

Determining priority areas for an Endangered cold-adapted snake on warming mountaintops

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Abstract Spatial prioritization in systematic conservation planning has traditionally been developed for several to many species and/or habitats, and single-species applications are rare. We developed a novel spatial prioritization model based on accurate estimates of remotely-sensed data and maps of threats potentially affecting long-term species persistence. We used this approach to identify priority areas for the conservation of the Endangered Greek meadow viper *Vipera graeca*, a cold-adapted species inhabiting mountaintops in the Pindos Mountains of Greece and Albania. We transformed the mapped threats into nine variables to estimate conservation value: habitat suitability (climate suitability, habitat size, occupancy, vegetation suitability), climate change (future persistence, potential for altitudinal range shift) and land-use impact (habitat alteration, degradation, disturbance). We applied the *Zonation* systematic conservation planning tool with these conservation value variables as biodiversity features to rank the areas currently occupied by the species and to identify priority areas where the chances for population persistence are highest. We found that 90% of current habitats will become unsuitable by the 2080s and that conservation actions need to be implemented to avoid extinction as this is already a threatened species with a narrow ecological niche. If threats are appropriately quantified and translated into variables of conservation value, spatial conservation planning tools can successfully identify priority

areas for the conservation of single species. Our study demonstrates that spatial prioritization for single umbrella, flagship or keystone species is a promising approach for the conservation of species for which few data are available.

Keywords Climate change, habitat suitability, land use, protected area, range shift, reptile, spatial conservation planning, *Vipera graeca*

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Introduction

Biological diversity has experienced significant losses as a result of a number of factors that directly or indirectly affect species. Amphibians and reptiles are among the groups most affected (Böhm et al., 2013; Ceballos et al., 2015). Reptiles are specifically threatened by habitat loss, degradation and fragmentation, introduction of invasive species, pollution, pathogens and climate change, resulting in global population declines (Cox & Temple, 2009).

Global climate change plays a key role in the biodiversity crisis (Butchart et al., 2010), as it causes a redistribution of biodiversity patterns (Pecl et al., 2017). Many species are predicted to shift their range, mostly towards the poles or higher altitudes (Hickling et al., 2006; Chen et al., 2011). Species adapted to high altitude habitats are thus particularly threatened by climate change because they often have low dispersal ability, a high level of habitat specialization and fragmented distributions, all of which predict low probability of range shift (Davies et al., 2004). Ectothermic animals such as reptiles are further threatened by climate change because of their sensitivity to changes in the thermal landscape and low dispersal ability (Sinervo et al., 2010). Mountain-dwelling species usually escape the changing thermal landscape by shifting their distributions to higher altitudes (Haines et al., 2017) but this is possible only if the local topography allows this (Şekercioğlu et al., 2008).

Meadow vipers (*Vipera ursinii* complex) are among the most threatened reptiles of Europe. The Greek meadow viper *Vipera graeca*, a small venomous snake endemic to the Pindos mountain range of Greece and Albania that has recently been recognized as a separate species (Mizsei et al., 2017), is the least known meadow viper in Europe

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and is categorized as Endangered on the IUCN Red List (Mizsei et al., 2018). The species has only 17 known populations, inhabiting alpine–subalpine meadows above 1,600 m on isolated mountaintops (Mizsei et al., 2016). The occupied habitats are the highest and coldest in the region; as the species is adapted to cold environments it is sensitive to climate change. These alpine habitats are threatened by overgrazing and habitat degradation, which simplify vegetation structure and reduce cover against potential predators. The species is strictly insectivorous, specializing on bush crickets and grasshoppers (Mizsei et al., 2019), and thus it is vulnerable to changes in its primary prey resource caused by land use. Shepherds are known to intentionally kill these snakes, which are held responsible for 1–4% of lethal bites to sheep annually in Albania (E. Mizsei, unpubl. data).

Here we identify priority areas that could facilitate the long-term persistence of *V. graeca*. We performed single species spatial prioritization to identify areas based on conservation value attributes of the currently suitable landscape. We aimed to identify any populations likely to disappear by the 2080s and any populations likely to be strongholds where the species could benefit from targeted management and conservation. To provide guidelines for conservation, we studied the overlap between priority areas and protected areas and explored the interrelationships of the conservation value variables to identify opportunities for potential interventions.

Methods

Approach We used spatial prioritization, an approach rarely applied to single species (Adam-Hosking et al., 2015), which is based on quantifying known threats and transforming them into variables describing conservation value based on current conditions. The process consisted of (1) delimiting the study area, (2) collecting and processing data on threats to derive conservation value variables, (3) spatial prioritization of the study area based on the conservation value variables, and (4) evaluation of overlaps with current protected areas and analysis of any interrelationships between conservation value variables (Fig. 1).

