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PRIMARY RESEARCH PAPER

Using ecological niche modeling to predict the distributions of two endangered amphibian species in aquatic breeding sites

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Abstract Amphibians are among the most threatened taxonomic groups worldwide. A fundamental step in species conservation is identifying the habitat requirements of the target species. However, this determination can often be problematic in endangered species because, by definition, they often only occupy a very limited number of sites. Moreover, when found, they are often in low abundance, and thus their detectability is low, yielding false "absence" data. Maximum entropy niche modeling provides a tool using only the presence data to predict potential habitat distributions of endangered species whose distributions have become highly limited. We provide two examples in the current study for the fire salamander, *Salamandra infraimmaculata*, and the green toad, *Bufo viridis*. *S. infraimmaculata* is considered endangered in Israel and near endangered worldwide. *B. viridis* is classified as locally endangered in Israel. Soil type was the most important predictor of the distribution of *S. infraimmaculata* and, to a lesser extent, also predicted the distribution of *B. viridis*. In addition, *S. infraimmaculata* larvae were also associated with high elevation areas. *B. viridis* was negatively associated with distance to urban areas and low solar radiation level. The potential distribution maps determined for *S. infraimmaculata* and *B. viridis* can help in planning future wetland use management around its existing populations, discovering new populations, identifying top-priority survey sites, or set priorities to restore its natural habitat for more effective conservation.

Keywords *Bufo viridis* · Maxent · *Salamandra infraimmaculata* · Small sample size · Species distribution model

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Introduction

Numerous studies have documented declines in amphibian species abundance across the globe in the last two decades (Blaustein & Wake, 1995; Stuart et al., 2004). Habitat fragmentation, degradation, and loss are probably the most important drivers of population decline worldwide (Hendrickx et al., 2007; Billeter et al., 2008). Studies that evaluate the relationship between amphibian distribution and their habitat can provide vital scientific information helping us to set up conservation plans. To protect these species, we need a better understanding of what constitutes suitable habitat and where such habitats exist. Habitat suitability mapping can identify areas in need of restoration or preservation (Gibson et al., 2004), and identify candidate areas for species reintroduction (Olsson & Rogers, 2009) or for construction of artificial breeding pools in the case of amphibians (Stratman, 2000).

Prediction and mapping of potential distributions of endangered species are required to assess species status and guide conservation plans (Gaston & Williams, 1996). However, data on threatened and endangered species' distributions are often sparse (Ferrier et al., 2002; Engler et al., 2004), both in the number of sites and in densities, which makes the probability of detection low. These problems make commonly used habitat modeling approaches that use the presence/absence data problematic.

Employing species distribution modeling tools in ecology is becoming increasingly popular. These models describe the environmental requirements of species and use it to produce distribution maps that are a crucial stage in targeting conservation and recovery efforts (Guisan & Zimmermann, 2000; Elith et al., 2006; Peterson, 2006). Improvements in geospatial databases and predictive algorithms have increased the reliability of habitat models (Guisan & Thuiller, 2005). A variety of species distribution modeling methods are now available to predict potential suitable habitat for a species (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Elith et al., 2006; Guisan et al., 2007; Wisz et al., 2008). The performances of most species distribution modeling methods are poor when sample size is small (Wisz et al., 2008), thus these modeling methods may not accurately predict habitat distribution patterns for threatened and endangered species.

In this study, we employed maximum entropy distribution (Maxent) modeling. Maxent, unlike other distributional modeling techniques, uses only presence and background data instead of presence and absence data. This method has been shown to perform well in comparison with alternative approaches (Elith et al., 2006; Hernandez et al., 2008; Navarro Cerrillo et al., 2011) and may remain effective even when the number of sites in which presence has been recorded is quite low (Hernandez et al., 2006; Papeş & Gaubert, 2007; Pearson et al., 2007; Wisz et al., 2008; Costa et al., 2010). Both Pearson et al. (2007) and Hernandez et al. (2006) suggest that reliable predictions with Maxent can be attained even when the number of sites in which presence is recorded is <10, and this presents positive implications for the scope of applying Maxent for predicting endangered species' distributions. Maxent has been used to model the potential distribution of species in terrestrial (Pearson et al., 2007; Attias et al., 2009), freshwater (Puschendorf et al., 2009; Tarkhnishvili et al., 2009), and marine (Lefkaditou et al., 2008; Hermosilla et al., 2011) ecosystems.

