Understanding the summer roosting habitat selection of the greater mouse-tailed bat (*Rhinopoma microphyllum*) and the small mouse-tailed bat (*Rhinopoma muscatellum*) in Iran

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Abstract

Roost for bats, which are responsible for a wide range of vital ecological and economic services, is crucial. Their availability affects both the geographic occurrence and the diversity of bat communities. Hence, understanding how bats use roosts and variables that influence these patterns could contribute to the development of management plans to ensure their survival. In this study, species distribution modeling of two bat species, the greater mouse-tailed bat (*Rhinopoma microphyllum*) and the small mouse-tailed bat (*Rhinopoma muscatellum*), were carried out using the sdm package in R. To do so, 16 environmental variables were used as the predictors to explore their relationships with the occurrence of the two species using 12 modeling algorithms. The prediction models for each species were then combined into an ensemble model. The random forest modeling algorithm showed better performance than the other individual models in this modeling. Moreover, the prediction performance of the ensemble model was more substantial than all the individual models for both species. For the greater mouse-tailed bat, elevation, annual mean temperature, temperature seasonality, and distance to roads-railways were identified as the essential variables for summer roosting habitat selection. Meanwhile, distance to roads-railways, annual mean temperature, elevation, and distance to the ridge were significant for the small mouse-tailed bat. Since this study facilitates the management of future and suitable habitats by identifying important environmental conditions, it can be used in conservation plans.

Keywords Summer roost · Mouse-tailed bat · SDM · Ensemble model · Spatial niche

Introduction

Since bats are responsible for a wide range of essential ecological and economic services, such as pollination, seed dispersal, pest control, food transmission, and environmental

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health indicators (Kunz et al. 2011; Boyles et al. 2011), it is essential to conserve roosting habitat to protect bats (Evelyn et al. 2004). Roosts are critical resources for bats (Kunz 1982) and play a vital role in their biology and affect their geographical distributions and diversity (Findley 1993). Understanding how bats use roosts and how variables influence their distribution patterns could contribute to developing management plans to ensure their survival (Fenton 1997; Lino et al. 2015). It is not easy to understand the relationship between bats' distribution and their habitat (Fenton 1997) because bats are elusive, nocturnal mammals that are difficult to observe and identify (Razgour et al. 2016). They can fly high above the canopy, are highly maneuverable, and, therefore, can evade nets or roost in inaccessible sites, such as trees, scattered in large forest patches, making their direct observation problematic. Although the widespread use of acoustic monitoring has dramatically increased the chances of recording bats, some species cannot be easily detected because of low intensity, high frequencies emitted, or highly directional echolocation calls. In contrast, others

are difficult to differentiate based on their echolocation calls (Razgour et al. 2016).

Species distribution models (SDMs) present an essential tool to tackle questions on bat distribution, biogeography, past and future responses to environmental changes, and conservation biology (Razgour et al. 2016). Several statistical methods are now available and commonly used for species distribution modeling (Guisan and Zimmermann 2000; Elith et al. 2006), and in a large number of studies, the performance and prediction of the models have been compared with different methods (Segurado and Araujo 2004; Elith et al. 2006; Heikkinen et al. 2006; Pearson et al. 2006; Dormann et al. 2008; Roura-Pascual et al. 2009). The efficiency of the methods to generate spatial predictions of species distributions has been significantly different. Thus, due to the differences between the predictions of species distribution models, it has been recommended to simultaneously use several models and combine them through a procedure called ensemble modeling (Araujo et al. 2005; Araujo and New 2007). Such a modeling framework is appropriate because it improves predictions of a species range (Thuiller 2004; Araujo et al. 2005; Marmion et al. 2009a), patterns in species richness (Parviainen et al. 2009), and diversity (Mateo et al. 2012). It also reduces the prediction uncertainty of models by combining their predictions (Araujo et al. 2005), and it can contain more vital information than using each of the individual models (Araujo and New 2007).

Despite the high richness of small-sized mammalian species in Iran (more than 150 species), most research studies have focused on the ecology and conservation of large-sized species (because of their high population reduction rate), and small-sized species have been overlooked. However, the subjects of some studies conducted on rodents and, in rare cases, bats have often been focused on taxonomy (IUCN 2012; Farhadinia et al. 2015). Among the 50 species of mammals with the high conservation priority in Iran, 22% of them (11 of the 51 identified bat species) are bats (Farhadinia et al. 2015; Yusefi et al. 2019). Nevertheless, only two studies have been conducted about assessing bats' distributions. Kafaei et al. (2020) used an ensemble model to predict the potential distribution of the small mouse-tailed bat in Iran, and Kafash et al. (2021) generated the first richness map of bats in Iran.

As a result, the present study aimed to determine the suitable areas for summer roosting habitat selection of the greater mouse-tailed bat (*Rhinopoma microphyllum*) and the small mouse-tailed bat (*Rhinopoma muscatellum*) in Iran and identify the environmental variables that affect the habitat selection that can be important for these species in other landscapes. In addition, the variables that are common between two species in habitat selection were determined along with the spatial niche overlap of their habitats. Finally, the individual and ensemble species distribution models

were compared to show which method is more suitable for bat studies.

Materials and methods

Study area

This study was carried out based on various sources in the distribution range, habitat range, and summer roosting habitat recorded from the greater mouse-tailed bat and the small mouse-tailed bat throughout Iran. The study site encompasses the Persian Gulf and Oman Sea basins, including nine sub-basins. Additionally, two sub-basins adjacent to the Persian Gulf and Oman Sea basins were used. This area covers the provinces of Kermanshah, Lorestan, Ilam, Khouzestan, Chahar Mahal and Bakhtiari, Kohgiluyeh and Boyer Ahmad, Bushehr, Fars, Hormozgan, and parts of Kerman and Sistan and Baluchestan provinces (Fig. 1).

Bat data

In this study, summer roosting sites of two species in caves were collected based on field observations and from studies conducted in Iran, such as Akmali et al. (2011), Benda et al. (2012), Fathipour et al. (2016), Shahabi et al. (2017), and also from GBIF database (2017a, b). Then field visits were conducted to ensure the presence of the two species in the caves. Travel corridors and foraging sites were identified as the presence points of these species in summer habitats according to the species distribution range and based on direct observation and evidence in the caves. Finally, these points were registered by a GPS device. Generally, 81 occurrence points of the greater mouse-tailed bat and 65 occurrence points of the small mouse-tailed bat were recorded and used in the modeling (Fig. 1).