Habitat suitability modelling to define the study area We defined our study area to include all *V. graeca* habitats identified by a habitat suitability model (Fig. 2). The model was constructed using 351 records of *V. graeca*, 83% of which were taken from our previous publications (Mizsei et al., 2016, 2017) and 17% of which were new, unpublished records. Our dataset contained all known localities of *V. graeca*, and also included absence data from 31 localities (55 records) predicted in an earlier habitat suitability model (Mizsei et al., 2016), and where the species has not

been found despite extensive searches. To account for potential spatial biases in sampling effort among sites, we re-sampled the presence dataset to obtain a spatially balanced subset of 71 presence records, which represented all known populations (Fig. 2). We used BIOCLIM climate variables, which have been successfully used to model the distribution of several European reptiles, including vipers (Scali et al., 2011; Martínez-Freiria, 2015; Mizsei et al., 2016). To ensure compatibility with our previous work (Mizsei et al., 2016), we used the same set of predictors: annual mean temperature (BIO1), temperature seasonality (BIO4), annual precipitation (BIO12) and precipitation seasonality (BIO15). These variables had high predictive performance and low intercorrelations ($r < 0.7$). We obtained these variables for current climatic conditions (mean of 1950–2000) from the *WorldClim 1.4* database at 30 arc seconds resolution (Hijmans et al., 2005). We generated the habitat suitability model using ensemble modelling (Thuiller et al., 2012) in the *BIOMOD2* package in *R 3.3.0* (R Core Team, 2016). We used two linear model algorithms (Generalized Linear Models, GLM; Generalized Additive Models, GAM) and three machine learning algorithms (Artificial Neural Networks, ANN; Random Forest, RF; Maximum Entropy, MaxEnt). Default settings were used to build the models (Thuiller et al., 2012). To increase model accuracy we generated 10 datasets of pseudo-absences, which included real absence data and random points at least 5 km from the presence localities (a total of 10,000 points per dataset). We ran 10 replicates with each of the five modelling algorithms for the 10 pseudo-absence datasets, which resulted in 500 habitat suitability model replicates. In each model replicate we randomly divided the presence data into training (70%) and testing subsets (30%). We used the four BIOCLIM variables as predictors. We scored all individual model replicates by the true skill statistic (TSS; Allouche et al., 2006), retaining only models with $TSS > 0.95$. This filtering resulted in 275 models, which always correctly classified the testing subset and that were used to produce ensemble projections by consensus (i.e. raster cells predicted suitable in each of the 275 models). Finally, we generated a binary suitability map using the ensemble projection of the best models and defined the resulting patches as the study area for the analysis (Fig. 2).

Variables for estimating conservation value We used nine environmental variables of three classes to estimate the conservation value of planning units (1 ha raster cells) over the entire study area: (1) habitat suitability: climate suitability, habitat size, habitat occupancy, vegetation suitability; (2) climate change: future persistence, potential for altitudinal range shift, (3) land-use impact: habitat alteration, habitat degradation, disturbance (Fig. 1). Each variable was standardized to 0–1, where 0 represented minimum and 1 represented maximum conservation value.

