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Range expansion and redefinition of a crop-raiding rodent associated with global warming and temperature increase

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Abstract

Since the 1970s, the crested porcupine *Hystrix cristata* has shown a marked range expansion in Italy. A web page has been created to collect occurrences of this species to monitor its distribution redefinition. Thus, aims of this work were (i) to identify the main predictors promoting the distribution of this large rodent in Italy and (ii) to predict its potential expansion under future climate change scenarios. A total of 1674 locations were used for this analysis, i.e., all those collected through the web page, with the exception of recently introduced populations (Sardinia, Western Liguria and Province of Varese). The current distribution of the crested porcupine covers a total of 135,177 km^2, as estimated through ensemble predictions. Future climate change scenarios for 2050 and 2070 show that a further range expansion by this species would occur up to 225,576 km^2, mainly towards areas where the species was historically absent. The increase of isothermality (i.e., the ratio between the mean diurnal and the annual temperature range) and the mean temperature of the driest months would help crested porcupines to reach high altitudes, e.g., in the Alps. In mountain habitats, the ongoing global warming is shifting the distribution of European forests to high elevations, thus potentially providing porcupines with suitable habitats. A reduction in snow cover and the snow period at ground level would remove an important barrier to the range expansion of the crested porcupine in Italy, and thus facilitate digging and food search by this large rodent. Despite being protected at national and international levels, the crested porcupine is reported to be an introduced species to Italy and, therefore, monitoring its range expansion is required. Furthermore, there are complaints about crop damage in agriculture ecosystems, and the species is still widely poached, thus additional management practices are required. Thus, given the conservation interest of this large rodent, an integrated and constantly updated monitoring system that sustains an addressed set of decision-making tools is recommended.

Keywords Climate change · *Hystrix cristata* · Italian peninsula · Management practices · Range redefinition

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1 Introduction

The current global climate change is one of the main threats to biodiversity worldwide, mostly enhanced by human activities (Parmesan and Matthews 2006). Accordingly, all ecosystems are virtually affected by global warming, and have to adapt to new climatic conditions. Living organisms may react to climate change through phenotypical alterations (Huey et al. 2000), phenological shifts (Luna et al. 2017), abundance changes (Sillett et al. 2000), and distribution range redefinition (Urban 2015). Animal species distribution is linked to biome distribution, which is dramatically altered by the ongoing increase in mean temperatures and precipitation and by the change in sea level, due to land ice melting (Andrewartha and Birch 1954; Woodward 1987; Root et al. 2003). Extents of occurrence of living species represent the result of a dynamic balance potentially influenced by physical phenomena, physiological levels of tolerance, and biotic and abiotic interactions (Parmesan 2006; Svenning et al. 2008; Sexton et al. 2009). Therefore, ranges may change over time due to climate change, human-mediated alteration of landscapes and land use, as well as biological invasions (Ching-Cheng et al. 2011; Ancillotto et al. 2016; Balestrieri et al. 2016). A strong attention has been paid to this topic by conservation biologists, especially for the development of management plans and preservation actions (Gaston 2009). Range dynamics over time deserve detailed studies especially for invasive alien species, which may rapidly colonize new suitable habitats (Alexander and Edwards 2010; Mori et al. 2015a; Su et al. 2017). As to native species, range modifications usually involve specialized taxa (Carone et al. 2014; Balestrieri et al. 2016) with respect to generalist and ecologically plastic species (Mori and Plebani 2012; Ancillotto et al. 2016). Urbanization and alterations of land cover represent common examples of habitat loss, i.e., the main cause of the global species extinction process (McKinney 2006; Carone et al. 2014); generalist and commensal species may adapt to live within human settlements by expanding or by modifying their ecological niches (Mori and Bertolino 2015; Ancillotto et al. 2016). Furthermore, since the end of World War II, the abandonment of cultivations on mountains and hilly landscapes allowed the re-expansion of forests and uncultivated fields (Piussi 2000; Mori et al. 2013). This phenomenon triggered an increment in population size and distribution range of many woodland mammal species (Levinsky et al. 2007; Balestrieri et al. 2016; Milanesi et al. 2016a, b). Landsat thematic mapper imagery (1984–2010) showed that, in the last 35 years, forests considerably increased in Italy, also (about by 20%) on degraded soils (e.g., in drought-prone Mediterranean areas: Mancino et al. 2014).

