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Invasion risk assessment using trait-environment and species distribution modelling techniques in an arid protected area: Towards conservation prioritization

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ABSTRACT

Invasive species are considered as one of the key threats to biodiversity and human livelihoods globally. The most effective strategy for handling invasion would be based on profiling invasive species and identifying areas at risk of invasion before they occur. The current study used a trait-environment modelling approach to identify alien species with high probability of invasiveness and combined this with the species distribution models (SDMs) to predict areas in the arid Saint Katherine Protectorate (SKP) in Egypt that were at highest risk of invasion by these species. The specific leaf area, number of leaves, soil nitrogen, and prevalence of disturbances were the most important biotic and abiotic indicators for predicting invasiveness in SKP. Of the investigated 33 alien plant species, three species were identified to have the highest probability of invasiveness, including *Salvia rosmarinus, Eucalyptus globulus,* and *Acacia saligna*. The outcome of the SDMs revealed that precipitation seasonality and temperature-related variables were the most important bioclimatic predictors determining the potential invasion risk of the studied alien species. Potential invasion is more likely in the eastern and northern parts of SKP, where biodiversity-rich common microhabitats are found and where there is a prevalence of disturbances such as tourism activities. The Etalaa, Shaq Mosa, and El-Mesirdi wadis microhabitats, in particular, were identified in the current study to be potentially highly suitable microhabitats for alien invasiveness and should be prioritized for monitoring and conservation actions. Moreover, the three identified species could be used as early indicators for microhabitats at risk of invasion along the environmental gradients of temperature and precipitation in arid ecosystems. This approach can be applied to other taxa and other ecosystems and can provide opportunities for formulating proactive management strategies against biological invasions.

1. Introduction

Concerns over the potential invasion risks of alien species and the resulting impact on biodiversity have been growing quickly in recent years (Liu et al., 2020; Schulze et al., 2018; Shackleton et al., 2020). Increasing trade and tourism activities are enabling alien species to continue to invade at higher rates (Seebens et al., 2018). Additionally, the advancement in means of transportation and communication has led to an increase in landscape connectivity, human movement, and ease of access to remote areas, which in turn has facilitated introduction of alien species into protected areas all over the world (Dean et al., 2019; Jones et al., 2018; Macdonald, 1989). However, due to the lack of resources and to large areas infested by invasive species, identifying the potential invasive species and the potential areas under invasion risk has been an enduring, and yet to be accomplished, goal in invasion biology (Kolar and Lodge, 2001; Packer et al., 2017; Ward, 2007). Using modelling techniques, such as species distribution models (SDMs) and trait-environment models, to predict invasion can therefore be beneficial

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when addressing the risk of invasive alien species on biodiversity and on natural ecosystems such as protected areas. Indeed, they are cost-effective and can make predictions at a large-scale especially if integrated together. These management- and monitoring- approaches represent appropriate tools for identifying priority conservation areas that are vulnerable to potential alien invasion (Vicente et al., 2013).

Species Distribution Models (SDMs) are based on correlations between the bioclimatic variables and species occurrence and can be used to predict areas potentially suitable for specific species to occupy (Araújo and Peterson, 2012). SDMs, even if based on climatic variables alone, have been widely recognized as powerful tools to predict the potential distribution of invasive plant species (Roura-Pascual and Suarez, 2008), and therefore can help to identify areas at high risk of invasion by well-known invasive species (Bellard et al., 2013; Bertelsmeier et al., 2015; Bomford et al., 2008; Fournier et al., 2019). Numerous ecologists have employed SDMs to predict the suitability of regions to invasion based on bioclimatic variables and to project changes in the distribution of invasive species under climate change scenarios (e.g., (Halmy et al., 2019; Larcombe et al., 2013; Watt et al., 2009; Xu, 2015). So far, studies that have employed SDMs indicate that without control actions in place, the distribution of numerous invasive alien species will increase under different land-use and disturbance scenarios (e.g., Bellard et al., 2013; Bertelsmeier et al., 2015).

Trait-based approaches, on the other hand, concentrate on the ecological traits that enhance invasiveness under varying environmental conditions, and incorporate other key factors causing invasions. The use of trait-based approaches, such as trait-environment models, is crucial for an accurate prediction of future invasions, the management of existing invasions, and for the proper application of restoration techniques needed for mitigating invasive species spread (Cousens, 2008; Drenovsky et al., 2012; Zakharova et al., 2019). In addition to SDMs, they can help to identify future invasive species and to predict the areas that will be potentially invaded by these species (Fournier et al., 2019). Few studies, however, have integrated trait-environment models with SDMs to assess invasion risk (Fournier et al., 2019), with this integration particularly in arid regions or drylands, and especially at local-scale hotspots.

One of the most important mountainous arid protected areas that is vulnerable to the risk of invasive species is Saint Katherine Protectorate (SKP), South Sinai, Egypt. The biodiversity in this protectorate is threatened by human activities including overgrazing, over-collection, over-exploitation of resources, and unmanaged tourism activities (Omar, 2016). The recent development in SKP, particularly in the tourism sector, has instigated more pressures and disturbances on the natural ecosystems and may have increased the risk of invasion by alien species (Fouda et al., 2006; Kamel, 2020; Shaltout et al., 2021).

