiseri* and cause upward shifts in elevation in portions of its range. This finding is somewhat consistent with other studies on

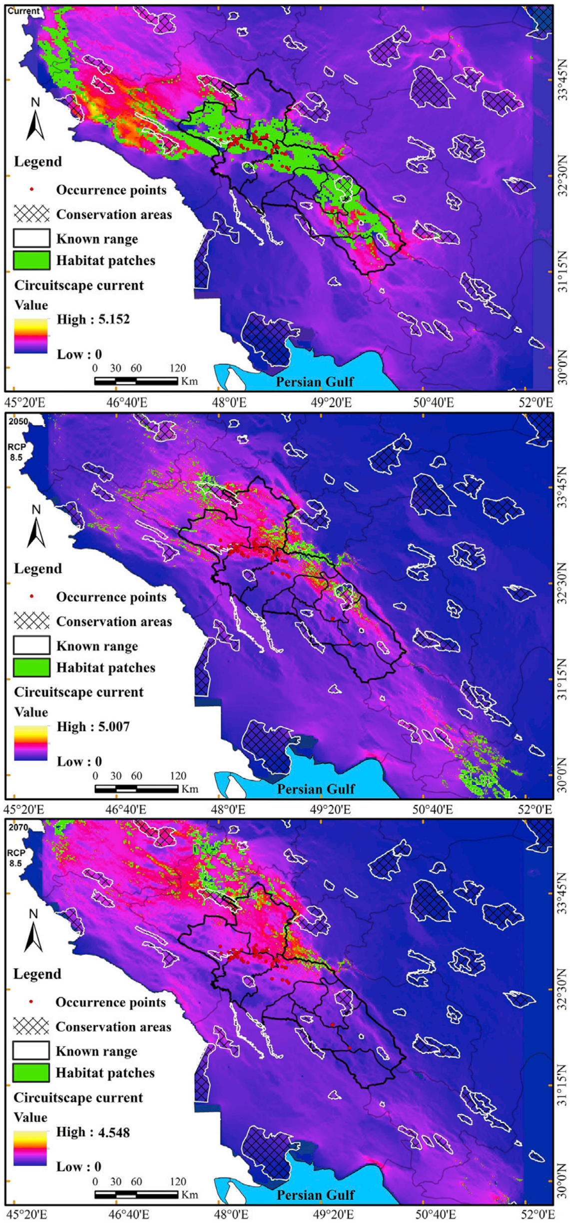

Fig. 5. Connectivity map among the habitat patches for *Neurergus kaiseri* under current climatic conditions and the near future and later (2050 and 2070) according to MRI-CGCM3 model (RCP8.5).

amphibians, particularly in relation to increasing temperatures (Milanovich et al., 2010; Ochoa-Ochoa et al., 2012; Velo-Antón et al., 2013; Barrett et al., 2014; Sutton et al., 2015; Tok et al., 2016). All GCMs predicted that suitable landscapes for the newt will decrease under all four RCP in 2050 and 2070. The findings indicate that the scenarios RCP8.5 (2070), RCP8.5 (2050), and RCP6 (2050) of BCC-CSM1-1 will have habitat losses of 98.1, 98.0, and 97.8%, respectively. Overall, the ability of species to adapt or adjust to climate change will depend on both the velocity of the climatic changes and species' dispersal abilities (Moritz et al., 2008; Loarie et al., 2009; Schloss et al., 2012). If warmer temperature causes *N. kaiseri* to shift their geographic ranges upward, the reduction in range size and available habitat will likely increase extinction risk and reduce connectivity among populations (Segelbacher et al., 2010; Hermes et al., 2018). The low dispersal abilities of *N. kaiseri* further increase the probability of isolation and reduce the likelihood of adaptive migration, rescue effects, or recolonization (Schloss et al., 2012). However, amphibians that use both aquatic and terrestrial habitats, such as *N. kaiseri,* sometimes behave contrary to expectations by moving considerable distances (e.g., >1 km) to reach distant suitable habitats (Smith and Green, 2005; Sinsch, 2014).

Other studies have painted a bleak picture of amphibian responses to climate change. For example, Ochoa-Ochoa et al. (2012) projected that the total number of amphibian species in Mexico dramatically decreased from 333 to 300 in 2020 (29 endemics extinct), to 258 (14 endemics extinct) in 2050 and finally to 254 (2 endemics extinct) species by 2080. These authors supposed the extinctions will be particularly intense during the period 2020—2050. Sutton et al. (2015) predicted all 24 evaluated salamander species in the northeastern United States to lose a portion of their current climatic niche (within an average range 3%—100%) by the year 2050. They suggested 14 species out of the 24 species to lose at least 50% of their climatic niche in the same timeframe. Further, recent analyses of negative effects of climate change on amphibians found some empirical evidence that certain species are more sensitive than others (Miller et al., 2018) and some locations are more likely to be affected than others (Grant et al., 2016). However, these authors also suggest that other stressors may be playing a bigger role, at least currently (Grant et al., 2016; Miller et al., 2018).

Survival in a rapidly changing climate will depend on whether or not susceptible species can find refuges that buffer against extreme conditions (Scheffers et al., 2014). Microhabitats, providing suitable microclimates (Ibanez et al., 2013), may act as key refuges (microrefuges) to moderate the ecophysiological consequences of changing climate on ectotherm communities (Huey and Tewksbury, 2009; Scheffers et al., 2014). While these microrefuges may help to buffer climate-sensitive organisms against extreme temperatures (Keppel et al., 2012; Rodhouse et al., 2017), reduced fitness and fragmented habitat and metapopulation dynamics may finally increase the risk of extinction (Huey and Tewksbury, 2009).

