TITLE: **How the South was won: current and potential range expansion of the crested porcupine in Southern Italy**

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RUNNING TITLE: Range expansion of the crested porcupine

Abstract

Since the 1970s, the crested porcupine has expanded his range into Northern regions in Italy, where it was historically absent, helped by climatic change, legal protection, and forest re-expansion. In the last ten years, a remarkable range expansion has also been observed in the southernmost Italian regions. The aim of our work is to summarize the distribution of this species in Southern Italy and assess potential range expansion under multiple future scenarios of global warming. We collected 1783 occurrence records of the crested porcupine through *ad-hoc* web pages, online platforms, and some data directly collected by authors (N = 976 occurrences between 1998 and 2008; N = 807 between 2008 and 2019). A remarkable increase in occurrences occurred in Lucania, Campania, and Apulia regions, in Southern Italy, mostly along the coastlines. Species distribution models showed that porcupine presence is associated with warm temperatures and an intermediate level of precipitation. Although land-cover showed lower importance compared to climate, the species was positively associated with forests and negatively associated with agricultural, grasslands and shrublands, and urban landscapes. Model projections suggested that future global warming can improve suitability for porcupines in the Apennine ridge, including the Southern Calabria and the Aspromonte National Park. However, increase in drought and urbanization may reduce the habitat suitability for the crested porcupine in the Salento peninsula, limiting the success of the range expansion by this large rodent, and in Eastern Calabria, wih possible range contractions along the Tyrrhenian coast.

Keywords. Global warming; *Hystrix cristata*; Southern Italy; range expansion; range reassessment.

Introduction

Climate and land-use changes are important factors shaping species distribution and diversity (Burns et al. 2003; Long et al. 2005; Lundy et al. 2010; Reis et al. 2018). Notably, the ongoing global warming is bringing thermophilous species to reach higher latitudes (Albano et al. 2010; Winwood-Smith et al. 2015; Ancillotto et al. 2016). Moreover, re-expansion of woodlands due to human urbanization – together with species legal protection – helped many forest animals to reach new areas, where historically absent or where they were recently extinct (Gainzarain and Fernàndez-Garcìa 2013; Escribano-Avila et al. 2014).

In this context, the crested porcupine *Hystrix cristata* (Mammalia: Rodentia) represents a paradigmatic case (Mori et al. 2013). Before 1970, this rodent was present in Italy only in Central-Southern regions on the Tyrrhenian coast, and in the Southern areas of the Adriatic coast (Toschi 1965). Climatic change and agricultural abandonment promoted the re-expansion of woodlands, which represent a paramount habitat for the crested porcupine, particularly for denning (Monetti et al. 2005; Mori et al. 2018). Furthermore, legal protection (National Italian Law n. 968/1977, Annex II of the Bern Convention in 1979, Annex IV of the Habitat Directive 1992/43/EEC, and National Italian Law n. 157/1992) probably reduced killing events towards this species (Mori et al. 2013). Therefore, despite its limited dispersal abilities, the crested porcupine almost doubled its Italian distribution range since the 1970s (Mori et al. 2018; Mori and

Fattorini 2019). The porcupine first crossed the Apennines from the Tyrrhenian coast in the west to the Marche region in the east, then expanded to the North reaching the northernmost regions, including Piedmont, Veneto, and Trentino Alto-Adige (Mori et al. 2013; Mori and Brugnoli 2019). Only three human-mediated colonization events are known to have occurred in Sardinia, Western Liguria, and the province of Varese (Lombardy region) (Balletto 1977; Mori et al. 2013). In the Elba island, where several introduction events have been carried out in the past, the current status of the species is uncertain (Vecchio et al. 2018). Recent species distribution models showed that northern Italy is suitable for the species establishment, mostly in Central and Western parts of the Po valley (Mori et al. 2013, 2018).