The current study uses a profiling approach by integrating trait-environment model with species distribution models (SDMs) to predict future invaders and future areas under invasion risk by these recognized invaders. This integration is especially needed for assessing the risks of invasions at protected areas threatened by the disturbances escalating due to human activities (e.g., overcollection, overgrazing, land use changes, agricultural and tourism activities), as is the case for SKP. The main objectives of the current study were to: 1) classify the alien plant species in SKP into groups of invasion levels by using a trait-environment model, 2) identify the alien plant species that can be indicators for microhabitats at high invasion risk, 3) evaluate the invasion risk of each group in response to the bioclimatic variables using species distribution models, 4) assess the range of the most significant climatic variables that indicates the invasion suitability, and 5) to identify the priority conservation areas of high invasion risk based on alien species richness maps of each group.

The outcome of the study provides insights that have the potential to guide prevention measures and control strategies, to assist in the mapping of dispersal routes, and to help guide actions of early detection and rapid response. It highlights the role or importance of the trait-environment models when integrated with SDM models in the assessment of invasion risk and conservation planning. Lastly, this study provides ecological- and trait profiles for the current alien species in this arid, protected area, acting as an informative tool to predict the rate of invasiveness and to determine the key factors shaping invasion.

2. Materials and methods

2.1. Study area and microhabitats

SKP is located in the arid North African belt of South Sinai, Egypt. The protectorate is composed of igneous and metamorphic rocks with the highest peaks being Gebel Saint Katherine, Gebel Um Shomer and Gebel Musa (about 2642, 2586, 2285 m a.s.L. respectively). Generally, southern Sinai climate is extremely arid, with hot rainless summers and cold winters, and the region receives on average <60 mm of rainfall annually. However, the high mountains in SKP receive higher amounts of precipitation in the form of rain and snow. The diversity in geomorphological and geological structures of SKP has resulted in six types of unique microhabitats, namely: Wadis (valleys), Terraces, Slopes, Gorges, Cliffs, Farsh (basins) and Caves (SKP Management Plan, 2003, Omar, 2014). Wadis are the most common microhabitats in the current study area, and act as catchment areas for the accumulation of water and nutrients, with typically higher resource availability compared to the surrounding areas.

2.2. Species occurrence, traits, and soil data

First, we obtained the occurrence (presence/absence) data of 33 alien plant species from field surveys that were carried out during the spring and summer seasons (March to July) of 2019 in SKP. This was accomplished by sampling 166 plots of 10 m^2 that were invaded by at least one alien plant species. Second, we obtained the following measurements for abiotic environment and resource availability: soil moisture, soil nitrogen, organic matter content, and anthropogenic pressures. These measurements were taken for each plot using a hygrometer for soil moisture, by calculating the ratio of total C and CaCO3% for organic matter (Klute, 1986), and with standard methods using a CNH analyser (EA1108, Carlo Erba Instruments, USA) for soil nitrogen concentration (Allen et al., 1974). A detailed description of the methods can be found in the previously published (El-Barougy et al., 2020). We estimated the anthropogenic pressures in the studied plots based on their intensity into three levels (low, medium and high). These pressures included grazing, tourism activity, urbanization, and over-collection considering that land-use, litter layers, and human wastes influence the occurrence of alien species in natural ecosystems (Mooney and Hobbs, 2000; Sanderson et al., 2002).

Third, we non-destructively measured three traits on all alien plants in the plots. These traits were plant height from the ground (cm), the number of leaves, and the number of reproductive organs (flowers and fruits). In addition to these three traits, we also determined aboveground biomass (kg) and specific leaf area, SLA [cm^2/g]. To obtain measurements for above-ground biomass of alien plants, all aboveground parts (leaves and stems) of all alien plants were dried in a drying oven (VWR International) at 50 °C for three days, and then weighed using a Mettler Toledo ML Series Precision Balance (ML Analytical balance). To calculate SLA, leaf area was estimated by using the IMAGEJ software, version 1.49. Then we dried the leaves and determined the leaf dry weight, and calculated the SLA (cm^2/g) as the leaf area divided by the leaf weight (Basuki et al., 2009)

2.3. Predictive model building

2.3.1. Potential future invasive species

We constructed a series of generalized mixed-effect models (trait-environment models) with binomial distribution, using alien species occurrence as a response variable, while alien species traits (height, SLA, biomass, number of leaves and flowers), soil resource measures (organic matter, nitrogen, soil moisture), and anthropogenic pressures (grazing, over-collection, urbanization, tourism activity) were included as explanatory variables (Fig. 1, Appendix A; Table 2A). The analyses were implemented using "*lme4*" R package (version 1.1–20; (Bates et al., 2015). Then, we ran 100 models on the list of 33 alien species and used model predictions to project the future alien invasive species distribution. For each model, we identified the potential probability of invasiveness for each alien species, with species that were selected in at least 90 of the 100 models considered to be potentially invasive. In addition, we verified whether our models were able to correctly classify the studied alien species by recoding the species as non-invasive and predicted them from the models with the remaining 32 alien species using 33–1 leave-one-out sensitivity analysis (Fournier et al., 2019). From this analysis, we classified all the studied alien species based on