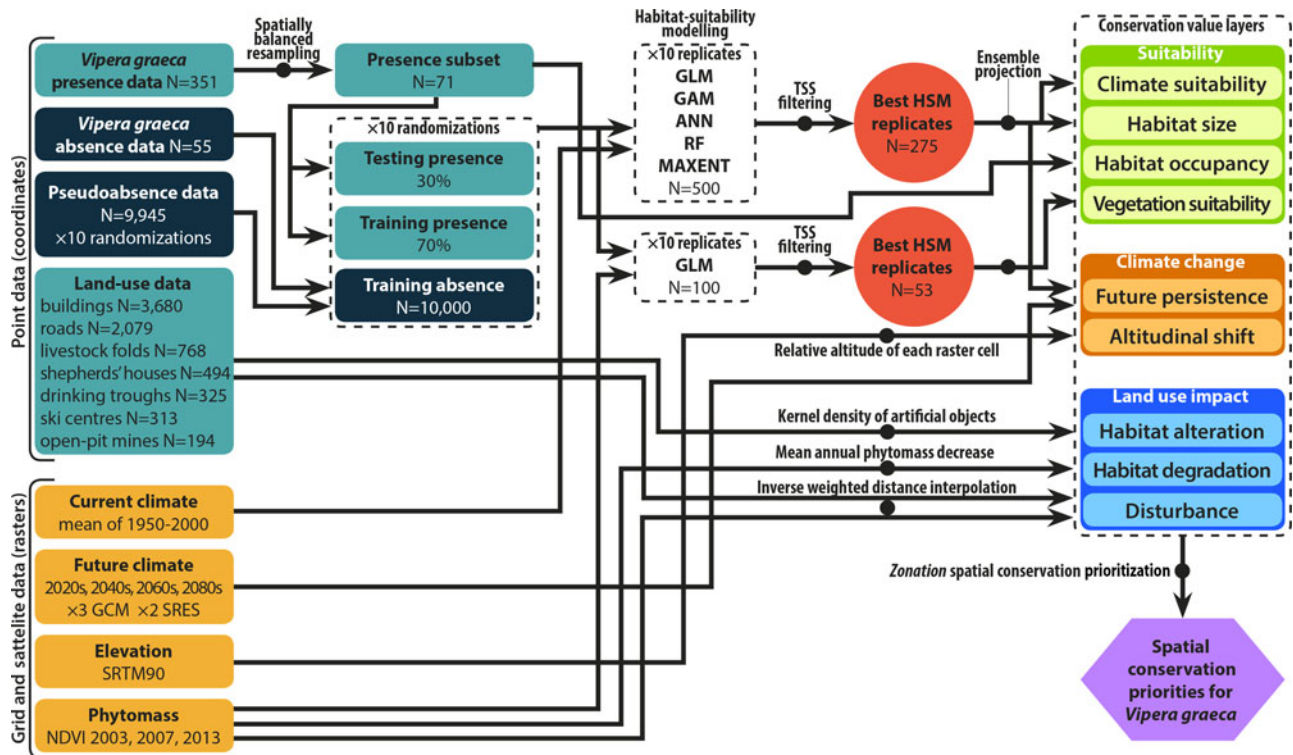


FIG. 1 Flow chart of data processing and conservation value layer construction and analysis. For abbreviations, see Methods.

Climate suitability Annual mean temperature (BIO1) and precipitation seasonality (BIO15) were the most important climate variables in the habitat suitability models, and thus we selected these variables as the primary predictors for the distribution of *V. graeca*. The response curves of predictors showed that *V. graeca* preferred habitats where the annual mean temperature was $< 8^{\circ}\text{C}$, temperature seasonality was less than average, and precipitation was high and seasonal across the coldest quarter (Fig. 2). We produced an ensemble projection of habitat suitability model replicates (TSS > 0.95) for current weather conditions and used the suitability values to represent climate suitability of sites downscaled from 30 arc seconds (c. 720×920 m) to a cell size of 100×100 m using bilinear interpolation.

Habitat size We calculated habitat size based on the area of suitable patches resulting from the species distribution model built to define the study area. We transformed this raster to polygons of climatically suitable habitats, and then calculated the area of each polygon. We then rasterized the polygons so that each cell inside the former polygons had the value of patch area and rescaled the area values to 0–1.

Habitat occupancy To assess habitat occupancy we visited all locations identified as climatically suitable for *V. graeca* (Mizsei et al., 2016), carrying out 32 surveys in Albania and

Greece during 2010–2016. We spent multiple days at each location, with a search effort adequate to infer *V. graeca* presence or absence (Mizsei et al., 2016). To determine habitat occupancy we used data for 351 individuals found in our surveys. We transformed the study area raster to polygons (climatically suitable patches) and allocated 0 (absence) or 1 (presence) to each patch. The polygons were then rasterized, with all cells within a patch receiving either a 0 (unoccupied patches) or 1 (occupied patches). This ensured higher scores in the prioritization for sites where *V. graeca* populations are known to be present.

Vegetation suitability We modelled the spatial distribution of suitable vegetation using the Normalized Difference Vegetation Index (NDVI), which quantifies the amount of phytomass on the surface from satellite-based imagery data. Because the availability of these data depends on satellite activity, we employed data from three Landsat sensors: Landsat 5 (TM; Thematic Mapper) from 2003, Landsat 7 (ETM+; Enhanced Thematic Mapper Plus) from 2007 and Landsat 8 (OLI; Operational Land Imager) from 2013. We used a 30×30 m spatial resolution and ArcGIS 10.2 (Esri, Redlands, USA) to pre-process satellite data. We built a habitat suitability model similar to that built for climate suitability but using one response variable (NDVI) and only the GLM algorithm (10 pseudo-absence datasets with 10 model replicates) with the BIOMOD2 package, as described above. We then projected the consensus model