Despite the species is also expanding in Southern Italy (Varuzza et al. 2019), less attention has been provided to this area. In the Calabria region, the porcupine is widely distributed north to the 39^{th} parallel (Mori et al. 2013). Conversely, in the Apulia region, the last records in the Gargano promontory (Northern Apulia) date back to the 1990s, and the presence of crested porcupine in the rest of the region was reported to be scarce and irregular in the first decade of 2000s (Mori et al. 2013). In 2013, the Red List of Mammals of Campania reported the crested porcupine as "Near Threatened" in this region (Fraissinet and Russo 2013), with populations only occurring in the northernmost part of the region, i.e. in the Province of Caserta, while being extinct elsewhere (Caputo 1989; Picariello et al. 1999; Maio et al. 2000). In the Lucania region, most records occurred in the Matera province, whereas scattered presences were recorded towards the westernmost area (province of Potenza: Amori et al. 2008; Mori et al. 2013). Given the peculiar morphology and the large size of the crested porcupine, the expansion in new areas by this species is frequently documented by local newspapers and photos of road-killed individuals posted on social networks, which helps the reconstruction of its range expansion (cf. Mori et al. 2019). Furthermore, because this mammal is a species of European conservation concern, updated monitoring of its distribution range is constantly required (Stoch and Genovesi 2016).

The aim of this work is to update the distribution range of the crested porcupine in Southern Italy, where range expansion occurred since 2010, and to identify potential areas of range expansion. We used Species Distribution Models (hereafter, SDM) to (i) assess the role of climatic and land-cover variables on the changes in the Italian distribution of this species including its future range expansion, and to (ii) identify areas of potential occurrence and range expansion in the future, under different scenarios of greenhouse gas concentration (Representative Concentration Pathway, RCP). We predicted that, given its climatic and geographic characteristics, Southern Italy now hosts broad areas where the porcupine can expand its range. Given the importance of wooded and concealed habitats for porcupines, we also predicted that open areas (including farmlands and fallows) and human settlements, as well as increasing drought, would limit its future range expansion.

Materials and methods

Collection of occurrences

Available occurrences of crested porcupines from Apulia, Lucania, and Campania regions were obtained from (i) published works (Mori et al. 2013, considered as the time 0 for the range expansion in Southern Italy; Varuzza et al. 2019), (ii) the citizen-science platform iNaturalist (validated data on the project on Italian Mammals: https://www.inaturalist.org/projects/mammiferi-d-italia Accessed on 10th October 2019), (iii) reports, videos, and photos posted on social networks (Facebook and Instagram) and (iv) private datasets of some of the authors. Not validated videos and pictures on citizen-science platforms underwent a blind identification procedure by the authors and doubtful records were discarded. In the absence of photos, records were considered as reliable whenever forwarded by professional zoologists. Further occurrences were collected by three authors (RB, GC, and PV) through camera trapping. Then, we filled a dataset including coordinates, observation date, and altitude for each record.

Climatic and land-cover data

Current climatic conditions were retrieved from the CHELSA monthly time-series dataset, version 1.2 (http://chelsa-climate.org/; Karger et al. 2017a; Karger et al. 2017b). From this dataset, we obtained two sets of maps including annual mean temperature and total annual precipitation at 30 × 30 arc seconds resolution (~1 km). The first set included the average climatic conditions between 1998 and 2008, whereas the second set included average climatic conditions between 2009 and 2013 (2013 is the last year available in this dataset).

Land-cover data were retrieved from the CORINE Land Cover dataset (https://land.copernicus.eu/pan-european/corine-land-cover) and our analyses used three maps representing the land cover in 2006, 2012, and 2018. Each map was aggregated from a resolution of 100 × 100 m to a resolution of 30 × 30 arc seconds and, for each cell, we calculated the percentage cover of four different variables: agricultural cover, urban cover, forest cover, and cover of open natural vegetation (grasslands and shrublands).