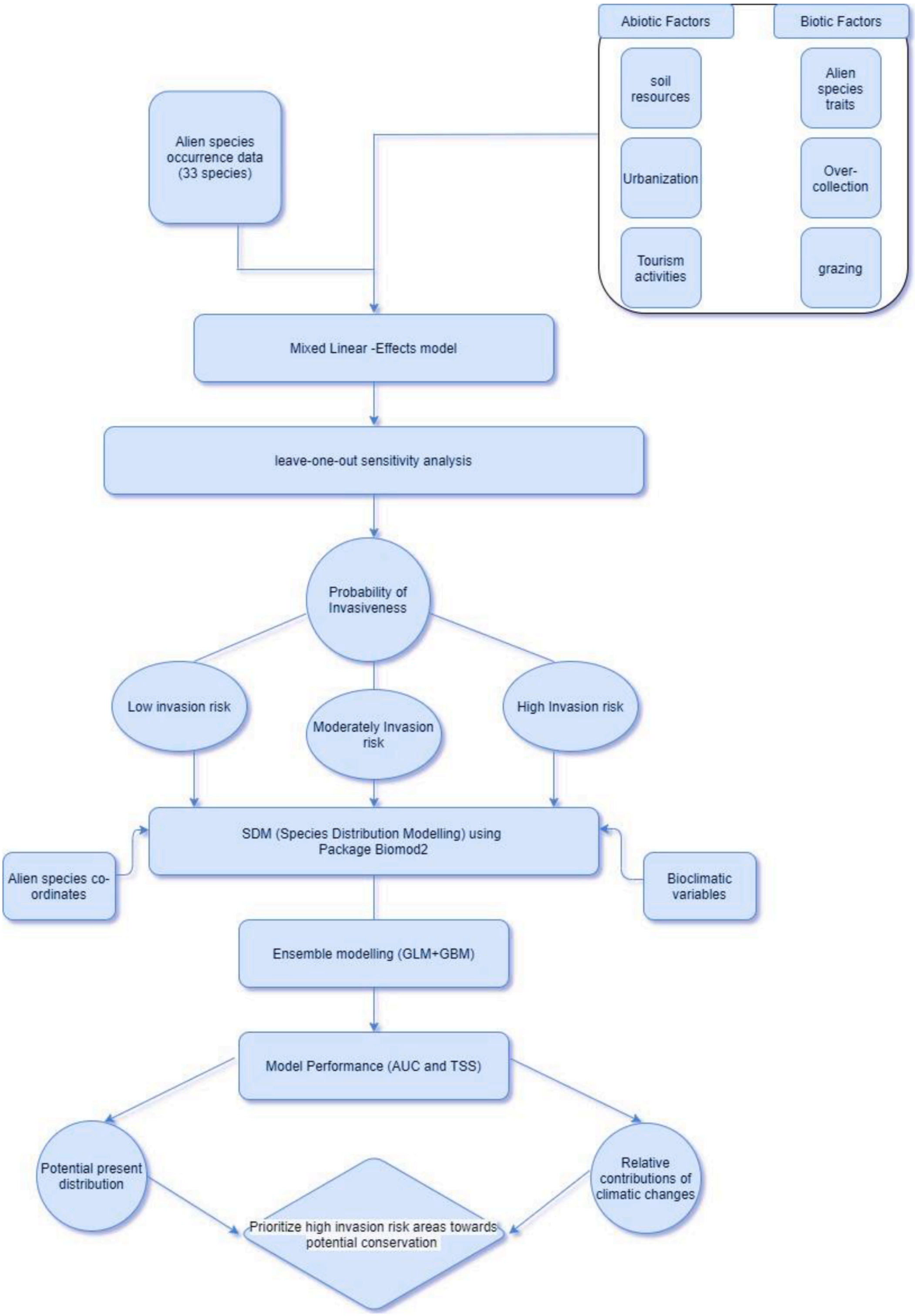

Fig. 1. Flowchart of the methodology and steps followed in the current study.

their probability of invasiveness into either a high invasion risk, moderate invasion risk, or low invasion risk group.

2.3.2. Estimation of areas under the invasion risk using SDMs

We built SDMs for the three groups of alien species in order to identify the areas that present suitable environmental conditions for these species and thus areas at risk of invasion. We used the presence points (species coordinates) that were determined with a 5 m resolution, with duplicate observations removed, before running the SDMs. In addition, pseudo-absences were selected (1000 occurrences) in order to 1) include presences as absence locations (same niche), (2) to avoid pseudo-replication and (3) to consider the possible issue that absences occur in locations that are potentially suitable for the species, but the species has not yet had the time to reach that environment. We also made sure that they were equally weighted to the presences, as recommended to obtain the greatest accuracy of the predictions (Barbet-Massin et al., 2012).