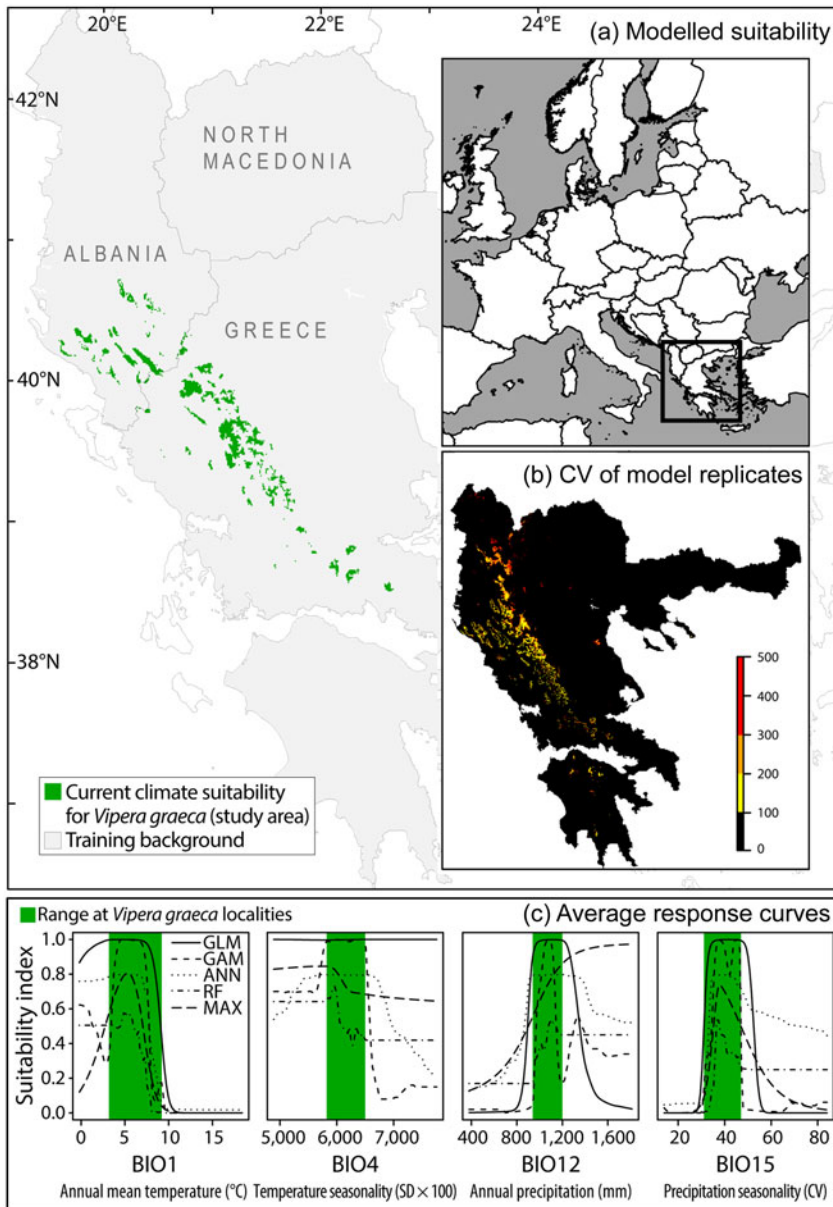


FIG. 2 (a) Area identified by the climate habitat suitability model for *V. graeca* in the western Balkans, (b) coefficient of variation (CV) of habitat suitability model replicates, and (c) average response curves of modelling algorithms for each predictor variable of the model, with range of values measured at *V. graeca* presence locations.

(based on 53 models, TSS > 0.95) and used the estimated suitability values to represent vegetation suitability of sites upscaled to the spatial resolution used in this study (1 ha).

Future persistence in the face of climate change We used scenario modelling to predict areas with high population persistence under future climate change. Data on future climate were obtained from the Global Circulation Model (GCM) database (CCAFS, 2016), which is projected based on the Fourth Assessment Report of the Intergovernmental Panel on Climate Change and on the CMIP3 protocol (IPCC, 2013). Future climate data have the same resolution as contemporary climate variables, and we used three frequently used GCMs available for use with BIOCLIM variables: CSIRO Mk 3 (Gordon et al., 2002), MIROC 3.2 (Watanabe et al., 2011) and HadCM 3 (Collins et al., 2001).

To account for the uncertainty in modelling future climatic patterns, we modelled climate suitability for *V. graeca* under two scenarios based on climate data from the Special Reports on Emissions Scenarios (SRES; Carter, 2007): under scenario A1B (a pessimistic scenario), 1.4–6.4 °C global change in mean temperature is expected, and under scenario B1 (an optimistic scenario), the expected change is 1.1–2.9 °C. We projected the most reliable (TSS > 0.95) habitat suitability model replicates (N = 275) for future climate in six combinations (three GCMs, two SRES) for the decades beginning in 2020, 2040, 2060 and 2080, applying the *BIOMOD_EnsembleForecasting* function of the *BIOMOD2* package (Thuiller et al., 2012). For each decade and SRES we calculated the mean suitability of the three GCMs. Finally, we calculated a mean of each SRES from all the decades as a value of persistence of suitable sites.

Potential for altitudinal range shift Upward altitudinal shifts of species' ranges are a common response to climate change but are limited by mountain height. We considered this by calculating a variable describing potential altitudinal shift based on elevation data from the Shuttle Radar Topography Mission (Jarvis et al., 2008) at a resolution of 30×30 m. We calculated the ratio of the elevation of the highest site in the species distribution model patch and the elevation of individual raster cells using the *calc* function from the *R* package *raster* (Hijmans, 2016) and assigned this value to characterize the opportunity for altitudinal shift for each raster cell.