Many ectothermic organisms are able to remodel their physiology and behaviour to cope with a changing environment (Abram et al., 2017), but rapid climate change presents serious challenges. Seebacher et al. (2015) showed that the average temperature increase over the past 20 years resulted in increased physiological rates of ectotherms, such as heart rate, metabolic rate and locomotor performance. Although animals may be able to maintain their physiological integrity in warmer temperatures, increased rate of metabolism could result in increasing demand for food resources. Novel climates may also disrupt interspecific interactions, such as when predator and prey populations exhibit different responses to rapid climate change (Seebacher et al., 2015).

4.2. Habitat fragmentation and connectivity

In addition to climate change, anthropogenic landscape alteration and habitat fragmentation are major threats to biodiversity in the Zagros Mountains. Recent habitat loss and fragmentation may limit the movement of species with low dispersal rates, such as our study species (Velo-Antón et al., 2013). However, mountain ranges have considerable environmental heterogeneity and could function as ‘biogeographic crossroads" (Hortal and Lobo, 2006). The mountains could also act as movement corridors to new habitats under future climates. Preservation of those areas, as open management habitats (Sutherland, 2002), could maintain the pathway for many species (Ochoa-Ochoa et al., 2012), particularly *N. kaiseri,* to survive episodes of regional or global climate change.

Landscape change may decrease the connectivity and gene flow among populations (Fischer and Lindenmayer, 2007; Ashrafzadeh et al., 2018), leading to increased extinction risk and lower colonization after local extinctions (Ferraz et al., 2007; Velo-Antón et al., 2013). Habitat loss and fragmentation is a major threat to Iran's biodiversity, including in the Zagros Mountains where wetlands, rivers, forests, grasslands and other ecosystems have been lost or degraded by intensive human use. The degradation rate of the country's biodiversity is at least 166% faster than the global average (Kolahi et al., 2012). Deforestation due to urbanization, infrastructure and industrial expansion into forest ecosystems is a considerable challenge in the Zagros Range (Soltani et al., 2014). Presently, *N. kaiseri* is associated with oak-pistachio open woodland areas. So, the predicted consequences of climate change cannot be easily disconnected from the direct human impacts on the woodlands. In general, landscape alteration along with climate change can create some uninhabitable or unreachable patches within otherwise suitable habitats.

Our connectivity analysis revealed that while there is relatively good permeability among many habitat patches within these landscapes in the current climatic model, the connectivity between the habitat patches may be significantly reduced by 2050 and 2070. We expect this loss of connectivity would result in reduced gene flow among populations, resulting in a reduction in genetic diversity and adaptive capacity to climate change (Segelbacher et al., 2010; Hermes et al., 2018). Sharifi et al. (2013) suggested that many of the newt populations may already be isolated from each other due to the long distances between many of the recorded localities and the inhospitable intervening terrain. However, there are consequences as low habitat suitability is not always the same as high resistance to movement. In the other words, animals may utilize the landscape differently during dispersal movements than in the home range (Keeley et al., 2017). For instance, while a certain habitat may be unsuitable for the species to occupy permanently, it may be crossed during a dispersal event (Engler et al., 2009). Several studies have concluded that resistance to dispersal movements or gene flow was less than expected based on habitat suitability for several wildlife species (e.g. Wasserman et al., 2010; Elliot et al., 2014; Keeley et al., 2017) such as salamanders (*Plethodon albagula*, Peterman et al., 2014). A population genetic study of *N. kaiseri* would help resolve some of this uncertainty and provide an important baseline for conservation strategies and action.

4.3. Implications for conservation

Our findings emphasize the potential risks that many montane species face under forthcoming climates (Milanovich et al., 2010; Ashrafzadeh et al., 2019; Hermes et al., 2018), especially salamander species (Velo-Antón et al., 2013; Sutton et al., 2015). The Zagros Range is one of the most vulnerable regions of Iran to warming-caused aridization over the forthcoming 30-year projections (Jowkar et al., 2016). It is anticipated that micro-endemic amphibians will be severely threatened by climate change (Ochoa-Ochoa et al., 2012), so our effort to find new occurrences, identify potentially suitable habitats now and under different climate scenarios hopefully will aid in conservation of the species. Recently, *N. kaiseri* has been recorded from new geographical localities and its extent of occurrence is assessed to be about 10,000 km^2, which is still small compared with previously estimated extent about 250 km^2 (IUCN SSC Amphibian Specialist Group, 2016). This range expansion is hopeful, but our future projected distributions for the newt indicate continued habitat loss and reduced spatial connectivity. The implications of such changes in *N. kaiseri* distribution suggest that the long-term persistence of the species is at risk. Conservation actions that focus on preserving habitats, especially aquatic habitats, which maintain connectivity and linkages for dispersal and genetic exchange among populations have high conservation priority (Wan et al., 2018). The development of a species conservation and monitoring plan would be an important first step to meet this need.

Since our findings focus on the macroecology, research into physiological and behavioural plasticity is needed to refine estimates about the influence of climate change on individual populations of the species. Population genetic studies could help us better interpret and refine our connectivity analyses (e.g., Pilliod et al., 2015). Additional research into the importance of microhabitats and microrefuges (Keppel et al., 2012) for population persistence is also warranted, far smaller than we could model within 1-km pixels.

Conflicts of interest

The authors have declared that no competing interests exist.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00637.

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