To predict the potentially suitable areas for the three groups of alien species, we downloaded the 19 bioclimatic variables (Table 1) of the current climate (averaged from 1970 to 2000) available from the Worldclim 2.0 database (http://www.worldclim.org) at 10 arc min resolution (Hijmans et al., 2005). These variables represent a combination of means, extremes, variability, and seasonality of temperature and precipitation data that are known to influence species distribution (Root et al., 2003). To avoid the multicollinearity among the 19 bioclimatic variables, we tested Variance Inflation Factors (VIFs) of 19 bioclimatic variables. VIFs are based on correlation coefficients (R^2) that were obtained from regression among all predictors and was implemented through the 'usdm' package in the R-environment (version 3.1.1). Consequently, eleven variables with VIFs > 5 were excluded (Chatterjee and Hadi, 2006) and only eight variables were used to establish the distribution model of the three groups of alien species under the current conditions. The selected variables were annual mean temperature (Bio1), mean diurnal range (Bio2), isothermality (Bio3), mean temperature of driest quarter (Bio9), annual precipitation (Bio12), precipitation of driest month (Bio14), precipitation seasonality (coefficient of variation, Bio15) and elevation (Elev). Notably, the inclusion of soil variables in the SDMs was constrained by sites with rocky and hard mountainous soil that prevail SKP, which may lead to some bias towards less mountainous sites than others and thereby leading to arbitrary selective sampling (Lepš and Hadincová, 1992).

Then, we used four algorithms using 'biomod2′ R. package (version 3.3–7.; Thuiller et al., 2020) including: generalized linear model (GLM), generalized boosting model (GBM), maximum entropy, and multiple adaptive regression splines, which are characterized by high stability and transferability compared to other models (Thuiller et al., 2009). We used these algorithms to build an ensemble model (i.e. TSS-weighted average of all models used) that encompassed the variability between the models and provided the central tendency (Araújo and New, 2007). Two metrics were used to evaluate the accuracy of each SDM: the True Skill Statistics (TSS) (Allouche et al., 2006) and the Area Under the receiver operating characteristic Curve (AUC) (Fielding and Bell, 1997). Ensemble models (Thuillier et al., 2016; Fournier et al., 2019) were run for each alien species group with sufficient occurrence points in order to produce invasion suitability distribution maps for each of the three groups (high-, moderate- and low-invasion risk).

Table 1
Environmental variables used for SDM modelling. Problems related to collinearity were avoided by removing variables with a correlation coefficient > 0.75. The variables highlighted in bold were selected with a multicollinearity test and were used in modeling.

Code/ Unit	Description	Source
Bio_1 (°C)	**Annual mean temperature**	**www.worldclim.org**
Bio_2 (°C)	**Mean Diurnal Range (Mean of monthly (max temp - min temp))**	**www.worldclim.org**
Bio_3	**Isothermality (Bio2/Bio7) × 100**	**www.worldclim.org**
Bio_4 (°C)	Temperature seasonality (SD × 100)	www.worldclim.org
Bio_5 (°C)	**Max temperature of warmest month**	**www.worldclim.org**
Bio_6 (°C)	Min temperature of coldest month	www.worldclim.org
Bio_7 (°C)	Temperature annual range (Bio5-Bio6)	www.worldclim.org
Bio_8 (°C)	**Mean temperature of wettest quarter**	**www.worldclim.org**
Bio_9 (°C)	**Mean temperature of driest quarter**	**www.worldclim.org**
Bio_10 (°C)	**Mean temperature of warmest quarter**	**www.worldclim.org**
Bio_11 (°C)	Mean temperature of coldest quarter	www.worldclim.org
Bio_12 (mm)	**Annual precipitation**	**www.worldclim.org**
Bio_13 (mm)	**Precipitation of wettest month**	**www.worldclim.org**
Bio_14 (mm)	**Precipitation of driest month**	**www.worldclim.org**
Bio_15	**Precipitation seasonality (Coefficient of variation)**	**www.worldclim.org**
Bio_16 (mm)	Precipitation of wettest quarter	www.worldclim.org
Bio_17 (mm)	Precipitation of driest quarter	www.worldclim.org
Bio_18 (mm)	**Precipitation of warmest quarter**	**www.worldclim.org**
Bio_19 (mm)	**Precipitation of coldest quarter**	**www.worldclim.org**
DEM (m)	Digital elevation model	U.S. geological survey (https://www.usgs.gov)

3. Results

3.1. Trait-environment model and invasion probabilities

The trait-environment model (generalized linear mixed effect model) showed high accuracy with area under the receiver operating characteristic Curve (AUC) = 0.78. It indicated relatively strong relationships between species traits and invasion potential (marginal $R^2 = 0.45$). It also revealed that the most important biotic and abiotic factors for predicting invasiveness probability are specific leaf area (SLA), number of leaves, soil nitrogen, and a frequent association with disturbances (tourism and grazing, see Table 2).

The leave-one-out sensitivity analysis provided a classification of the 33 studied alien species into three groups based on the predicted invasion probability (Fig. 2) as follow: high-invasion risk group (with probability > 0.26), moderate-invasion risk group (with probability 0.094–0.189), and low- invasion risk group (with probability ≤ 0.075) (Table 3). Out of the 33 investigated alien species, 18% were estimated to have high invasiveness potential, 27% with moderate invasiveness potential, while the rest (55%) were estimated as low invasiveness potential. The three species *Salvia rosmarinus, Eucalyptus globulus,* and

Table 2
Results of multivariate generalized linear mixed effects model showing the significant biotic predictors (SLA, number of leaves, grazing), and abiotic predictors (soil nitrogen, soil organic matter, tourism activity) that explain alien species occurrence.