Habitat alteration by humans We inferred habitat alteration from the presence and density of artificial objects in the landscape (Plieninger, 2006). We identified 3,680 objects using satellite imagery from *Google Earth* (Google, Mountain View, USA) from 2017. These were mainly roads (2,079), livestock folds (768), shepherds' buildings (494), drinking troughs for livestock (325), other buildings (e.g. ski resort infrastructure, 313) and open-pit mines (194). We performed kernel smoothing to estimate spatial density of these objects using the *bkd2D* function of the *R* package *Kernsmooth* (Wand, 2015). Conservation values were specified to be inversely related to the density of artificial objects in the raster cells.

Habitat degradation by grazing Because grazing by livestock (sheep and cattle) is a major driver of habitat quality in *V. graeca* habitats (Mizsei et al., 2016), we estimated the degree of habitat degradation by quantifying grazing pressure from the mean annual change in phytomass. We used two seasonal intervals: (1) after snowmelt but before the start of livestock grazing (summer, 1–15 July) and (2) at the end of grazing but before snowfall (autumn, 1–15 October), for 2003, 2007 and 2013. We estimated grazing pressure by changes in phytomass between summer and autumn, as quantified by NDVI values taken before and after the livestock grazing period. We estimated the phytomass decrease from summer to autumn by subtracting the summer NDVI values from the autumn values. We then upsampled the 30×30 m resolution to 100×100 m using the *resample* function of the *R* package *raster* (Hijmans, 2016).

Disturbance by traditional grazing Grazing pressure is not homogeneously distributed in these high mountain landscapes and is concentrated near livestock folds. To account for this spatial heterogeneity we calculated a proxy for disturbance by livestock grazing (Blanco et al., 2008). We selected 768 livestock folds from the artificial objects dataset and weighted them by phytomass decrease values. We then performed an inverse weighted distance interpolation

using the spatial linear model fit of grazing pressure values over distance from the coordinates of the folds using the *R* packages *gstat* and *spatstat* (Baddeley et al., 2015).

Spatial prioritization We used the *Zonation* systematic conservation planning tool for spatial prioritization, with our raster data layers as inputs, because this tool primarily uses raster data (Lehtomäki & Moilanen, 2013). We performed the prioritization separately for both future climate scenarios (A1B, B1). We used the *R* package *rzonation* (Morris, 2016), which runs *Zonation 1.0* (Moilanen, 2007). Finally, we calculated the mean conservation value of each cell, to compare the results of the spatial priorities.

Evaluation of current protection and opportunities for future conservation We used the high-priority raster cell networks obtained by the spatial prioritization to evaluate the degree of overlap with current protected areas. We aimed to identify areas where current protection ensures the long-term persistence of *V. graeca* populations and areas where further conservation actions such as protection, habitat management and/or restoration are necessary to ensure long-term persistence. We first converted the high-priority networks identified in the spatial prioritization into polygons and then intersected them with polygons of current protected areas. Spatial data on current protected areas were obtained from the World Database of Protected Areas (UNEP-WCMC, 2018), which included areas protected by both national and European Union laws (Natura 2000 sites). Finally, we examined the interrelationships of the conservation value variables using a cluster analysis, to identify closely related variables that can identify targets for future conservation.

Results

Spatial priorities for long-term persistence The consensus of *Zonation* solutions for the two future climate scenarios identified eight separate mountain ranges as high priority areas (priority rank > 0.8 ; Fig. 3). However, only three of these mountain ranges are known to hold at least 10 km^2 of contiguous suitable habitat that will also be suitable by the 2080s (Nemercke in Albania, Tymfi and the Lakmos-Tzoumerka chain in Greece) and can thus be considered as key areas for the persistence of *V. graeca* (Fig. 4). Other known populations have high probability of extinction in the future, mainly as a result of climate change. Some mountain ranges that are not known to hold *V. graeca* populations are high-priority areas (Fig. 3). The *Zonation* solutions for both climate scenarios protected a larger area than the sum of the areas with high mean conservation value (Fig. 3). This was because core sites with high spatial