Environmental data

In this study, we used the information from the natural history of two species and from the literature reviews to select environmental variables from three different groups, including topographic, land cover/land use, and bioclimatic variables (Table 1). In addition, to construct all layers with a spatial resolution of 1 km, ArcGIS 10.3 software was used. We selected the topographic variables, including elevation, slope, aspect, and ridge curvature, that have often been used in landscape analyses for bat habitats (Gumbert 2001; Bellamy et al. 2013) to show potential microclimate variations within the landscape (Hammond et al. 2016). These variables, including elevation, slope, aspects, distance to the ridge, and ridge curvature, were constructed from a digital elevation model (DEM) dataset over the study area. The
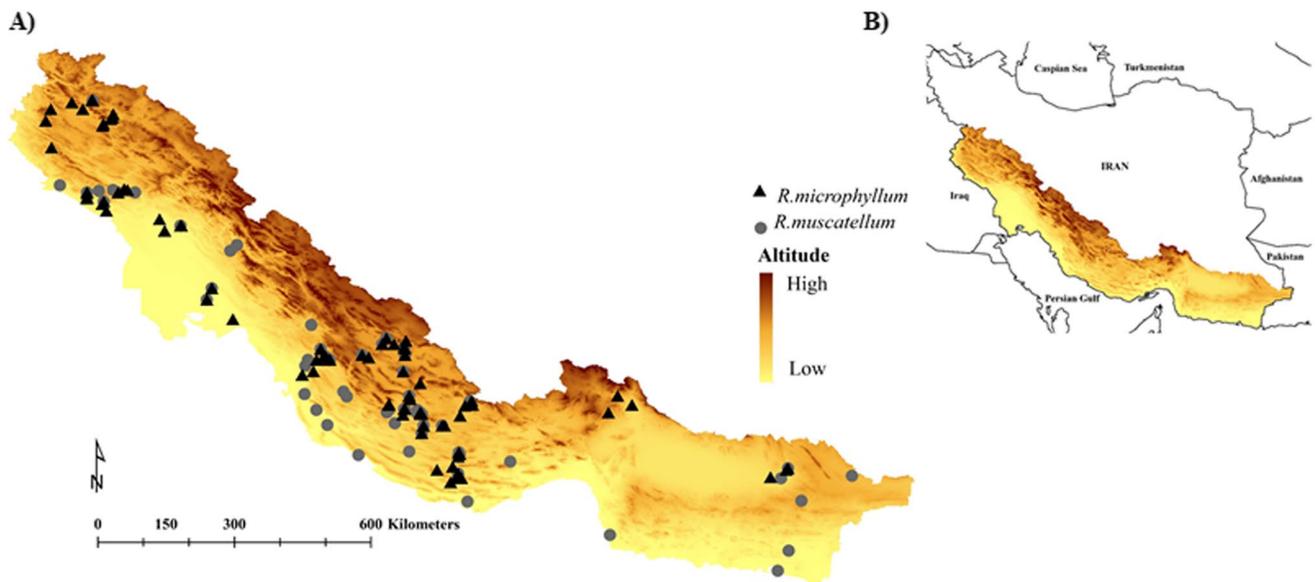
Fig. 1 A Study area showing elevation and observation data of the greater mouse-tailed bat and the small mouse-tailed bat. B Location of the study area in Iran

Table 1 Environmental variables used in research

Category	Variable	Data source
Bioclimatic	Annual mean temperature	Hijmans et al. 2005
	Isothermality	Hijmans et al. 2005
	Temperature seasonality	Hijmans et al. 2005
	Mean temperature of driest quarter	Hijmans et al. 2005
	Annual precipitation	Hijmans et al. 2005
	Precipitation seasonality	Hijmans et al. 2005
	Precipitation of driest quarter	Hijmans et al. 2005
Topography	Elevation	DEM
	Slope	DEM
	Aspect	DEM
	Ridge curvature	DEM
Land cover/land use	Distance-to-roads and railways	Forests, Rangelands, and Watershed Management Organization
	Distance-to-Ridge	Forests, Rangelands, and Watershed Management Organization
	Distance-to-water	Forests, Rangelands, and Watershed Management Organization
	Distance-to-agriculture	Forests, Rangelands, and Watershed Management Organization
	Distance-to-range	Forests, Rangelands, and Watershed Management Organization

spatial analyst tools were used to prepare layers of the slope, aspect, and ridge curvature. The aspect values were classified into five main categories including no direction or flat (0–1), North (0–45, 315–360), East (45–135), South (135–225), and West (225–315). Calculation of the distance to ridges needed more processing than other variables. Although the flow tools were commonly used to identify the low points in topography, we used the tools to determine ridge tops by multiplying the outputs by −1 (Hammond et al. 2016). We

merged flow lines such as rivers and streams and added a buffer of 1 m to transform lines to a polygon feature. Then we merged it with the wetland layer to prepare a water body layer. The road layer (including major and minor roads) and railway layer were merged to make a layer. Forests, rangelands, and farmlands were considered as the bats' foraging resources and travel corridors extracted from a layer prepared by Iran's Forests, Range, and Watershed Management Organization. In this layer, land cover and land use types are

classified into 12 categories (e.g., forests, range, agriculture, wetlands, drylands). We selected distance to features that seemed to be essential for bats as potential travel corridors, foraging resources, or for higher solar exposure (i.e., distance to ridge top; Duchamp et al. 2007) (Hammond et al. 2016). The Euclidean Distance tool was used in ArcGIS 10.3 software to generate the distance to the features' layer. The 19 bioclimatic variables with the resolution of 30 s (~1 km^2) were extracted from the WorldClim dataset (Hijmans et al. 2005) and prepared for the study area. The pairwise correlation among the environmental layers was examined using ENMTools 1.4.4 (Warren et al. 2010), and all correlation coefficients were under 0.7 (Pearson ≤ 0.70), suggesting that the variables have no collinearity issue (Table 1, Fig. 2).