Niche modeling of amphibians at the landscape scale has often studied the relationship between amphibian assemblages and the degree of landscape alteration (e.g., Knutson et al., 1999; Lehtinen et al., 1999). These studies have typically included a significant agricultural (Knutson et al., 1999; Lehtinen et al., 1999), urbanized (Gibbs, 1998), or forested (deMaynadier & Hunter, 1998) component. Indeed, such studies suggest that amphibians in altered landscapes are susceptible to forest fragmentation (Gibbs, 1998), urbanization (Richter & Azous, 1995), and agriculture (Knutson et al., 1999; Lehtinen et al., 1999). These and other factors can lead to barriers to a single breeding site, or in the case of metapopulation structure, isolation from other wetlands (Vos & Stumpel, 1996). In unfragmented landscapes, the effect of land-use cover on species distribution may be weaker as the habitat-matrix character is less obvious (Hartel et al., 2010). Another important factor affecting the distribution of amphibians, which is sometimes overlooked, is soil type. Soils that drain quickly limit the hydroperiod for the developing amphibian larvae and reduce a species' ability to dig into the soil and provide moist refuge sites during estivation periods (Hardy, 1945). In this study, we investigated landscape variables correlated with the larval distribution of the fire salamander, *Salamandra infraimmaculata;* and green toad, *Bufo viridis*. Both species are of conservation concern. *S. infraimmaculata* is considered endangered in Israel (Dolev & Perevolotsky, 2004) and near endangered worldwide (Papenfuss, 2008). Israeli populations occupy the southern-most, and most xeric habitats of this genus worldwide (Degani, 1996 ;Bar-David et al., 2007). *B. viridis* has recently experienced population decline along the heavily developed coastal plain of Israel (Elron et al., 2005) and is now classified as locally endangered in Israel (Dolev & Perevolotsky, 2004).

We used maximum entropy niche modeling as a tool to assess potential habitat suitability for *S. infraimmaculata* and *B. viridis* and to map the potential distribution for the entire Mt. Carmel area, which contains the southern-most populations of

S. infraimmaculata worldwide. More specifically, our objectives were to (1) predict potential distributions of the threatened *S. infraimmaculata* and *B. viridis* using known presence observations; and (2) identify the landscape factors associated with *S. infraimmaculata* and *B. viridis* habitat distribution.

Methods

Study region

Mount Carmel is a mountain belt in northern Israel, covering an area of 240 km^2 with an altitude range of 40–546 m a.s.l (Fig. 2a). It is few kilometers away from the sea and characterized by sharp borders with the surrounding lowlands—to the west by a coastal abrasion escarpment, to the northeast by a steep escarpment, and to the southeast by a moderate escarpment formed by a river valley. The lithology is composed of upper Cretaceous carbonate rocks, mainly dolomite, limestone, marl, chalk, and local exposures of volcanic tuff. Mt. Carmel's climate is eastern Mediterranean, characterized by relatively hot, dry summers, and cool, wet winters (Carmel & Stoller-Cavari, 2006). The area receives approximately 600 mm rainfall annually, mainly between November and March. Most stream systems of Mt. Carmel are ephemeral. The only exceptions are short sections of a few streams that are fed by springs including during the summer. Stream flow events occur sporadically, mainly after intense rainstorms. Breeding sites can be found along these intermittent streams. Rain pools not associated with these streams can also serve as breeding sites for amphibians. The vegetation of Mt. Carmel is characterized by a complex of pines (*Pinus halepensis*), and the *Quercus calliprinos–Pistacia lentiscus* associations which together form a Mediterranean evergreen sclerophyll forest type referred as maquis.

Amphibian sampling

Salamandra infraimmaculata and *B. viridis* breeding habitats in the Mt. Carmel region are patchily distributed. We checked 66 water bodies that might be potential breeding sites (ponds, pools, ancient wine presses, and wells). Between November 2009 and April 2010, these sites were sampled for the occurrence of *S. infraimmaculata* and *B. viridis* larvae. All ponds were surveyed by sweeping a dip net and visual survey of the ponds. All sites were visited during each of the four sampling periods spanning the season in which larvae of these species occur in temporary habitats. Larvae were identified at the breeding site and immediately released upon identification.