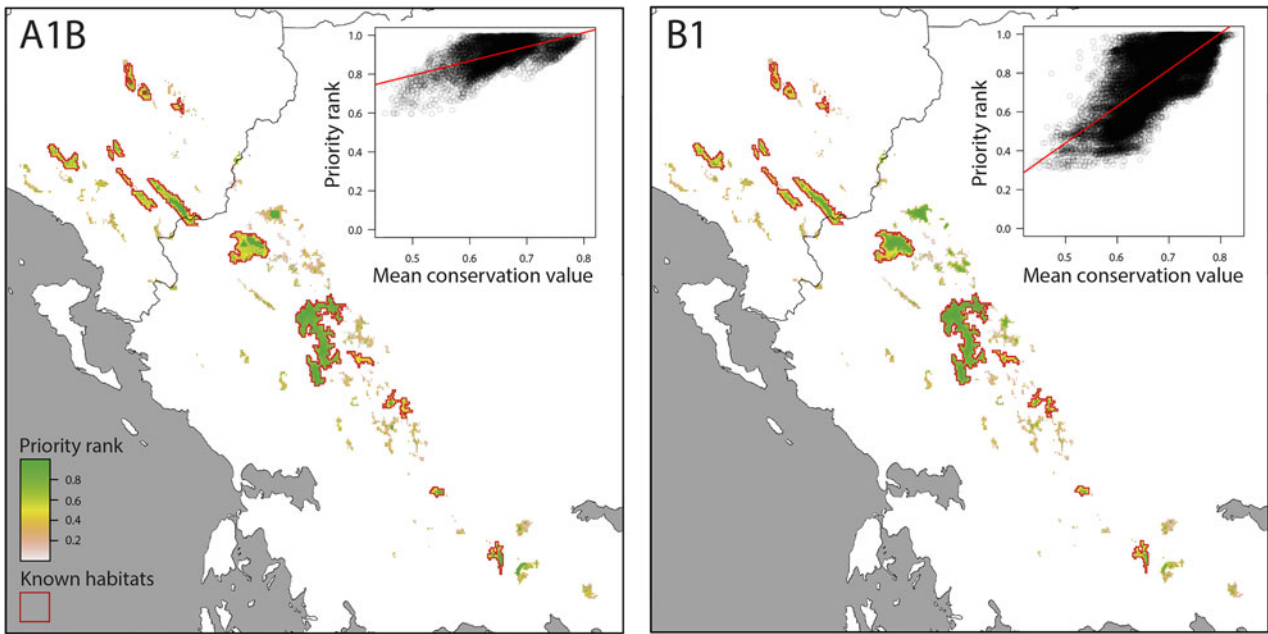


FIG. 3 Spatial conservation priorities for pessimistic (A1B) and optimistic (B1) future climate scenarios (main panels) and linear regression of priority rank over mean conservation value per cell (insets).

compactness but with a number of low-ranking cells were selected, and marginal and low-connectivity cells were discarded in the prioritization (Fig. 3). Priority rank increased with conservation value of the cells in both scenarios (Fig. 4; linear regression, $b = 0.732$, $P < 0.0001$ for A1B; $b = 1.883$, $P < 0.0001$ for B1).

Current protection Protected areas covered 13.3% of the area known to hold *V. graeca* populations in Albania and 90.6% in Greece (Fig. 4). Under the A1B scenario, the total area of high-priority cells covered by protected areas was 242.7 km², or 81.8% of the high-priority areas that are protected, but none of the high priority areas were located

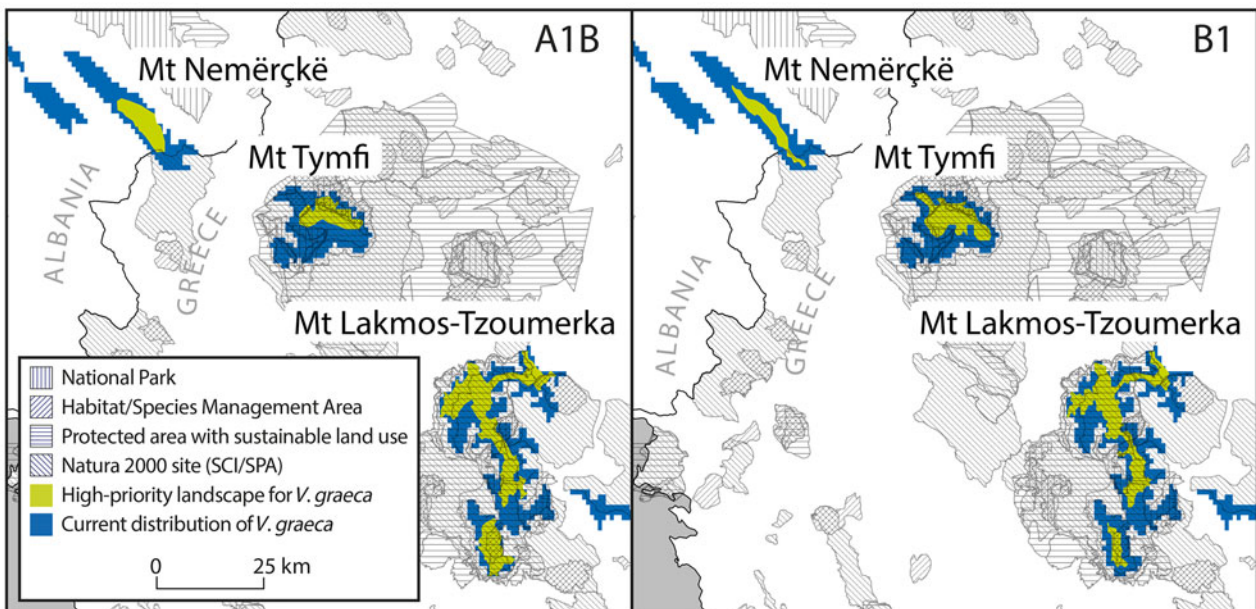


FIG. 4 Key areas for the persistence of *V. graeca* populations and their inclusion in protected areas in pessimistic (A1B) and optimistic (B1) future climate scenarios. SCI, Site of community importance (EU Natura 2000 Habitats Directive site); SPA, Special protection area (EU Natura 2000 Birds Directive site).