Predictors	Coeffecient	Std. E	df	t value	Pr(>|t|)
log. Nitrogen (mg/L)	0.028	0.008	42.37	2.71	0.001**
log. Organic matter (g/ml)	0.025	0.012	86.768	2.1	0.03*
Grazing	0.053	0.026	108.16	2.06	0.04*
Tourism activities	0.062	0.02	64.94	3.14	0.002**
log. SLA (Cm2/gm)	0.023	0.007	193.91	3.31	0.001**
log. number of leaves	0.046	0.004	196.03	12.056	<0.0001***

Significant association test (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.)

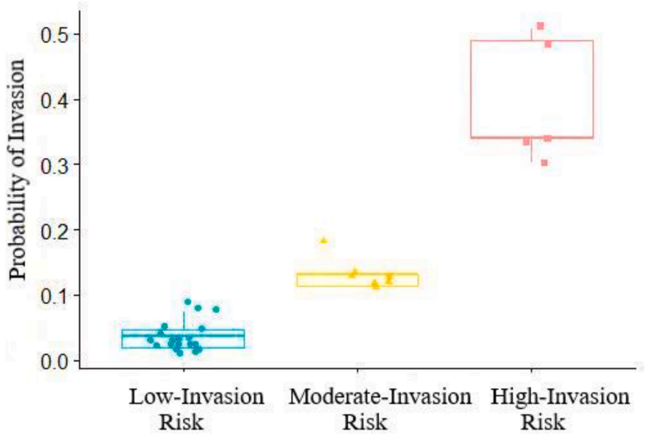

Fig. 2. Predicted invasion probability distribution for alien species. Three classes of invasion risk (low, moderate, and high).

Acacia saligna, which are known to be invasive globally (CABI, IUCN, see details in the discussion section), have the highest invasion-risk probabilities (0.51, 0.49, and 0.34, respectively; see Table 3).

3.2. Potential invasion risk

Species distribution ensemble models allowed us to predict and identify the suitable climatic areas for each group of alien species. These predictions indicated excellent model performances, with values of True Skill Statistics (TSS) ranging from 0.89 to 0.97, and AUC values ranging from 0.98 to 0.996 (Fig. 4). Temperature bioclimatic variables were the most important factors explaining the probability of occurrence of the three groups of alien species. For moderate and high-invasion risk groups, the annual mean temperature (bio1), mean temperature of the driest and warmest quarters (bio9 and bio10), and precipitation seasonality (bio15) were the most important bioclimatic variables determining the distribution of alien species (Fig. 3). These variables contributed between 20% and 60% of the predicted suitability of these alien species groups.

3.3. Local areas at invasion risk

Four distinct local areas at the northern part of SKP are expected to be of high potential suitability for the alien group with high invasion risk (Fig. 4). The potential suitability in these areas were mostly between 40% and 95% (Fig. 4). In addition, the potential invasion is more likely in the eastern parts of north SKP, where the biodiversity-rich microhabitats “Wadis” (Etalaa, Shaq Mosa, and El-Mesirdi) are found.

4. Discussion

4.1. Trait-environment models and invasion risk

The capacity of species distribution models to deliver robust and accurate predictions may be impeded by a shortage of ecologically pertinent predictors. For example, the species traits that limit species distributions may influence model performance (Regos et al., 2019). By revealing the relative importance of environment-species traits in influencing the invasiveness probability of alien species, trait-based approaches can help identifying the ecological profile of existing alien plants and detect species with low or high invasiveness. The integration of trait-environment models with species distribution models leads to robust predictions that help to understand the response of alien species to the environmental conditions in a new area, and thus its potential invasiveness (Vesk et al., 2021).

Table 3
Predicted invasion probabilities of the 33 alien species, generated by linear mixed effect model.

Group	Species	Global invasiveness status	Predicted invasiveness probability
High Invasion Risk	*Salvia rosmarinus* Schleid.	Invasive	0.509
	Eucalyptus globulus Labill.	Invasive	0.491
	Acacia saligna (Labill.) H. L. Wendl.	Invasive	0.340
	Mentha longifolia (L.) Huds.	Invasive	0.340
	Nerium oleander L.	Invasive	0.302
	Salvia fruticosa L.	unkown	0.264
	Rosa gallica L.	unkown	0.189
Moderate Invasion Risk	*Beta vulgaris* L.	unkown	0.132
	Mentha spicata subsp. *spicata*	Invasive	0.132
	Origanum majorana L.	unkown	0.132
	Amaranthus caudatus L.	Invasive	0.113
	Papaver somniferum	unkown	0.113
	Pistacia lentiscus L.	unkown	0.113
	Yucca gloriosa L.	unkown	0.113
	Camellia sinensis (L.) Kuntze	unkown	0.094
Low Invasion Risk	*Aloe vera* (L.) Burm.f.	Invasive	0.075
	Nicotiana rustica L.	unkown	0.075
	Agave americana L.	Invasive	0.057
	Crocus sativus L.	unkown	0.057
	Casuarina cunninghamiana Miq.	Invasive	0.038
	Selenicereus triangularis (L.) D. R. Hunt	unkown	0.038
	Opuntia ficus-indica (L.) Mill.	Invasive	0.038
	Pelargonium peltatum (L.) L'Hér. ex Aiton	Invasive	0.038
	Rhus coriaria L.	unkown	0.038
	Azadirachta indica A. Juss.	Invasive	0.019
	Cynara cardunculus L.	Invasive	0.019
	Lantana camara L.	Invasive	0.019
	Erepsia lacera (Haw.) Liede	unkown	0.019
	Moringa oleifera Lam.	Invasive	0.019
	Myoporum laetum G. Forst.	unkown	0.019
	Plectranthus hadiensis (Forssk.) Schweinf. ex Sprenger	unkown	0.019
	Simmondsia chinensis (Link) C. K. Schneid.	unkown	0.019
	Platycladus orientalis (L.) Franco	unkown	0.019