Model selection

Species distribution modeling was performed using the presence records of species as the response variable (dependent variable) and 16 environmental variables as the predictor variables (independent variables) on the sdm R package (Naimi and Araujo 2016). In this study,

12 potential algorithms were tested, including maximum entropy (Maxent) (Phillips et al. 2006), generalized linear models (GLMs) (McCullagh and Nelder 1983), flexible discriminant analysis (FDA) (Hastie et al. 1994), boosted regression tree (BRT) (Friedman 2001), classification and regression tree (Cart) (Breiman et al. 1984), Glmnet (Friedman et al. 2010), multivariate adaptive regression splines (MARS) (Friedman 1991), maximum likelihood (Maxlike) (Royle et al. 2012), mixture discriminant analysis (MDA) (Hastie et al. 1994), recursive partitioning and regression trees (rpart) (Breiman et al. 1984), support vector machines (SVM) (Cortes and Vapnik 1995), and random forest (RF) (Breiman 2001) (Table 2).

In order to evaluate the efficiency of individual models and compare them with each other, the area under the curve (AUC) and correlation (Cor) statistics were used (Elith et al. 2006). On the other hand, for comparing the performance of the ensemble model with individual models, the AUC was used as the index of the model's performance, as well as the amount of uncertainty of the model that was obtained by the normalized Shannon entropy on sdm R package (Naimi and Araujo 2016).
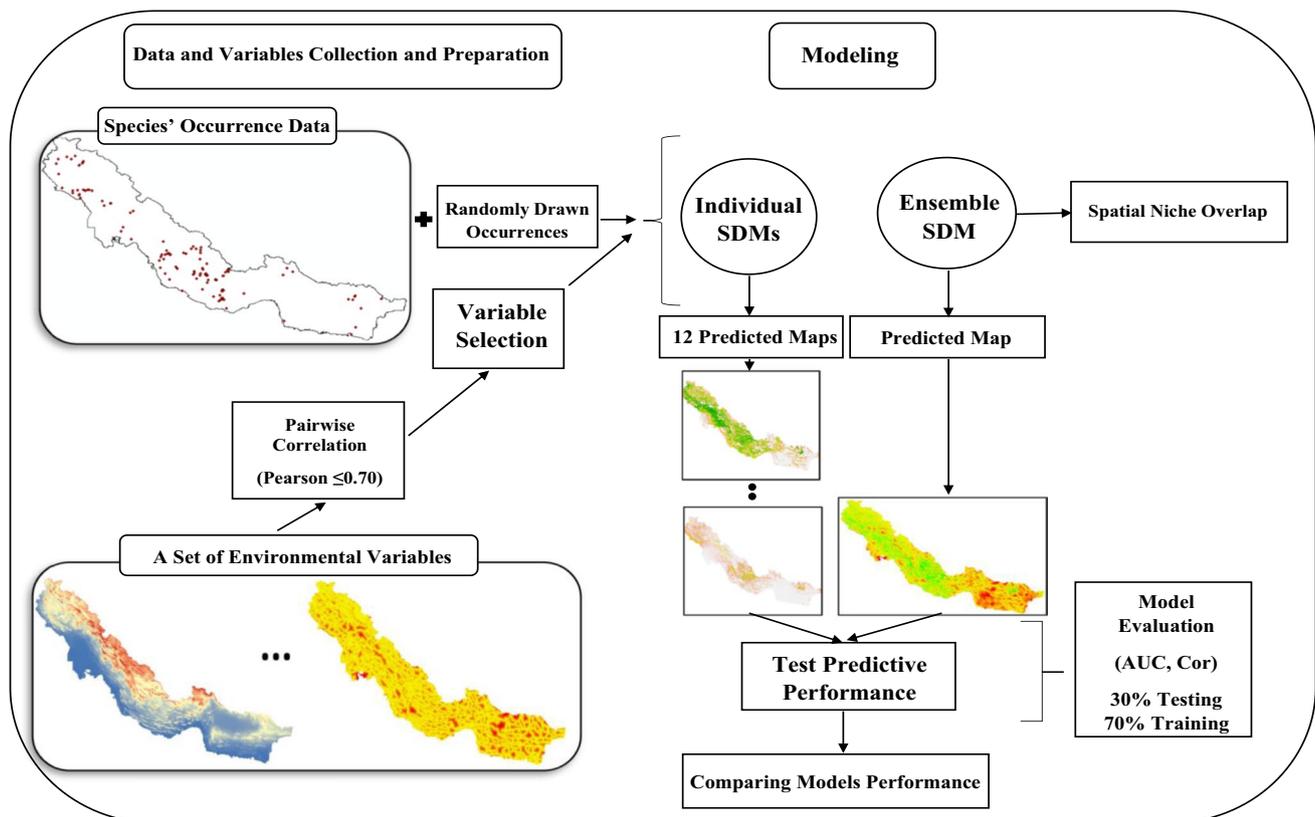

Fig. 2 Flow diagram showing the procedure of modeling

Table 2 The modeling algorithms in SDM package used in this research, brief description, and their required species data type

Modeling methods	Species data type*	Brief description	Key references
Maximum entropy (Maxent)	P/B	Maxent is a machine learning approach that estimates species distributions by finding the distribution of maximum entropy (i.e., closest to uniform) subject to the constraint that the expected value of each environmental variable (or its transform and/or interactions) under this estimated distribution matches its empirical average	Phillips et al. 2006
Boosted regression tree (BRT)	P/A	BRT, also called stochastic gradient boosting, is a machine learning approach that combines two algorithms: the boosting algorithm iteratively calls the regression-tree algorithm to construct a combination or "ensemble" of trees	Friedman 2001
Random forest (RF)	P/A	RF belongs to the learning machine methods. It generates hundreds of random trees. A selective algorithm limits the number of implemented parameters in each tree. A training set for each tree is chosen as many times as there are observations among the whole set of observations. For each node of the tree, the decision is taken according to randomly selected environmental parameters. The trees thus constructed are not pruned and are as large as possible. After the trees have been built, data are entered into them, and all trees will classify each grid square. At the end of the run, the classification given by each tree is considered as a "vote," and the classification of a grid square corresponds to the majority vote among all trees	Breiman 2001
Classification and regression tree (CART)	P/A	CART is a non-parametric technique that produces either classification or regression trees, depending on whether the dependent variable is categorical or numeric, respectively. It allows the rules to be induced directly from the observations	Breiman et al. 1984
Flexible discriminant analysis (FDA)	P/A	A classification model based on a mixture of linear regression models uses optimal scoring to transport the response variable so that the data are in a better form for linear separation and multiple adaptive regression splines to generate the discriminant surface	Hastie et al. 1994
Multivariate adaptive regression splines (MARS)	P/A	MARS is a non-parametric regression technique that combines classical linear regression, mathematical construction of splines, and binary recursive partitioning to produce a local model in which relationships between response and predictors are linear or non-linear	Friedman 1991
Generalized linear models (GLMs)	P/A	GLMs is a flexible generalization of ordinary least square regression which generalizes linear regression by allowing the linear model to be related to the response variable via a link function (let handling distributions such as the Gaussian, Poisson, binomial, or gamma) and by allowing the magnitude of the variance of each measurement to be a function of its predicted value. This parametric approach is the most common method in predictive habitat distribution modeling	McCullagh and Nelder 1983