Environmental predictor variables

We considered eight environmental variables as potential predictor variables of *S. infraimmaculata* and *B. viridis* distribution. We used "Band Collection Statistics tool" of ArcToolbox in ArcGIS 9.0 (ESRI, Redlands, CA), to compute the correlation coefficients matrices between these layers (Table 1). Only two variable pairs were collinear ($r > 0.60$): "distance to road" versus "distance to urban areas", and "distance to agricultural areas" versus "distance to forest"; thus, we excluded distance to road and distance to agricultural fields. These predictor variables were selected based on their potential ecological relevance to amphibians. Various studies found different associations between these predictor variables and amphibian species (Table 1). For example, Segev et al. (2010) found positive correlation between urban cover and *S. infraimmaculata* population size but suggested that this is because human settlements were established close to permanent springs. Knutson et al. (1999), on the other hand, found that most anurans they surveyed were negatively associated with the presence of urban land because of conversion of natural habitats to industrial uses, roads, and home site and because of wetland contamination.

Three topography predictor variables were selected for the analysis: mean topographical wetness index (TPI), mean solar radiation, and elevation. These predictor variables were derived from the digital elevation model (DEM obtained from the Survey of Israel; Hall et al., 1999) at 25-m resolution using ArcGIS and ArcView software (ESRI, Redlands, CA). The wetness level of the area was calculated by defining the TPI (Beven & Kirkby, 1979), also called the compound topography index (Gessler et al., 2000). TPI is defined as

$$\mathrm{TPI} = \ln\left[\alpha/\tan(\beta)\right]$$

where α is the specific catchment area expressed as m^2

Table 1 Environmental predictor variables used in the analysis to determine potential distribution of *S. infraimmaculata* and *B. viridis*

Environmental predictor variables	Unit	Mean (min–max)	Association found in other amphibian studies
Mean radiation	Mj cm^{-2} $year^{-1}$	0.98 (0.5–1.12)	− (Pahkala et al., 2000)
Mean TPI	–	6.68 (4.89–14.44)	∩ (Penman et al., 2007)
Elevation	Meter	238.45 (9–540)	− (Bradford et al., 2003; Suzuki et al., 2008)
			+ (Kirk & Zielinski, 2009)
Soil type	–		+ water holding soils (Dayton et al., 2004)
Distance to urban areas	Meter	780.5 (0–3154)	+ (Segev et al., 2010)
			− (Knutson et al., 1999; Lehtinen et al., 1999)
Distance to forested areas	Meter	844.6 (0–7745)	+ (Knutson et al., 1999; Hartel et al., 2008)
			± (Van Buskirk, 2005)
			± (Guerry & Hunter, 2002; Van Buskirk, 2005)

Two other variables—distance to roads and distance to agricultural fields—were originally also considered but deleted because of colinearity with other variables

+, positive association; −, negative association; ±, species dependent; ∩ species is more common at intermediate values

per unit width orthogonal to the flow direction, and β is the slope angle. TPI describes the local relative differences in moisture conditions (Gessler et al., 2000). Small values represent upper catenary positions (dry), and high values represent lower catenary (wet) positions.

Mean spatial solar radiation (Mj cm^{-2} $year^{-1}$) was estimated using a computer model of clear sky insolation and exposure of different slopes. Estimations were made using the Solar Analyst extension on ArcView (McCune et al., 2002). Accurate maps of insolation would require building and maintaining a dense network of stations. However, spatial solar radiation models are a cost-efficient means to characterize spatial variation of insolation over landscape scales (Tovar-Pescador et al., 2006). Solar radiation is a direct ecological factor affecting the habitat conditions (Austin & Meyers, 1996). Thus, it is more reasonable to use solar radiation than slope or aspect predictor variables (Bennie et al., 2008).

Urban areas and roads were manually digitized from high resolution (1 m pixel size) aerial orthorectified images acquired in 2008. Distance to urban and forest areas were calculated using the ArcGIS spatial analyst distance function (ESRI, Redlands, CA). Soil type layer was derived from polygons of soil association produced by the Ministry of Agriculture and Rural Development of Israel.

Distribution data for the two amphibians, along with data for the six predictor variables, were collected from 100 × 100 m grid cells.