Out of the 33 investigated alien species, seven were estimated to have high invasiveness potential, eight with moderate invasiveness potential, while the rest (17) were estimated to have low invasiveness potential. In accordance with our finding, three of the highest invasion-risk probabilities in the current study (*Salvia rosmarinus*, *Eucalyptus globulus*, and *Acacia saligna*) are well-known aggressive invasive species in different parts of the world and are listed in the Invasive Species Compendium of Centre for Agriculture and Bioscience International (CABI) and the IUCN Global Invasive Species Database (GISD). Our findings appear to be in accordance with information available from the literature that regard these species as having the characteristics to become future invaders and negatively impact natural ecosystems. For example, *A. saligna* is recognized as ‘one of the worst woody invaders’ (Cronk and Fuller, 2014) because it has invaded and caused harmful impacts on biodiversity and ecological services in parts of Algeria, Cyprus, Italy, Portugal and Spain, and is naturalized in Australia (Thompson et al., 2015). In Egypt, *A. saligna* negatively impacted the diversity of native species within the Mediterranean protected areas (El-Bana, 2008). E. globulus has been reported as invasive in parts of

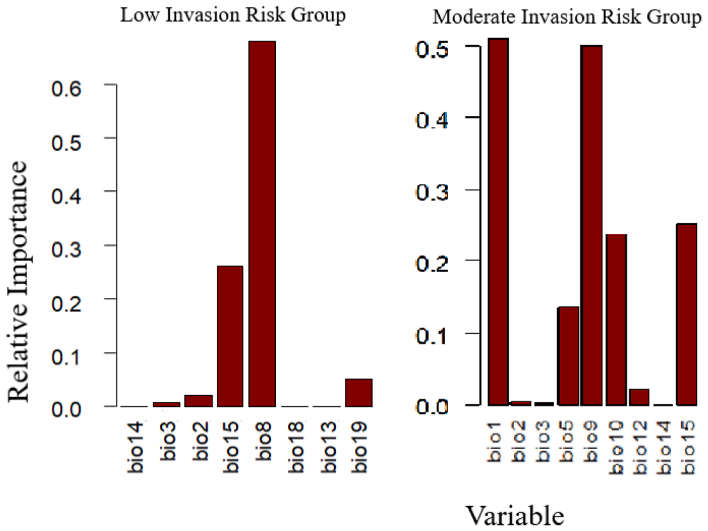

Fig. 3. Relative importance or contribution of the predictor variables used in ensemble modelling of the three invasion-risk groups of alien species. Abbreviations: bio1-annual mean temperature (C); bio2-mean diurnal range (C); bio3-isothermality; bio5-max temperature of the warmest month(C); bio8-mean temperature of the wettest quarter(C); bio9-Mean temperature of driest quarter (C); bio10-Mean temperature of the warmest quarter; bio12-annusal precipitation (mm); bio13-precipitation of the wettest month (mm), bio14-precipitation of the driest Month (mm); bio15-precipitation seasonality (C of V); bio18-precipitation of warmest quarter (mm) and bio19-precipitation of coldest quarter (mm).

Australia, the US and Portugal (Deus et al., 2019; Richardson and Rejmánek, 2011); and R. officinalis is considered as a ‘casual alien’ (Randall, 2012), and has been reported as invasive in Cuba (Oviedo Prieto et al., 2012). The alien species that attained low and moderate invasiveness probability in our study have not been reported as posing any threats yet in Egypt, thus giving support for the proactive potential of the approach used in this study. In addition, the studies assessing the invasion status of most of these species are insufficient, which stresses the need for more investigations and monitoring efforts.