The crested porcupine *Hystrix cristata* is the largest Italian rodent (up to 12–15 kg: Mori and Lovari 2014). It lives in several types of habitats, from woodlands to rural environments to suburban areas (Mori et al. 2014a; Lovari et al. 2017), even if denning sites are mainly linked to densely vegetated areas (Monetti et al. 2005; Lovari et al. 2017). Population genetics (Trucchi & Sbordoni, 2009; Trucchi et al. 2016), paleontology (Masseti et al. 2010), reproductive phenology (Mori et al. 2016), behavioral ecology (Mori et al. 2014a) (Mori et al., 2014b), and ectoparasite load (Mori et al. 2015b) strongly suggests a North African origin of the Italian population of the crested porcupine in the early medieval times (Bertolino et al. 2015; Trucchi et al. 2016). During the last 30 years, this species underwent a marked and abrupt range expansion in Italy (Mori et al. 2013); until the 1970s, this large rodent was only distributed in Central and Southern Italy, mostly on the Thyrrenian coast (Ghigi 1917; Tomei and Cavalli 1976; Mori et al. 2013).

Then, between 1975 and 2015, it crossed the Apennine ridge, where the expansion to the North may have begun, prior to reaching the northernmost regions (Piedmont, Trentino Alto-Adige, Lombardy and Veneto: Orsomando and Pedrotti 1976; Pandolfi 1976; Mori et al.

2013). In most cases, the first records were followed by observations of cubs or reproductive adults, suggesting successful colonization of new areas (Spada et al. 2008; Bollin and Leo 2013; Chiodo and Mori 2015). Even if some local anthropogenic introductions occurred throughout Italy (i.e., in Sardinia, Northern Lombardy, and Western Liguria: Mori et al. 2013), this abrupt range expansion is most likely due to climate change, which also contributed to the re-expansion of the forest cover in Italy (Mori et al. 2013). Given its high ecological plasticity to many different habitat types from lowlands to mountain forests and to urban areas (Mori et al. 2014a; Grano 2016; Lovari et al. 2017), climatic factors rather than non-climatic ones (i.e., linked to physiology: see Mathewson et al. 2017) are suggested to have promoted this range expansion. Accordingly, the crested porcupine evolved in areas characterized by hot-warm climates (Trucchi et al. 2016) and, thus, its range expansion might have been promoted by the current global warming (cf. Levinsky et al. 2007). The Indian crested porcupine *Hystrix indica* was reported to be unable to colonize only snow covered areas in high mountains (Alkon and Saltz 1988), a finding also confirmed for the crested porcupine in Italy by a habitat suitability model (Mori et al. 2013). On the other hand, the ongoing climate change may represent one of the factor helping porcupines to colonize high mountains (cf. Wilson et al. 2005; Levinsky et al. 2007), as number of days of snow cover is decreasing year by year (Bertolino et al. 2016; Klein et al. 2016; Mori 2017).

The crested porcupine is subjected to a strong poaching pressure both in response to crop and riverbank damages, and for its meat (Cerri et al. 2017; Lovari et al. 2017). Future projections obtained through Species Distribution Models (hereafter, SDMs: Guisan et al. 2013) can be useful to correctly address conservation plans (and, thus, to set up actions for the prevention of damage) by providing knowledge about the species potential distribution range. Given the conservation interest of the species and its appeal to the general public, the range expansion of the crested porcupine in Italy has been widely documented by media (e.g., newspapers, television), social networks, and gray literature (e.g., Orsomando and Pedrotti 1976; Tomei and Cavalli 1976; Bollin and Leo 2013; Mori et al. 2013). Therefore, reliable and detailed data and long-term datasets distribution on its occurrence are available (Mori et al. 2013; www.naturaesocialmapping.it; www.inaturalist.org).