Table 2 (continued)

Modeling methods	Species data type*	Brief description	Key references
Maximum likelihood (Maxlike)	PO	Maxlike is a likelihood-based approach that estimates the probability of occurrence using presence-only data and spatially referenced covariates	Royle et al. 2012
Mixture discriminant analysis (MDA)	P/A	MDA is an extension of linear discriminant analysis (LDA). It assumes that the distribution of a class of each environmental variable follows a Gaussian distribution, allowing the classifier to handle different prototype classes such as a mixture of Gaussians. The environmental parameters form primal classes, which are divided into sub-classes. The classification results from these sub-classes, a mixture density, describe the distribution density of the primal classes of environmental variables (Marmion et al., 2009b)	Hastie et al. 1994
Recursive partitioning and regression trees (Rpart)	P/A	Rpart is a powerful machine learning used for building classification and regression trees. The rpart algorithm works by recursively splitting the dataset, which means that the subsets arising from a split are further split until a predetermined termination criterion is reached. At each step, the split is made based on the independent variable that results in the largest possible reduction in the heterogeneity of the dependent (predicted) variable	Breiman et al. 1984
Support vector machines (SVM)	PO	SVM is one of the popular and successful supervised learning methods widely used for classification and regression problems. SVM fits data by maximizing the margin around the separator. This leads to good generalization performance regarding new unseen data, i.e., training data are classified with the given labels with a separator that is the farthest as possible to both classes of points. This generalizes well to new data. The maximum margin of the separator of classes leads to the strong upper bound of the generalization error. SVM minimizes this upper bound (Byun and Lee, 2002)	Cortes and Vapnik 1995
Glmnet	P/A	Glmnet is used for estimating generalized linear models with convex penalties. The models include linear regression, two-class logistic regression, and multi-nomial regression problems, while the penalties include $\ell 1$ (the lasso), $\ell 2$ (ridge regression), and mixtures of the two (the elastic net). The Glmnet algorithms use cyclical coordinate descent, which successively optimizes the objective function over each parameter with others fixed, and cycles repeatedly until convergence. The methods can handle large problems and also deal efficiently with sparse features	Friedman et al. 2010

*Species data type: presence (P), absence or pseudo-absence (A), background (B), presence only (PO)

Spatial niche overlapping

One of the most used techniques to estimate spatial niche is the ecological niche models (ENMs), which allow identifying areas with the appropriate environmental conditions for the presence of a species (Chefaoui et al. 2005). In this study, we used the ENMTools 1.4.4 to calculate the spatial niche overlapping between the greater mouse-tailed bat

and the small mouse-tailed bat. ENMTools implements two quantitative tests of niche similarity introduced by Warren et al. (2008), including Schoener's (1968) *D* and a measure derived from Hellinger distance called *I* (Warren et al. 2008, 2010). ENMTools' method is dependent on overly simplistic binary predictions. In this method, both assume probability distributions defined over geographic space. These tests ask whether the ENMs generated from two populations are identical or, at the other extreme, only more similar than expected by chance (Warren et al. 2010). Schoener's *D* is defined as (Schoener 1968):

$$D\left(\rho_X, \rho_Y\right) = 1 - \frac{1}{2} \sum_i \left| \rho_{x,i} - \rho_{y,i} \right|$$

where $P_{X,i}$ and $P_{Y,i}$ are the normalized suitability scores for species *X* and *Y* in grid cell *i*. *I* is defined as:

$$I\left(\rho_X, \rho_Y\right) = 1 - \frac{1}{2} \sqrt{\sum_i \left(\sqrt{\rho_{x,i}} - \sqrt{p_{y,i}} \right)^2}$$

It is noticeable that *I* is 1—"Hellinger's distance" from probability theory; similarly, *D* is 1—"total variation distance." Both similarity measures range from 0, when species predicted environmental tolerances do not overlap, to 1, when all grid cells are estimated to be equally suitable for both species (Warren et al. 2010).

Results

Species distribution modeling

Individual modeling

Among the 12 algorithms implemented for the greater mouse-tailed bat species distribution modeling, the random forest model with an AUC of 0.93 showed the best performance, whereas the Glmnet model with an AUC of 0.76 compared to other models had a weaker performance. For the small mouse-tailed bats, the random forest model with an AUC of 0.93 showed the best performance. But the Cart model with an AUC of 0.79 had a weaker performance.

Assessments of modeling success using AUC and correlation indicate that methods can be analyzed in three groups (Elith et al. 2006). The first and highest performing group, such as the random forest model, performed relatively well according to each of the evaluation measures. The second group of methods showed intermediate performance for AUC and correlation. In the third group, all performed relatively poorly. Moreover, this group deviated from the generally linear relationship between AUC and correlation results, i.e., assessment of their predictive success depends on which measure is used (Table 3, Fig. 3).

Ensemble modeling

The area under the curve was obtained for ensemble modeling of the greater mouse-tailed bat 0.923 and the small mouse-tailed bat 0.914 (Fig. 4).

Variables' importance

The importance of predictor variables showed that elevation, annual mean temperature, temperature seasonality, and distance to roads and railways were most important to summer roosting habitat selection of the greater mouse-tailed bat. At the same time, the aspect was the least important (Fig. 5). Distance to roads and railways, elevation, annual mean temperature, and distance to the ridge were most important to summer roosting habitat selection of the small mouse-tailed bats, whereas the aspect was not significant (Fig. 6).