Trait-based modelling has been used to detect traits which can be utilized in predicting potential invaders (Zakharova et al., 2019). It has been emphasized that the identification of a set of ‘universal traits’ distinctively linked to invasion is uncommon because the comparative significance of certain traits can vary in different local environments (Gross et al., 2010; Zakharova et al., 2019). Our results highlighted some traits and environmental factors highly related to invasion risk, which might be key in explaining the success of invasive species in new environments. The most important species-traits were found to be the specific leaf area (SLA) and the number of leaves, and the environmental factors that were found to be highly associated with the occurrence of invasive species were soil nitrogen and the prevalence of disturbances (e.g., tourism). Some of these traits were previously emphasized as regularly associated with invasive plant species. For example, leaf production cost, as indicated by SLA and number of leaves, play a key role in resource acquisition, subsequently leading to higher invasion success (Wang et al., 2017). However, it should be noted that the invasion process is dynamic and, as such, certain alien species that are categorized as non-invasive at a particular time could turn into harmful invaders when disturbances alter the current environmental conditions (Schrama and Bardgett, 2016). This, in turn, will potentially affect the relative importance of the different traits being investigated.

Disturbances in general are indicated as one of the factors associated with the occurrence of invasive species (e.g., Halmy, 2019; Halmy et al., 2019; Rodríguez et al., 2017). Tourism activities may directly or indirectly affect the probability of invasiveness through unintentional or intentional human transport (Kumar Rai and Singh, 2020). Generally, tourism and related recreational activities are recognized as one of the main ways for the introduction of alien species to occur. Through the continuous development of these activities, their influence in spreading invasive species increases (Anderson et al., 2015). In addition, the overcollection of native plants by local people (Bedouins) is one of the causes of disturbance in the current study region, which may facilitate the spread of invasive species through the creations of open niches for these species to occupy. This practice usually occurs intensively before the onset of the tourism season, since local people sell the collected native plants to national and international visitors (Omar, 2012).

4.2. *Bioclimatic drivers of invasion risk*

Temperature has been reported as a key bioclimatic variable determining the distribution of alien species in previous studies (Larcombe et al., 2013; Terzano et al., 2018) and the considerable effect of temperature during the driest months on the potential distribution of invasive species have already been recognized (e.g., Terzano et al., 2018; Watt et al., 2009; Xu, 2015). The outcome of the SDM revealed that the temperature-related bioclimatic variables were the most important factors for predicting the potential distribution of the three groups of alien species. The tolerance of the studied species to drought and the dry conditions prevailing in SKP may explain why the precipitation-related variables had a limited role in predicting the distribution of the high risk species in the region (e.g. *R. officinalis*, *E. globulus*, and *A. saligna*) (Eggleton et al., 2007). The results also revealed that precipitation seasonality is one of the key determinants for the potential distribution of the moderate- and high-invasion risk groups. Sensitivity to variability in precipitation is known to act as one of the main factors determining invasive species distributions (Hierro et al., 2009; Xu et al., 2013), and an increase in precipitation seasonality is suggested as one of the factors that can negatively affect invasive plant species spread (Xu et al., 2013). Precipitation seasonality is assumed to negatively influence germination rate and to pose risks to invasive species in their initial developmental stages (Hierro et al., 2009). In contrast, low precipitation seasonality has been thought to contribute to an increase in invasion success, particularly in mountainous ecosystems (Paź-Dyderska et al., 2021). For example, it was found that the establishment of the invasive species *E. globulus*, one of the high-invasion risk species in the current study, has increased in areas with low precipitation seasonality (Larcombe et al., 2013). Thus, the likelihood that invasive species can develop fast adaptive germination strategies in response to changes in the precipitation seasonality may determine the success of these species in their new environments (Hierro et al., 2009).

4.3. *Priority conservation areas*

The high-invasion risk map revealed areas of high conservation priority. These areas are mainly at the northern and eastern parts of SKP, including unique wadis such as Wadi Etalaa, Wadi Shaq Mosa, and Wadi El-Mesirdi. These wadis are also among the most affected areas by tourism activities, notably visiting SKP for safari and camping (Omar,