Species distribution models

Species distribution models were built with Maxent, version 3.4.1 (Phillips et al. 2017), which proved to be useful to predict range shifts and expansions (e.g. Elith et al. 2010; Ficetola et al. 2010; Falaschi et al. 2018). For all the models, we used six environmental variables describing climate and land-cover: annual mean temperature, annual precipitations, agricultural cover, urban cover, forest cover, and cover of open natural vegetation. Furthermore, because easily accessible areas can be overrepresented, we added a map representing the density of roads as a bias file to sample background points (Phillips et al. 2009; Kramer-Schadt et al. 2013; Ramellini et al. 2020). We ran two different models. A) A *historical* model representing the past distribution of the species, based on occurrences collected between 1998 and 2008; this predates the known expansion of the Porcupine in Southern Italy. B) an *expansion* model, based on occurrences collected between 2009 and 2019; this represents the period when the Southern expansion took place. The *historical* model was based on land-cover data from 2006 and average climatic conditions between 1998 and 2008, while the *expansion* model was based on 2012 land-cover data and average climatic conditions between 2009 and 2013. Before running the models, we tested for possible correlations among environmental variables, finding no strong correlations (Table S1; pairwise correlation coefficients ≤ 0.7). All the models were run using linear, quadratic, and hinge features, for a maximum of 2000 iterations, sampling a maximum of 10 000 background points. In order to avoid overfitting, before running the *historical* and the *expansion* models, we ran preliminary models to select the most appropriate regularization multiplier (i.e. the smoothing of the model, where a higher number represents a simpler model: Elith et al. 2011). In so doing, we used the data for the *historical* model and performed eight different models with the same settings and only varying the regularization multiplier between one and eight. We then calculated the Bayesian Information Criterion (BIC) for each model and used it to select the value of the regularization multiplier. BIC represents a criterion for model selection and indicates the goodness of a model taking into consideration a penalty term for the number of parameters included in the model. BIC is closely related to Akaike Information Criterion but is more suitable for models including a high number of data (Raffalovich et al. 2008). The model with regularization multiplier = 2 showed the lowest BIC value; hence the *historical* and *expansion* models were run with this value (Table S2).

In order to test the performance of the models, we calculated the cross-validated AUC by splitting the occurrences into five groups and running five models for each scenario (*historical* and *expansion*) using 80% of the data for model fitting and the remaining 20% for testing. Additionally, we tested the ability of the *historical* model to predict the recent distribution of the porcupine. To do so, we projected the *historical* model on the *expansion* environmental data and reclassified the continuous output into "suitable" and "unsuitable" by using the 10^{th} percentile training presence as a threshold to discriminate unsuitable from suitable cells (Pearson et al. 2007). Then, we calculated the percentage area of Italy predicted to be suitable by the *historical* model projected on the *expansion* maps and compared it to the percentage of 2009/2019 occurrences located in suitable cells. If the model predictions are not better than random, the percentage of suitable area and the percentage of occurrences predicted to be in suitable cells should not differ (Roura-Pascual et al. 2004).

Future projections

To assess future suitability for the crested porcupine in Italy, we used the maps of projected climate in the year 2050 from the Coupled Model Intercomparison Project (CMIP5), for three different RCP scenarios (RCP 2.6, 4.5, and 6.0). In order to represent uncertainties in climatic projections, for each RCP, future suitability was based on five different climatological models. We used a stepwise model elimination procedure to select the most dissimilar models of future climate (Sanderson et al. 2015) and selected the following models: BCC-CSM1-1, NorESM1-M, GFDL-ESM2M, HadGEM2-AO, CCSM4 (Karger et al. 2017a). Because maps of future projections of land-use are not available at the 30 arc seconds resolution, we assumed no land-cover changes compared to 2018.

Results

We retrieved a total of 1783 occurrences of the crested porcupine, including 976 collected between 1998 and 2008, and 807 records between 2009 and 2019 (Fig. 1). In this period the porcupine remarkably expanded his range both in Northern and in Southern Italy (Fig. 1).

Both the models built using the *historical* and the *expansion* data showed a good cross-validate AUC value (*historical* = 0.751; *expansion* = 0.726). It must be remarked that maximum achievable AUC for maxent models is $1 - a/2$, where a is the proportion of pixels occupied by the species (Phillips et al. 2006). Therefore, widespread species have a maximum achievable AUC well below 1. According to the *expansion* model, suitability for crested porcupines was the highest in areas with annual mean temperature between 15 and 17°C and with annual precipitation between 600 and 1200 mm (Fig. 2). Suitability showed a negative relationship with agricultural areas, open vegetation, and urban cover, while increased with forest cover (Fig. 2). The *historical* model showed very similar relationships, with only small differences for annual mean temperature and urban cover (Fig. S1 in Supplementary Material 1). In both models, climatic variables showed the highest importance (total permutation importance > 70 %), while land-cover variables showed a limited contribution (Tables S3, S4).