Maximum entropy modeling

Maxent is a presence-only modeling method that estimates the probability distribution from incomplete information, and has recently been applied to modeling species distributions (Phillips et al., 2006; Kuemmerle et al., 2010). A detailed mathematical definition of Maxent, discussion of its application to species distribution modeling, and initial testing of the approach are described in Phillips et al. (2006) and Elith et al. (2011). The Maxent algorithm operates on a set of constraints that describes what is known from the sample of the target distribution. Maxent characterizes the background environment with a set of background points from the study region. However, unlike the presence–absence data, species occurrence at these background points is unknown. Maxent predicts the probability distribution across all the cells in the study area and, to prevent over-fitting, employs maximum entropy principles and regularization parameters (Phillips et al., 2006). Given that we consider only a portion of distribution of these species worldwide, the models generated do not necessarily predict the full fundamental niche, but our models

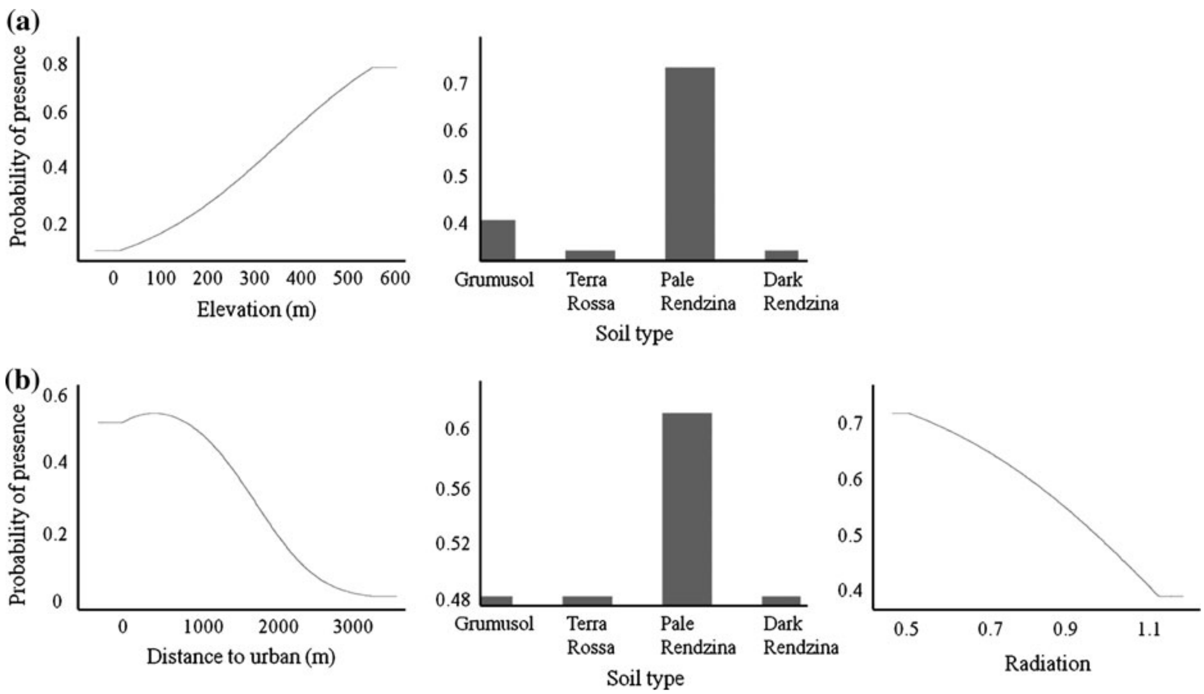

Fig. 1 Marginal response curves of the predicted probability of *S. infraimmaculata* (**a**) and *B. viridis* (**b**) occurrences for predictor variables that contributed substantially to the distribution models

likely predict an approximate distribution of these amphibians in the highly heterogenous study area.

We implemented Maxent using version 3.3.3e of the software developed by S. Phillips and colleagues (http://www.cs.princeton.edu/_schapire/maxent/). Distribution maps were obtained by applying Maxent models to all cells in the study region, using a logistic link function to yield a suitability index between zero and one (Phillips & Dudik, 2008). Recommended default values were used for the convergence threshold (10^5) and maximum number of iterations (500).