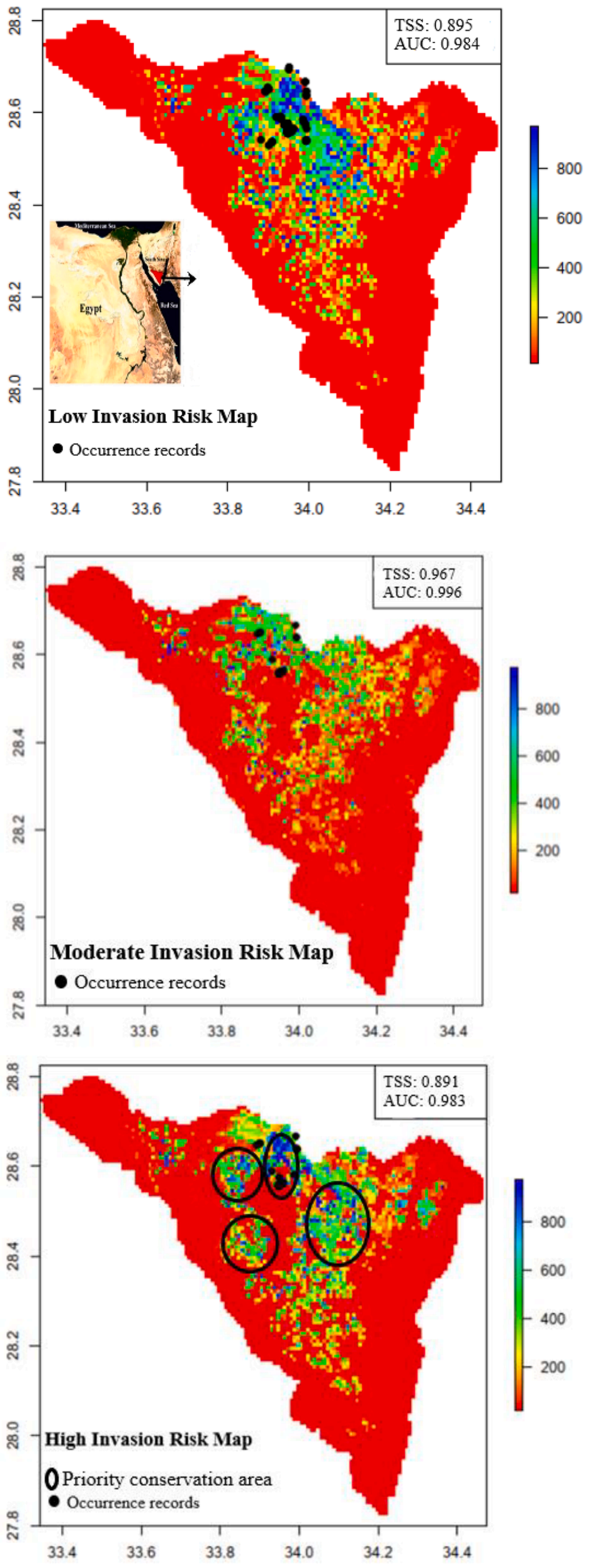

Fig. 4. Habitat suitability maps of Alien species richness for the three invasion-risk groups. Ensemble-Model Accuracy indicators: TSS = true-skill statistics, and ROC = receiver operating characteristic.

2016). The low altitude of these wadis makes them more vulnerable to invasion because they are easily accessible and thus heavily used by tourists and grazing animals (Guenther, 2005; Khafagi et al., 2018; Moustafa et al., 2001; Omar, 2012). For example, grazing by donkeys is known to cause severe negative impact on vegetation cover and plant regrowth, through the uprooting of plants and soil trampling and compaction (Khafaja et al., 2006, Omar et al., 2013). Moreover, the topography of these wadis acts as reservoirs for water (Omar, 2012), which highlights their value for human activities as well.

4.4. *Conservation implications and local management strategy*

Prevention is the most appropriate management approach for addressing biological invasion. However, nearly all current management endeavors are concentrating on established alien populations, with less attention given to future and potential invasion. The successful prevention and management of invasion risk need to be considered as an integral component for SKP management effectiveness. Formulating ways to identify the main vectors responsible for the introduction of invasive species in SKP would be an efficient strategy for prevention, early detection and rapid actions.

Wadis are the most threatened microhabitats by alien species and are also subjected to overgrazing, agricultural activities, and overcollection of the medicinal plants (Moustafa et al., 2001; Guenther, 2005; Omar, 2012, 2016; Khafagi et al., 2018). These wadis are predicted to have high potential suitability for alien species invasion and need to be prioritized for monitoring activities and conservation actions.

The management strategy needs to focus on the species that were revealed in this study as potential invaders. In particular, *R. officinalis, E. globulus, and A. saligna* should be the most targeted and monitored in “wadis” microhabitats, as they were found to be the most suitable habitats for these species. Besides monitoring activities, awareness programs should be developed for local people to avoid collecting native species, particularly in the highly suitable areas for invasion risk (i.e. priority conservation areas with high plant diversity and endemism). In addition, incentives and alternatives for local communities should be provided to encourage them to reduce the grazing activities in the areas at high risk of invasion.

5. Conclusion

This study provides a simple framework to identify biotic and abiotic factors related to invasion success in the arid protected area SKP, which can be implemented by other researchers to predict potential invaders, and their pattern of invasion under similar conditions as in the present study. Trait-environment based models revealed that the specific leaf area, number of leaves, soil nitrogen, and tourism activities were the most important factors for predicting invasiveness in SKP. Of the investigated 33 alien species, *Salvia rosmarinus, Eucalyptus globulus, and Acacia saligna* should be prioritized in any future invasion management actions aimed at establishing protected areas and any other relevant conservation actions.

The utilization of SDMs to predict areas at highest risk of invasion revealed that temperature and precipitation -related bioclimatic variables were the most important factors determining the potential distribution of the investigated species. In addition, the eastern and northern parts of SKP are recommended for any current or future actions involving in-situ or ex-situ conservation. Finally, we highlight that the inclusion of future land-use change scenarios should also be incorporated into integrative modelling approaches aimed at assessing the impact of future climate and environmental changes on alien species distribution and the availability of suitable habitats. In addition, more attention, should be given to study the variations in the suitability of alien species that might respond and adapt quickly to the climatic changes particularly outside their native range.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Authors' contributions

RFE conceived the approach with substantial contributions from LFB. RFE and AAK collected and compiled the datasets. RFE and MAD performed data analysis and visualization. RFE, MAD, MWH, SMG, MA, LFB drafted the manuscript. All authors contributed substantially to revise and edit the manuscript. All authors gave final approval for publication.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107951.

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