When we validated our models by projecting the *historical* model on the *expansion* environmental variables, we predicted recent occurrences significantly better than random (predicted suitable area = 48 % of the study area; successfully predicted recent occurrences = 83 %; $\chi^2 = 25.3$; $p < 0.001$).

Future scenarios of climate change suggest that the crested porcupine could further expand its range in Italy (Fig. 3; Figg. S2-S4 in Supplementary Material), gaining suitability both in Northern and in Southern regions. Other areas of the species' range could undergo a loss of suitability, including North-Eastern Italy, the Tyrrhenian and Ionian coastlines, and a large portion of Southern Sicily (Fig. 3).

Discussion

While the spread of the crested porcupine in Northern Italy has been widely studied (e.g. Spada et al. 2008; Borgo and Doria 2015; Chiodo and Mori 2015; Mori and

Brugnoli 2019), our work is the first to analyze its range expansion in Southern Italy, assessing scenarios of distribution change in the future. Climatic change and land use are involved in the most evident northwards expansion (Mori et al. 2013; Mori et al. 2018), whereas range re-expansion in Southern regions, where the species has been present until last century (Toschi 1965) has been long overlooked (cf. De Santis 2010; Varuzza et al. 2019).

In the last decade, the crested porcupine greatly expanded his range in both Northern and Southern Italy, with many new records in previously unoccupied areas (Fig. 1). Species distribution models provided a quantitative assessment of relationships between environmental variables and suitability for the crested porcupine, suggesting that its distribution is shaped by the joint effect of climatic and landscape variables (Fig. 2). Scenarios of future climatic change show a potential range expansion for the crested porcupine in Italy, also towards areas of Southern Italy where the species has never been present (Fig. 3)

In the last ten years, the crested porcupine has increased its presence in several regions of Sotuhern Italy. In Lucania it expanded its range mostly towards the Tyrrhenian coast (Toschi 1965; Amori et al. 2008; Mori et al. 2013), with many records in the South-Western part of the region (Varuzza et al. 2019). In Campania, the most recent records occurred in the northernmost and southernmost areas, while in Apulia, porcupines are spreading mainly in the northernmost part of the region, with new records from Gargano promontory, where the first records of the species occurred in the 1990s (Toschi 1965; Mori et al. 2013; Mori et al. 2018).

Species distribution models confirmed the importance of wooded areas, as they provide key shelter sites for the porcupines (Monetti et al. 2005; Mori et al. 2014; Lovari et al. 2017; Mori and Assandri 2019). Furthermore, we detected a negative relationship with agricultural areas, open vegetation, and urban cover, in line with Monetti et al. (2005) and with Mori (2017). Our models indicate that temperature and precipitation where the most influential variables shaping the species' distribution in Italy. Indeed, being the crested porcupine a habitat generalist (Amori et al. 2008; Mori et al. 2014), land-cover may have played a less important role compared to climate in shaping the species' distribution. However, fine-scale habitat features, not represented by the land cover layers used here (e.g. specific vegetation typologies, small bramble scrubland areas, small calcareous cave systems, orchards), can be important and high resolution analyses can provide improved information on processes occurring at the landscape-scale.

High mountains were confirmed to be unsuitable habitats for the crested porcupine, as snow cover prevents food search by this rodent (Alkon and Saltz 1988; Corsini et al. 1995; Mori 2017). The crested porcupine may occasionally exploit areas covered by snow in some periods of the year (i.e. > 1200 meters above sea level: Fig. S5 in Supplementary Material 1), but its spatiotemporal behavior is generally altered in these environments (Corsini et al. 1995; Mori 2017). Global warming and the abandonment of traditional agriculture are altering habitat composition on mountains, particularly in peninsular Italy (Stanisci et al. 2005; Rogora et al. 2018). Duration of snow and ice cover on the ground remarkably decreased in the last 50 years, and this may allow porcupines to dig for food search also in winter months and to search for food throughout the year in mountainous areas (Alkon and Saltz 1988; Mori 2017).