TABLE 1 Areas of high-priority landscapes predicted by spatial prioritization under two climate scenarios (A1B, B2) until 2080 for the conservation of *Vipera graeca* and that are covered by various categories of the current network of protected areas.

Protected area type description	Protected area coverage (ha)	
	A1B	B2
National park (IUCN type II)	1,959.5	2,039.9
Habitat/Species management area (IUCN type IV)	4,133.2	3,154.7
Protected area with sustainable use of natural resources (IUCN type VI)	35,471.8	31,356.4
Site of community importance (EU Natura 2000 Habitats Directive site)	16,881.4	13,359.7
Special protection area (EU Natura 2000 Birds Directive site)	22,381.3	20,809.5

in protected areas in Albania and all high priority areas were in protected areas in Greece (Fig. 4). Under the B1 scenario the total protected high priority area was 221.2 km² or 83.5% of all high priority areas, all of which were in Greece (Fig. 4, Table 1).

Interrelationships of conservation value variables Cluster analysis revealed four clusters of conservation value variables (Fig. 5). Habitat alteration was mostly independent of other variables. Vegetation suitability was clustered with disturbance and habitat degradation, and climate suitability was related to habitat size. Population persistence was closely related to the opportunity of altitudinal shift ($r = 0.64$, $r = 0.73$ for A1B and B1, respectively). No site had maximum conservation value for all variables.

Discussion

Our study provides four main results. Firstly, the modelling of future climatic conditions showed a significant 81–90% reduction in the area of habitats suitable for *V. graeca* by the end of the 2080s. Secondly, current protection appears adequate for the persistence of the species in Greece but not in Albania. Thirdly, conservation efforts are most likely to

succeed if they target habitat alteration, degradation and disturbance as these have similar effects and the other threats are not easy to address at local scales (Fig. 5). Fourthly, our approach shows that threats can be mapped and used to estimate the conservation value of areas, which can then be used in spatial conservation prioritization for single species.

Expected impact of climate change

Our analyses support the previous results of Mizsei et al. (2016) showing that the distribution of *V. graeca* is limited to the coldest and highest elevation habitats in the Southern Balkans. However, based on future climate scenarios, there will not be any remaining suitable habitats (i.e. with mean annual temperature < 10 °C) in the Southern Balkans by 2100 within the current range of the species (Lelieveld et al., 2012). Thus, the probability of the extinction of *V. graeca* is high, as unassisted long-distance dispersal to other high elevation mountains that may be suitable in the future is not possible. Besides increases in temperature, substantial aridification is expected throughout the Mediterranean basin (Foufopoulos & Ives, 1999). Precipitation quantity and frequency are predicted to decrease and the number of dry days is predicted to increase considerably by 2100 (Lelieveld et al., 2012; Mariotti et al., 2015). For ectotherms,

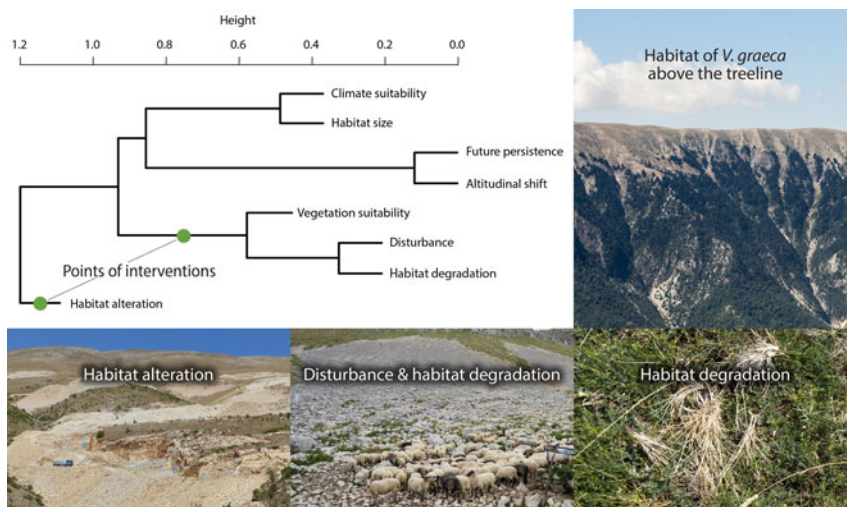


FIG. 5 Agglomerative hierarchical clustering of conservation value layers and illustrations of the habitat of *V. graeca* and the most important threats. Conservation management actions should be targeted at the points of interventions. Note that the binary habitat occupancy variable is not included.

a change in the thermal landscape will probably reduce the time available for daily activity, which will affect foraging, feeding and breeding success (Walther et al., 2002). For a cold-adapted species such as *V. graeca*, these changes will have an impact on the persistence of the species as it already occupies a narrow niche in a harsh environment.