Model evaluation

Ideally, for evaluating the model performance, an independent dataset should be used. However, when working with threatened and endangered species, such a dataset seldom exists. Therefore, the most commonly used approach is to partition the dataset randomly into "test" and "training" sets (Fielding & Bell, 1997; Guisan et al., 2007). However, this approach is problematic with a small number of samples because the "test" and "training" datasets will be too small (Pearson et al., 2007). Therefore, we used a jackknife procedure, in which the model performance is assessed based on its ability to predict one locality that was excluded from the "training" dataset (Pearson et al., 2007). According to the number of the presence records, different predictions are made for each species, with one of the occurrence records excluded in each prediction and the final potential distribution map generated using all records (Fig. 1). We used the P value program provided by Pearson et al. (2007) to test the significance of the model. Model performance was evaluated using "Area under the curve" (AUC). AUC is a widely used accuracy measure, although some criticism has been raised, suggesting that AUC may be an inaccurate measure if observations are unreliable (Lobo et al., 2008). However, it is an accepted practice, especially for the presence-only datasets. The range of AUC is from 0.0 to 1.0. A model providing excellent prediction has an AUC higher than 0.9, a fair model has an AUC between 0.7 and 0.9, and a model with AUC below 0.7 is considered poor (Swets, 1988).

The jackknife validation approach that we used requires application of a threshold above which the model output is considered to be a prediction of the

Table 2 Jackknife tests of distribution models for *S. infraimmaculata* and *B. viridis*

Species	Number of pools detected	LPT		T10	
		Success rate	*P* value	Success rate	*P* value
S. infraimmaculata	17	0.76	0.021	1	0.0017
B. viridis	9	0.44	0.77	0.88	0.002

presence (Pearson et al., 2004). We considered two alternative thresholds which are widely used in species distribution modeling applications (Liu et al., 2005): the "lowest presence threshold" (LPT, equal to the lowest probability at the species presence locations), and a fixed thresholds that rejected only the lowest 10% of possible predicted values (T10) (Pearson et al., 2007).

Results

Of the 66 sites monitored, we found 17 *S. infraimmaculata* breeding sites and nine *B. viridis* breeding sites. The AUC value for the training data was 0.814 and 0.769 for *S. infraimmaculata* and *B. viridis*, respectively indicating a good level of accuracy for the Maxent predictions. These results suggest that the models had relatively high predictive power. The jackknife tests indicated that when using the LPT rule the *S. infraimmaculata* model was significantly better than random with *P*-values below 0.005 but not significant for *B. viridis* (Table 2). However, jackknife test results show high success rates and statistical significance when using T10 for both *S. infraimmaculata* and *B. viridis*.

Table 3 Percent contribution of the selected predictor variables in Maxent model for *S. infraimmaculata* and *B. viridis* species

Variable	Percent contribution	
	S. infraimmaculata	*B. viridis*
Radiation	0	23
Wetness	0.1	1.6
Elevation	40	0
Soil	59.5	11.5
Distance to urban areas	0	64
Distance to forested areas	0.4	0

Evaluation of models and the importance of environmental predictor variables

Salamandra infraimmaculata occurrence was most strongly associated with elevation and soil type (Table 3). *B. viridis* occurrence was strongly associated with distance to urban areas and radiation but also influenced by soil type (Table 3). *S. infraimmaculata* was positively associated with elevation while *B. viridis* was negatively associated with distance to urban areas and radiation (Fig. 1). Both species preferred pale Rendzina soil type.

Maxent prediction for *S. infraimmaculata* pointed to the Central Carmel as the region of highest probability for the geographical range of the species (Fig. 2b). A close examination of Figure 2b shows areas delineated by elevation higher than 200 m and pale rendzina soil were suitable habitats. *B. viridis* highest probabilities (>0.6) were in the Central Carmel area (Fig. 2c). For descriptive proposes, we selected probability <0.2 to interpreted parts of the study area as unsuitable for the species. These Central Carmel areas are located in the Southwest of the Carmel area for *S. infraimmaculata* and characterized by elevation lower than 200 m and Terra-Rossa soil type. For *B. viridis*, low probability areas are located in the central part of Southern Mt. Carmel. These areas are characterized by Terra-Rossa soil type and they are relatively distant from urban areas.