The *historical* model correctly predicted recent occurrences with good performance (see results), indicating that our models are suitable for making predictions about future distribution of this species. Future predictions suggested that the crested porcupine may colonize mountain areas in the Southernmost Italian peninsula, including the Aspromonte National Park. Dry areas are unsuitable for the crested porcupine, preventing digging and burrowing; therefore, this large rodent tends to avoid xeric habitats, deserts, and urban areas (Cuzin 2003; Amori et al. 2008; Mori et al. 2013). An increase in farmlands and urbanization, as well as a reduction of annual precipitations, can thus represent limit the range expansion of this species, particularly in Salento (Southern Apulia) and along the Eastern Calabrian coastline. The crested porcupines may exploit cultivated areas for feeding (e.g. Zavalloni and Castellucci 1994; Pigozzi and Patterson 1990; Mori et al. 2014). Despite this, our results are in line with other studies, which suggest that agricultural areas are only occasionally exploited by porcupines, particularly when wild fruits are scarce (Bruno and Riccardi 1995; Laurenzi et al. 2016). Porcupines seem to be strongly associated with undisturbed habitats, which can provide food, suitable denning sites, and protection from predators (Bruno and Riccardi 1995; Monetti et al. 2005; Fattorini and Pokheral 2012; Laurenzi et al. 2016; Lovari et al. 2017). Conversely, the Alps seem to be unsuitable for porcupines, who cannot search for food in areas characterized by snow and ice cover (cf. Mori 2017). Moreover, an increase in average temperatures and a future reduction in annual precipitations is expected to reduce habitat suitability for this large rodent in some areas of Southern Italy. The increase in drought would limit water availability for physiological functions, prevent porcupines burrow stability (Monetti et al. 2005) and digging behavior, thus limiting the establishment of family groups (Mori et al. 2013; Lovari et al. 2017).

An updated and standardized monitoring of the range of the crested porcupine is required as the species is listed within the Annex IV of the Habitat Directive

(1992/43/EEC), to sustain an effective set of decision-making tools. Global warming and land use change are altering and influencing the distribution of most mammal species, thus bringing new challenges for biological conservation (Di Febbraro et al. 2019). Therefore, an active surveillance program should be carried out in areas where the porcupine is not yet present, i.e. near the borders of its current European distribution. Reduced snow cover on mountain tops and increasing wooded areas may eliminate the strongest barrier to the range expansion of the crested porcupine in Italy (Mori 2017; Mori et al. 2018). Conversely, increasing droughts may represent a future limit for this rodent and other semifossorial species.

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Author contributions

E.M., G.F.F., and M.F. conceived the idea, E.M and M.F. organized the dataset and wrote the first draft the manuscript; M.F. carried out statistical analyses; R.B., G.C., and P.V. collected recent occurrences of crested porcupine in Southern Italy. All authors approved the final draft.

Compliance with ethical standards

Conflict of interest: Authors certify that they have no affiliation with or involvement in any organization or entity with any financial or nonfinancial interest in the subject matter or materials discussed in this manuscript. Thus, they have no conflict of interest to declare.

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Figure Captions

Figure 1. Occurrences of crested porcupine used for this study. Green dots represent "historical" occurrences (1998-2008) and yellow dots represent recent records (2009-2019).

Figure 2. Response curves for the MaxEnt model fitted with presence data between 2009 and 2019. Relationships between suitability and a) mean annual temperature, b) annual precipitation, c) agricultural cover, d) forest cover, e) cover of open vegetation, f) urban cover. Black lines indicate the mean predicted suitability and grey areas represent one standard deviation from the mean.

Figure 3. a) Environmental suitability, as predicted by the MaxEnt model fitted with presence data between 2009 and 2019. 0.4 is the 10^{th} percentile training presence threshold; 0.05 is the minimum training presence threshold. b-d): predicted suitability changes under three different RCP scenarios. See Appendix 1 for the interpretation of suitability change. Grey areas represent unsuitable areas which remain unsuitable.