Model performance evaluation

Performance comparison of the individual and ensemble models based on AUC and the model uncertainty showed that the ensemble model had a stronger prediction than individual models due to high AUC and low uncertainty.

Spatial niche overlap

Spatial niche overlap of the greater mouse-tailed bat and the small mouse-tailed bat, based on two criteria: Schoener's *D* (Schoener 1968) and the Hellinger distance *I* were equal to 62% and 64%, respectively.

Table 3 Evaluation of the twelve models tested in sdm using the area under the curve (AUC) and correlation (Cor) for the greater mouse-tailed bat and the small mouse-tailed bat

	Brt	Cart	Glmnet	Mars	Maxlike	Mda	Maxent	Glms	Fda	Rpart	Svm	Rf
Greater mouse-tailed bat												
AUC	0.77	0.81	0.76	0.86	0.82	0.83	0.88	0.86	0.82	0.81	0.85	0.93
Cor	0.18	0.33	0.2	0.37	0.28	0.32	0.41	0.34	0.29	0.37	0.4	0.65
Small mouse-tailed bat												
AUC	0.85	0.79	0.87	0.9	0.87	0.85	0.9	0.9	0.86	0.87	0.87	0.93
Cor	0.43	0.45	0.3	0.54	0.44	0.4	0.51	0.49	0.42	0.44	0.51	0.71

Fig. 3 Mean AUC vs. mean correlation (Cor) for evaluation models of A the greater mouse-tailed bat habitat modeling and B the small mouse-tailed bat habitat modeling
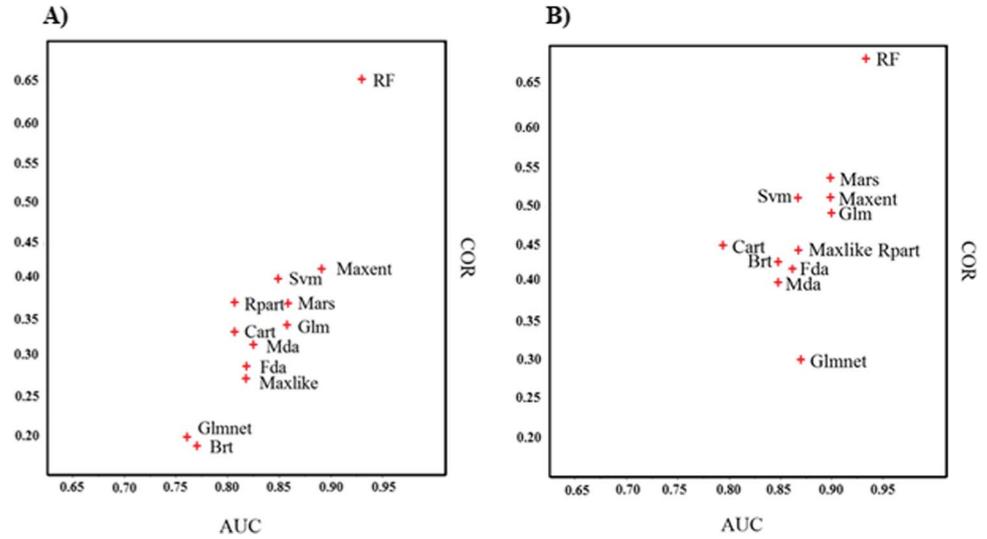

Fig. 4 The area under the curve (AUC) for ensemble modeling of A the greater mouse-tailed bat roosting habitat and B the small mouse-tailed bat roosting habitat
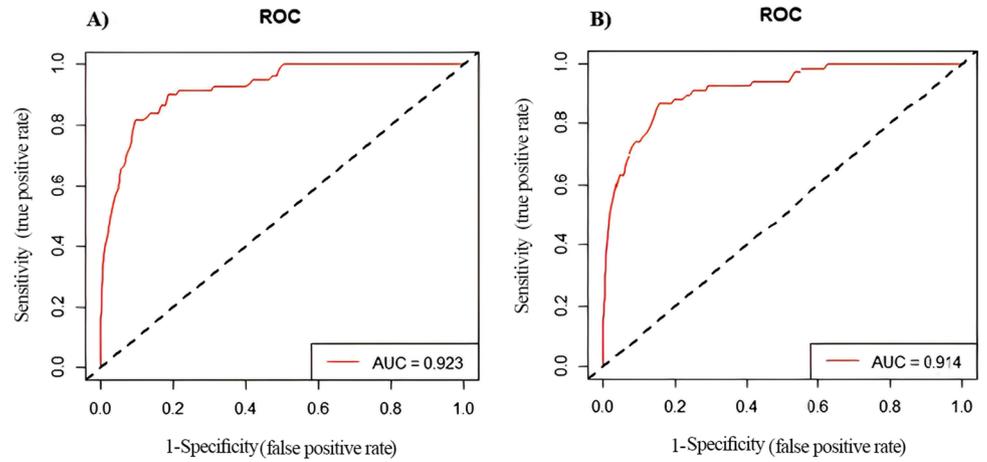