Novelties and limitations in estimating land use impact

Our approach involved two rarely used methods. Our layer for habitat degradation characterized grazing pressure by the decrease in phytomass between spring and autumn, which adequately represents grazing pressure in grasslands (Todd et al., 1998; Senay & Elliott, 2000; Kawamura et al., 2005). We developed this further by spatial interpolation of the distribution of livestock folds weighted by phytomass decrease, which is a novel approach to estimating the intensity of land use or the degree of disturbance. Further studies are needed to calibrate this type of derived variable accurately with on-site measurements or experiments.

One potential limitation of our study is that land-use intensity is probably higher at the lower elevations of *V. graeca* habitats (1,500–1,800 m) than at higher elevations. Lower elevations are easier to access for people and grazing livestock, snow melts are earlier, and thus the grazing season is longer than at higher elevations. Therefore it is possible that *V. graeca* may already have disappeared from lower elevations as a result of anthropogenic impacts, and that our suitability models based on current conditions are biased to colder climates and/or higher elevations. This is unlikely, however, because lower elevations are often secondary grasslands established in previously wooded areas below the former treeline, as evidenced by wooded areas remaining on slopes too steep for grazing livestock (Fig. 5). It is therefore unlikely that these lower elevation areas were formerly suitable for *V. graeca*. Moreover, overgrazing also occurs at higher elevations, where the species is present, albeit in lower abundance. Nevertheless, because the species was discovered only in the 1980s there are no historical data to test temporal patterns in habitat occupancy.

Prioritization for single species

Systematic conservation planning techniques were developed for multiple species (Lehtomäki & Moilanen, 2013) and have only recently been applied for single species (Adam-Hosking et al., 2015). Single species conservation planning follows the same protocol but ranks sites according to the spatial distribution of threat factors (or conservation value), and/or the cost of protection (Adams-Hosking et al., 2015; Nori et al., 2016). The scarcity of systematic conservation planning for single species is probably a result of the primary importance of biodiversity protection as opposed

to species protection. Our study shows that the approach can provide information of value for the conservation of umbrella, flagship or keystone species.

Recommendations for the conservation of *V. graeca*

Our study shows that *V. graeca* habitats may face significant losses or further fragmentation up to 2089, although some populations in a few contiguous habitats are predicted to persist. These results suggest that conservation should focus on sites of high importance by improving habitat quality, reducing disturbance and degradation, effectively protecting the species, educating local stakeholders and continuing to monitor the populations.

Raising awareness and involvement of local communities is central to any conservation action, to ensure its success, and to establish sustainable land use (Adele et al., 2015). Research by the Greek Meadow Viper Working Group on human–wildlife conflict resulting from sheep mortality as a result of snake bites is already underway and is trying to identify ways to involve local communities. This project has already recommended that shepherds follow two guidelines for grazing livestock in *V. graeca* habitats: avoid grazing on south-eastern slopes where vipers are more abundant, or, if the shepherd must utilize these slopes, do so between 11.00–15.00, when vipers usually shelter from the midday heat.

Our findings warrant slightly different recommendations for sustainable land use in the two countries. In Albania grazing pressure needs to be reduced to achieve an improved, more natural vegetation structure in meadows. In Greece a shift from cattle grazing to sheep grazing is required. Cattle grazing has a stronger and more negative impact because cattle uproot vegetation, which is detrimental to both the top soil layer and vegetation. Eradication of fescue tussocks (Fig. 5) has already changed the vegetation, resulting in the homogenization of microhabitats: there are fewer structures that provide shelter and shade for snakes, which in turn increases predation by birds of prey and reduces the abundance of the viper's Orthopteran prey (Lemonnier-Darcemont et al., 2018).

Along with habitat conservation, we recommend the launch of an ex situ breeding programme, similar to that for the threatened Hungarian meadow viper *Vipera ursinii rakosiensis* (Péchy et al., 2015), to help reinforce populations that are suffering from the symptoms of an extinction vortex. We suggest that a combination of ex situ and in situ conservation plans and continued research on the ecology and population genetics of *V. graeca* in high priority areas are necessary to ensure persistence. Further research, in conjunction with local and governmental support, is key for the development of a species conservation programme that will ensure the long-term survival of this Endangered, cold-adapted species trapped on mountaintops in the warming Mediterranean basin.

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Author contributions Study design: EM, MS, SL; collection and processing of spatial data: EM, LS, ZB, KM; collection of field data: EM, MS, SAR, MD, ZB, SL, YI; data analysis: EM, ZV; writing: EM, MS, SAR; contribution to writing: all authors.

Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards. Individual snakes were not collected or harmed in any way in the course of this study.

Data accessibility The R script of conservation value layers and the produced ASCII files are available as supplementary material. Occurrence data are not provided, to protect the species, but are available for bona fide researchers upon request from the corresponding author.

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