Discussion

Maps of potential distribution are very important for developing management programs to protect endangered species (Gaston & Williams, 1996). Using maximum entropy niche modeling, we produced such maps for *S. infraimmaculata* and *B. viridis*. However, it is important to stress that model predictions using low numbers of occurrence sites should not be interpreted as predicting actual range of a species but

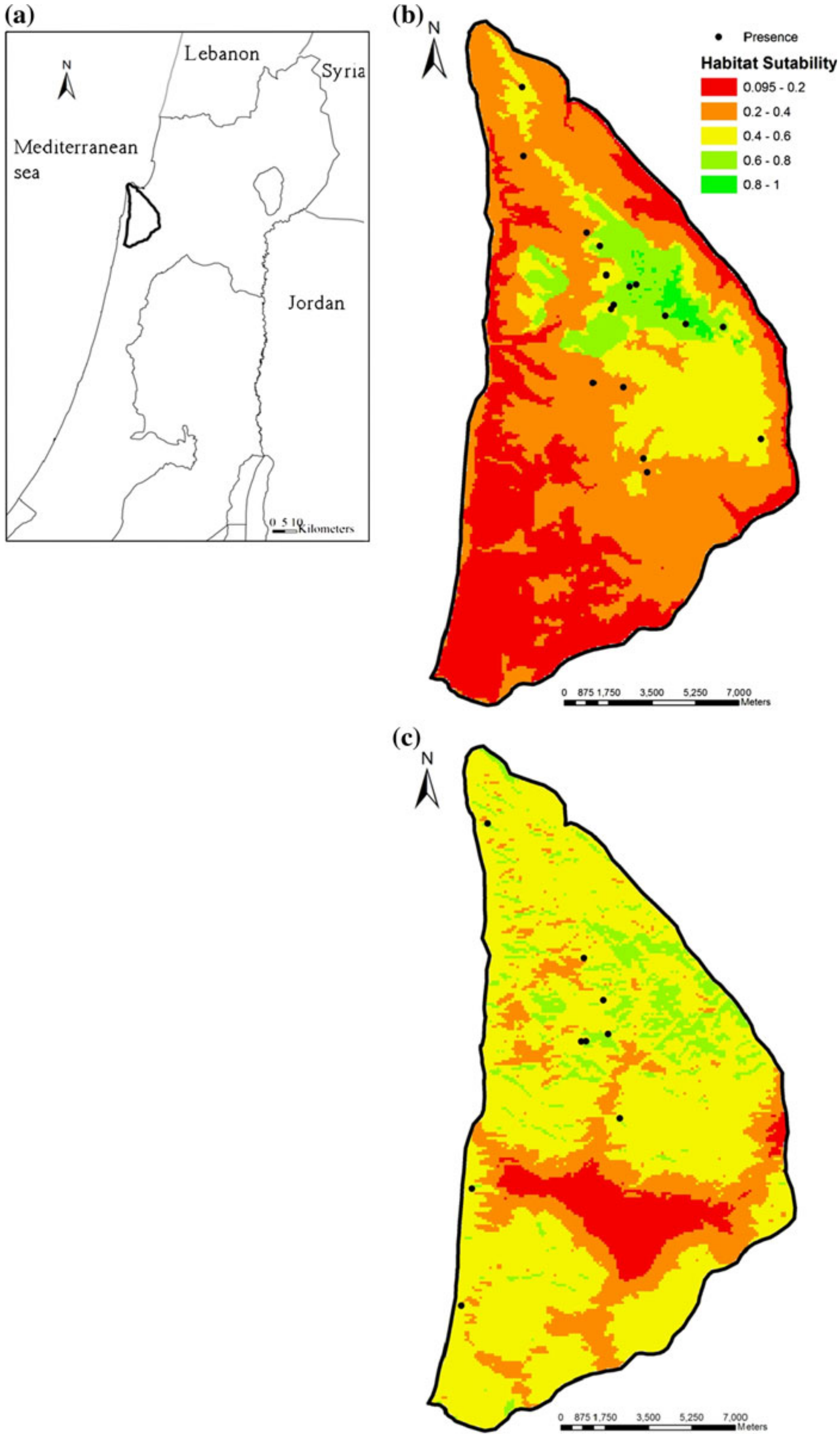

Fig. 2 Location of the study area in Israel (**a**). Predicted potential suitable habitat on Mt. Carmel for *S. infraimmaculata* (**b**) and *B. viridis* (**c**)