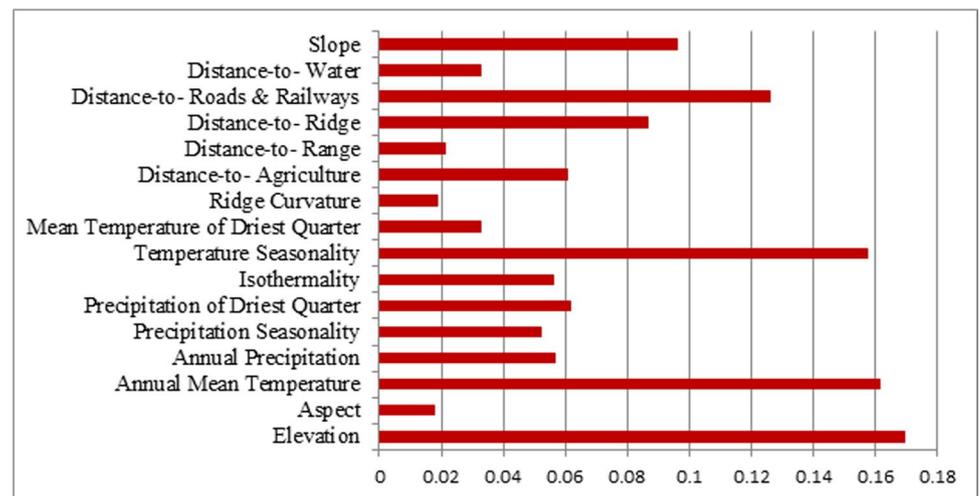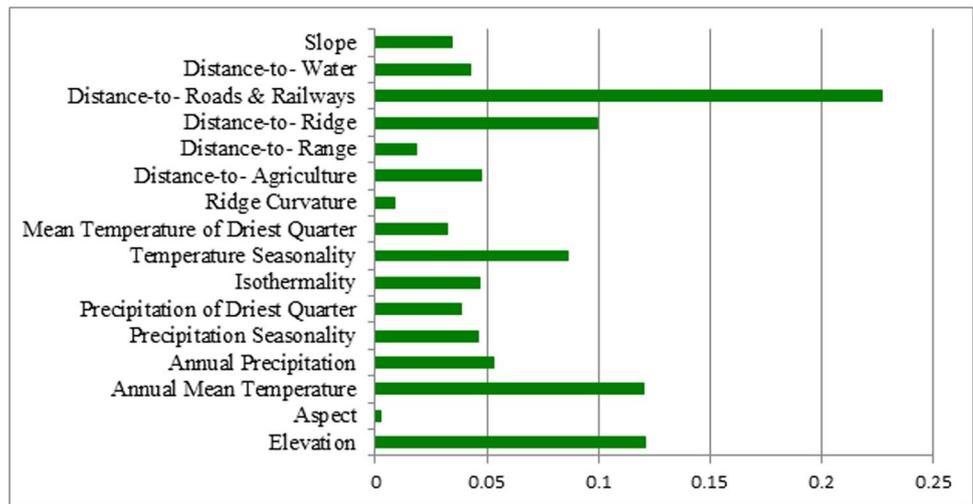**Fig. 5** Significant variables for the greater mouse-tailed bats' summer roosting habitat selection

Fig. 6 Significant variables for the small mouse-tailed bats' summer roosting habitat selection

Discussion

Summer roosting habitat modeling of the greater mouse-tailed bat

In the random forest, as the strongest model among individual models, annual precipitation was recognized as the most important predictor variable compared to other variables in the summer roosting habitat modeling for the greater mouse-tailed bats. According to the sources, this variable can have both negative and positive effects on this choice for several reasons, which can be attributed to the following.

The activity of bats with increasing precipitation decreases (Geluso and Geluso 2012). Also, increasing precipitation can prevent insects from flying; therefore, it reduces bats' access to insects (Anthony et al. 1981), which predicts these changes can reduce colony structure, productivity, and adolescent survival (Richter and Cumming 2008). However, precipitation causes a growth in the abundance of some insects such as order Diptera or Lepidoptera (Williams 1951; Sillett et al. 2000; Landesman et al. 2007).

Since this study area is located in arid and semi-arid regions of Iran where the long-term average precipitation is approximately 360 mm (Iran Water Statistical Yearbook 2018), it can be concluded that precipitation more and less than this amount leads to habitat suitability reduction by reducing preys or access to them. However, it should be remembered that precipitation in this amount also increases the frequency of some insects, which positively affects the foraging activity of this species. Overall, the higher number of insects resulting from precipitation has a positive effect on the foraging base.

Comparing the ensemble model with individual models based on two indicators, AUC as a model performance index and model uncertainty, the ensemble model showed a stronger performance than individual models. Therefore,

it is recommended to use an ensemble model to reduce the uncertainty of every single model. The elevation is the most important variable for species distribution modeling of the greater mouse-tailed bats. Then, the annual mean temperature, temperature seasonality, distance to roads and railways, and slope were important in summer roosting habitat selection (Fig. 7).

The elevation variable played a key role compared to other variables for this species. The elevation influences bat species distributions (Jaberg and Guisan 2001) and roost locations (e.g., Neubaum et al. 2006). Cryan et al. (2000) suggest that variation in temperature and insect availability at different elevation gradients may impact torpor and energy restrictions. Elevation influences the temperature regimes bat experiences while roosting and, thus, the amount of energy a bat expends for thermoregulation. The elevation range of the study area was estimated to be – 10 to 4208 m. According to the review of sources, the elevation range in which this species is scattered is between 0 and 1200 m (Monadjem et al. 2017), but the results of this study showed a suitable habitat roosting of this species is located in the elevation range of 2–3795 m. Therefore, these results provide a new view on the range of elevation distribution of this species, suggesting that a research study be conducted to modify this suggested range in the future. After elevation, annual mean temperature and temperature seasonality played roles in this selection, respectively. Studies have illustrated a positive relationship between bat activity and temperature (e.g., Wolbert et al. 2014). The activity of bats is strongly related to the temperature outside the roosts and is associated with the airflow at the entrance of roosts. Changes in airflow due to temperature differences between outside and inside the roost can be an efficacious sign of air temperature for bats (Meyer et al. 2016). Moreover, some studies, such as the study of Frick et al. (2012), showed that, for instance, the Brazilian free-tailed bat, when the surface temperature

Fig. 7 Summer roosting habitat selection ensemble modeling of the greater mouse-tailed bat
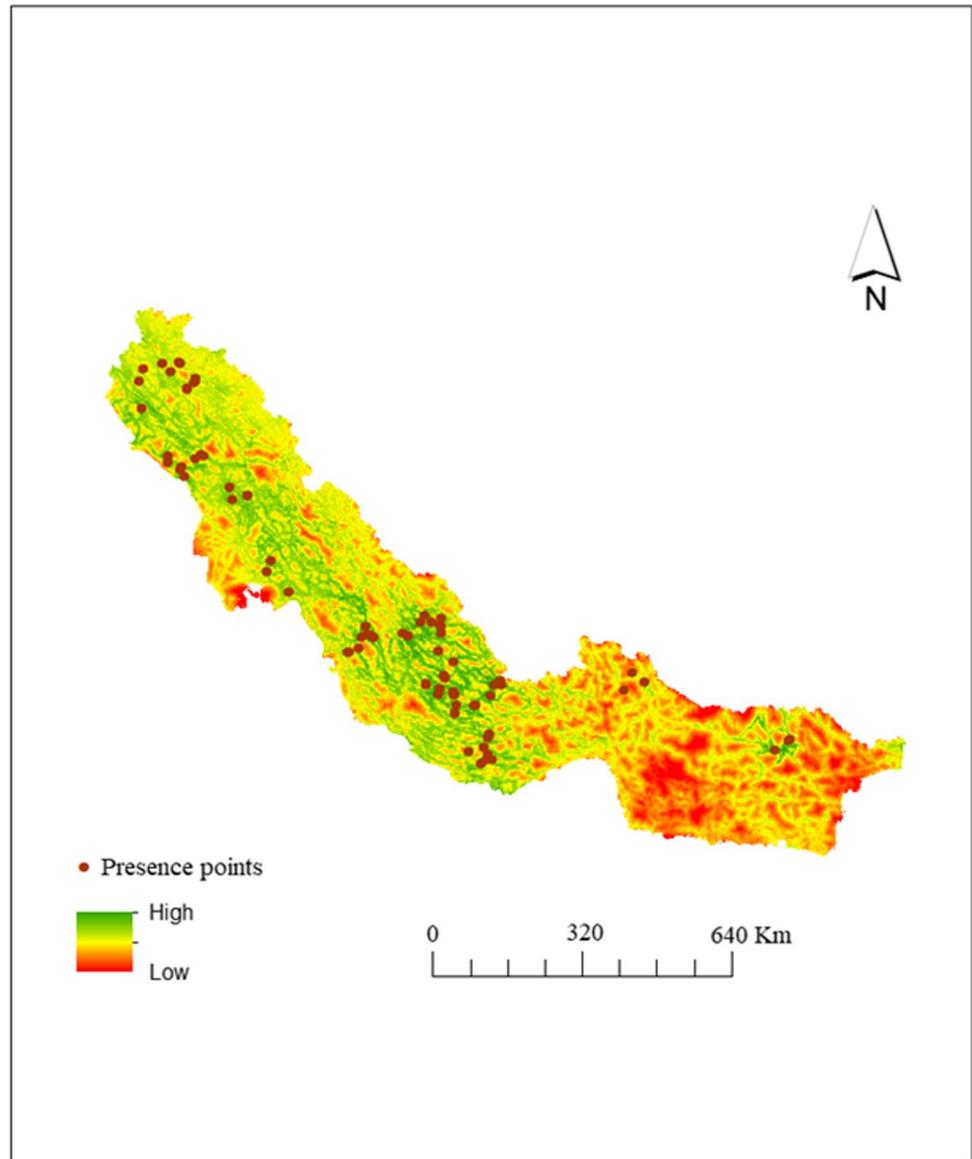
is high, comes out of the roost later in both dry and wet years. The inside temperature of the roosting caves is also essential because it is affected by the outside temperature. The greater mouse-tailed bats select hot and dry caves with a mean temperature of 28–32 °C as roosts (Levin et al. 2013).

Furthermore, temperature affects the abundance of insects as bats' diet (Meyer et al. 2016). Most insects enter diapause to pass the winter and become active again in spring when the weather warms up. The cues that insects use to break diapause are complex and differ across species but include temperature and photoperiod (Gullan and Cranston 2010). Insect numbers build as spring progresses as the triggers to break diapause are reached in various species, and as insects that overwintered in egg or immature steps resume development and reach the adult, flying stages (Meyer et al. 2016). Although bat activity may peak

before insects become abundant, bat activity coincides with insect activity when bats are at their summer colonies (Anthony et al. 1981). Temperature also affects the growth and development of vegetation (Hatfield and Prueger 2015), and vegetation influences insects' abundance.

The distance to roads and railways was also crucial for habitat selection. Transport infrastructures are likely to induce significant negative impacts on bats by impacting frequent road kills (Gaisler et al. 2009; Lesiński 2007; Lesiński et al. 2010; Medinas et al. 2013; Russell et al. 2009; Secco et al. 2017), reducing foraging activity near roads with street lighting (Hale et al. 2015; Stone et al. 2009, 2012), or intense traffic noise (Luo et al. 2015; Schaub et al. 2008; Siemers and Schaub 2011). In addition, some studies show that with approaching the major roads, bat activities and their species richness decrease

(Zurcher et al. 2010; Berthinussen and Altringham 2012; Kitzes and Merenlender 2014).

Even though the distance to agricultural lands and rangelands, known as habitats, foraging resources, and potential travel corridors (Hammond et al. 2016), were less important in this selection, distance to agricultural lands was more important than distance to rangelands. According to the classification of agricultural lands into rainfed and irrigated farming, rainfed agricultural lands were more significant than irrigated farming in this habitat selection.

Although the aspect was less important in this study than the other variables, it is noticeable that this species prefers the north/south aspect more than the east/west aspect, which appears to be related to solar exposure or optimal microclimates (Hammond et al. 2016).

Summer roosting habitat modeling of the small mouse-tailed bat

It was concluded that the random forest model appeared as a strong model compared to other individual models for the small mouse-tailed bat habitat modeling. The distance to main and secondary roads and railways in the RF model had the most significant impact on the roost selection. The significance of this was like what was described for the greater mouse-tailed bat.

Since the ensemble model has a stronger prediction than other individual models, therefore, it is still recommended to use an ensemble model to reduce the uncertainty of every single model. In the ensemble modeling, also distance to roads and railways was most important for summer roosting