rather identifying regions characterized by similar environmental conditions to where the species is known to occur (Pearson et al., 2007). Thus, such models can be considered to represent only conservative potential distribution of a given species. This is because areas that have similar environmental conditions to those used for constructing the model will be ranked as suitable areas for the species. However, with a small number of sampling units, it is possible that the dataset will not capture all suitable environmental conditions. This study contributes relatively simple models for the endangered *S. infraimmaculata* and *B. viridis*. The models provide valuable information on the major environmental predictor variables affecting the distribution of both species. However, species distributions are not only constrained by landscape scale abiotic (e.g., soil and elevation) factors. Other factors than the ones we used may affect these species distributions and in this case study, these might include biotic interactions (e.g., Stav et al., 2010), dispersal limitations created by geographic barriers (e.g., Calsbeek et al., 2003), stochastic events (Pulliam, 2000), and abiotic characteristics of the breeding site (such as turbidity, temperature, and pH (e.g., Herrmann et al., 2005). It is also expected that factors such as temperature and precipitation would have a strong impact on *S. infraimmaculata* and *B. viridis* distribution. However, our study is relatively homogeneous with respect to these factors, thus elucidating much of the net effect of the predictor variables we used.

The model for *B. viridis* was not accurate when we used the LPT threshold. This approach can be interpreted ecologically as identifying pixels predicted as being at least as suitable as those where a species' presence has been recorded; it is thus conservative. The T10 approach is intended to be more liberal by incorporating a larger predicted area. Thus, our map of *B. viridis* suitable habitat can help to inform conservation biologists of areas that may have suitable habitat for that species. In contrast, the *S. infraimmaculata* suitability map had high and significant success rate at both LPT and T10 indicating that the predictive power of the model was good.

Soil was the environmental feature most important to explain the distribution of *S. infraimmaculata* and, to a lesser extent, that of *B. viridis*. Soil properties influence the distribution of many amphibian species (Diller & Wallace, 1999; Bradford et al., 2003; Dayton et al., 2004). Soils that drain quickly limit the duration that water is available for breeding and reduce a species' ability to dig into the soil (Hardy, 1945). In addition, soils that retain water for longer time are likely to be important for burrowing amphibians, as they provide moist refuge sites that prevent amphibians from desiccating (Shoemaker, 1988). For both *S. infraimmaculata* and *B. viridis*, pale Rendzina was found to be the preferred soil type. The association with this soil type probably reflects its superior ability to hold water. Terra-rossa soil covers the limestone and dolomite while Rendzina soil characterizes chalk and marl. Marly chalk bedrock layers affords high water-holding capacity (Schiller et al., 2010). Henkin et al. (1998) found that the amount of available water was greater in the Rendzina soil than in the Terra-Rossa soil. In addition, *S. infraimmaculata* were also associated with high elevation areas. All breeding sites in the Carmel Mountain range were above 200 m a.s.l. Known breeding sites in other regions in Israel are all above 200 m (Goldberg et al., 2007; Sinai I. *unpublished data*). In addition to soil type, *B. viridis* was negatively associated with distance to urban areas. *B. viridis* is a broad habitat generalist species (Nevo & Yang, 1979). Amphibian species that are habitat generalists or have relatively low dispersal requirements appear to have greater survival probabilities (Hamer & McDonnell, 2008). *B. viridis* is often encountered in human settlements including many urban centers (Ensabella et al., 2003; Kovács & István, 2010). These observations are consistent with our results showing that that *B. viridis* breeding sites were found close to villages.

Low solar radiation level was also found to be an important condition for *B. viridis*. The amount of solar radiation on the surface is dependent on the slope and aspect of the ground, and has been identified as an important factor in determining the ecological conditions at a site (Geiger, 1965; Oke, 1987). Several studies have noted the effect of slope and aspect in determining soil moisture, near-surface air, and soil temperature, and hence habitat choice of invertebrates in grassland habitats (Nevo, 1995; Weiss & Weiss, 1998; Davies et al., 2006). Desiccation is one of the primary factors that prevent amphibian larvae from reaching metamorphosis (Ryan, 2007). High temperature causes faster habitat desiccation and can thus have particularly large impacts on species that use ephemeral habitats (Blaustein & Schwartz, 2001; Sadeh et al., 2011).

Maximum entropy niche modeling provides a tool using only the presence data to predict potential habitat distributions of endangered species whose distributions have become highly limited. We provide two examples in the current study for the locally endangered *S. infraimmaculata* and *B. viridis*. The information produced during this study is highly relevant given the potential threats to these species habitat. The potential distribution maps for *S. infraimmaculata* and *B. viridis* and other endangered species can help in planning wetland use management around its existing populations, discover new populations, identify top-priority survey sites, or set priorities to restore its natural habitat for more effective conservation.

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