Fig. 8 Summer roosting habitat selection ensemble modeling of the small mouse-tailed bat
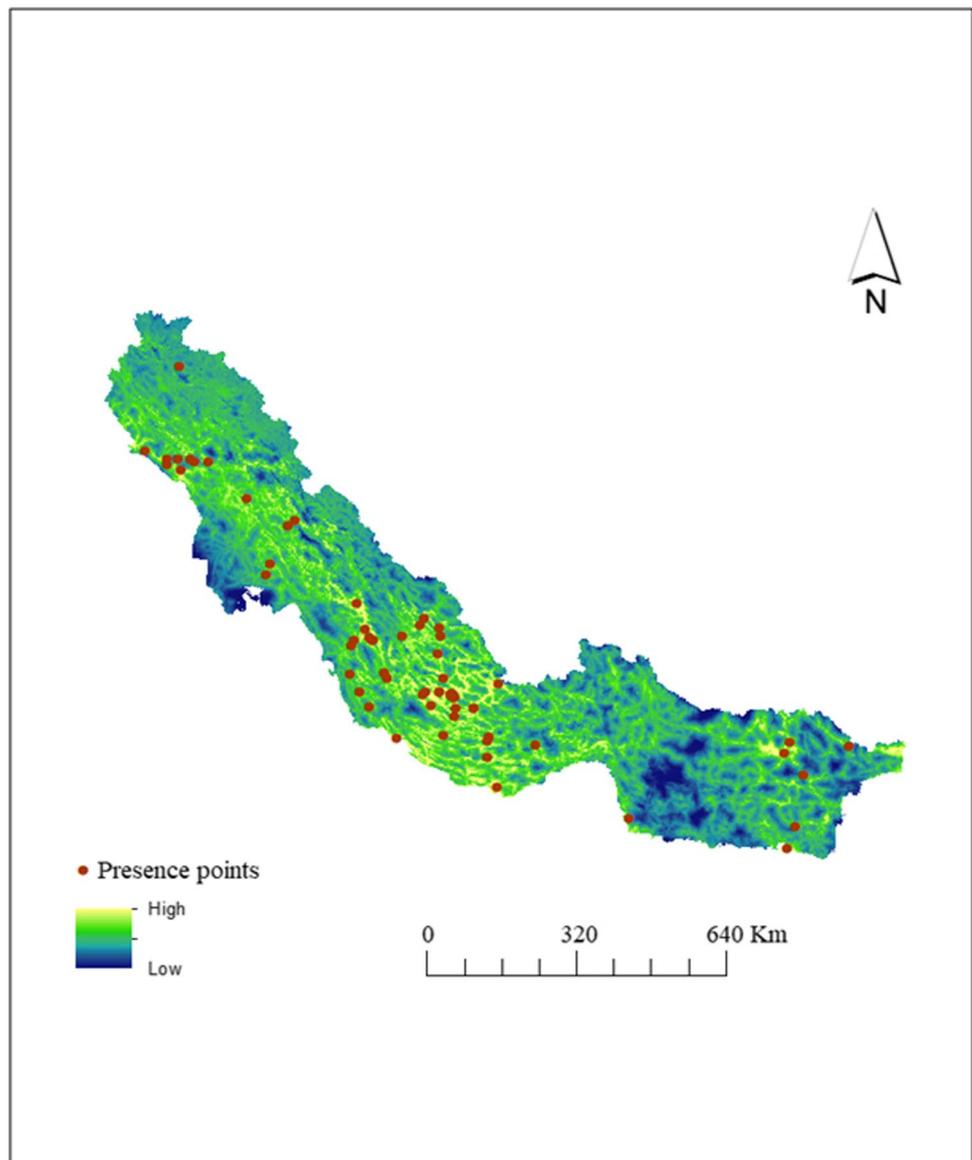
habitat selection of this species, which the reason for the importance of this variable was discussed earlier (Fig. 8).

Then the variables of elevation and annual mean temperature were equally important. The reasons why the elevation and annual mean temperature were important for the small mouse-tailed bat habitat selection are likely similar to those observed for the greater mouse-tailed bats.

The study area is located in the elevation range of − 10 to 4208 m; according to the review of the resources, they are present at the elevation range of 700–1100 m (Molur et al. 2008). In this case, the results displayed that the suitable summer roosting sites for the small mouse-tailed bats are at an elevation range of − 3 to 3778 m. Hence, these results provide a new view on the range of elevation distribution of this species, suggesting that a research study be conducted to modify this suggested range in the future.

For the small mouse-tailed bats, the distance to the ridge was identified as the fourth important variable, contrary to the greater mouse-tailed bats, indicating that they probably avoid sunlight when selecting summer habitat roosts (e.g., Duchamp et al. 2007). Due to the species distribution range, the small mouse-tailed bats live in arid and semi-arid areas, where summers are hot and long, and winters are short and without freezing periods (Molur et al. 2008). Thus, it can be concluded that such areas are suitable habitats for summer roosting, which is farthest from the sun's rays. Therefore, increasing distance to the ridge increases the suitability of roosting habitats for this species.

Among the least important variables, the distance to agricultural lands as foraging resources was more significant than rangelands in choosing the summer roosting habitat of small mouse-tailed bats. According to the results, this species is dependent on irrigated agricultural lands, in contrast to the greater mouse-tailed bats, with 54.6%, which compared to rainfed agricultural lands with 45.4% dependence showed a higher value, which seems associated with dietary niche partitioning. The aspect was the least important variable for the small mouse-tailed bats, similar to the greater mouse-tailed bats. In this variable, the north/south aspect plays a significant role in this selection rather than the west/east aspect, which seems to be related to solar exposure or optimal microclimates (Hammond et al. 2016).

Spatial niche overlap

According to the resources, Schoener's *D* (Schoener 1968) index performs better than the *I* (Rödder and Engler 2011). Consequently, a 62% of the spatial niche overlap indicates the similarity in the summer roosting habitats and the variables that play an essential role in these selections by these species. The slight difference in the importance of the predictor variables confirms these results. However, they seem to reduce competitive interactions by dietary niche partitioning. This study partly showed differences between foraging resources, but it needs more detailed research on the dietary niche of these species.

In conclusion, this study facilitates the management of future and suitable habitats by identifying important environmental conditions; thus, it can be used in conservation plans in Iran as one of the first studies in modeling summer habitat selection. Since the variables of elevation and distance to roads and railways have the most significant impact on this selection by the greater mouse-tailed bat and the small mouse-tailed bat, respectively, these are essential factors to consider in combination with habitat when designing conservation strategies. It is noticeable that because of the similarity in their spatial niche, a conservation program for each species can help protect the other species to some extent. In addition, comparing individual and ensemble models displayed that the latter has a more substantial performance than all individual models suggesting ensemble models may also be useful for other bat SDM studies. Therefore, it is recommended to use these models to reduce the uncertainty of every single model.

Declarations

Ethics approval No approval of research ethics committees was required to accomplish the goals of this study because we did not need to capture bat species and resample them.

Conflict of interest The authors declare no competing interests.

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