Aims of this research were (i) to identify the main predictors promoting the distribution of the crested porcupine in Italy and (ii) to predict the potential expansion of this large rodent under future climate change scenarios.

2 Materials and methods

2.1 Data collection

A high number of crested porcupine occurrences in Italy were recently reported by a study involving observations and photos by citizen scientists (Mori et al. 2013). Giving the rapid evolution of this phenomenon, a real-time, constantly updated map with all occurrences has been set up at the link: www.naturaesocialmapping.it/node/6. We selected a total of 1674 data from this online platform, i.e., all those with a geographical error lower than 150 m (reported in each website used for data collection). Other 33 occurrences (collected by 31 citizen scientists) were extracted from the iNaturalist project on Italian mammals (www.inaturalist.org/projects/mammiferi-d-italia). Data were evenly distributed throughout the Italian range of this species (Mori et al. 2013) and showed a highly fine geographical precision (i.e., < 150 m: www.inaturalist.org/projects/mammiferi-d-italia). Data from introduction areas (Mori et al. 2013) were excluded from the analysis, as well as those for which geographical precision was over 200 m. Occurrences were validated through an expert-based approach on photos, which allowed us to distinguish among different porcupine species according to their morphology (Mohr 1965; Mori et al. 2017, Supplemental Material). Quills were genetically analyzed to ascertain that the species was correctly identified (Viviani and Trucchi 2007; Trucchi et al. 2016; Mori et al. 2017). Molecular analyses always confirmed the morphological identification, and a different species from *H. cristata* was detected only once (i.e., *H. indica* in Central Italy: Mori et al. 2017).

2.2 Predictor variables

We took into account 11 bioclimatic variables, which represented the habitat requirements of our target species: for all these variables, continuous spatial data were available for the whole study area (Mori et al. 2014a; Lovari et al. 2017). Variables (Supplementary Material 1) were collected from the WorldClim dataset (www.worldclim.org) for the current period (1950–2000 average) at a 2.5-min resolution (≈ 5 km). We considered this spatial resolution as optimal for the species, since crested porcupines may range for over 3–5 km per night to reach feeding areas (Massolo 2000; Mori et al. 2014a). We calculated the variance inflation factor (VIF) for all the variables, and we removed predictor variables with values > 3 (i.e., highly correlated to other predictors; Zuur et al. 2010; Supplementary Material 1), to avoid multicollinearity among predictors. We used the same set (and the same spatial resolution) of bioclimatic variables of the current period for future scenarios in 2050 and 2070, projected under different climate change scenarios. Specifically, we considered four climate change scenarios, derived by 11 general circulation models (BCC-CSM1-1, CCSM4, GISS-E2-R, HadGEM2-AO, hadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM-CHEM, MIROC-ESM, MIROC5, MRI-CGCM3, and Nor-ESM1-M: Ihlow et al. 2016), which represent simulations of four representative concentration pathways (Moss et al. 2010; RCP 2.6, which assumes that global annual greenhouse gas emissions measured in CO2-equivalents will peak between 2010 and 2020, with emissions declining considerably from there on; RCP 4.5, peak around 2040, then decline; RCP 6, peak around 2080, then decline; RCP 8.5, emissions continue to rise throughout the twenty-first century) for 2050 and 2070. Scenarios were obtained from the fifth assessment of the Intergovernmental Panel for Climate Change (www.ipcc.ch). The selected RCPs represent four possible greenhouse gas emission trajectories ranging from low (RCP 2.6) to high (RCP 8.5) increases in global radiative forcing (Ihlow et al. 2016).

2.3 SDMs and prediction of future distribution

We used the average ensemble prediction (Thuiller et al. 2009) derived from 11 SDMs to assess species distributions and avoid biased estimation due to single model uncertainty. In detail, we developed (i) artificial neural networks (Ripley 2007); (ii) boosted regression trees (Friedman 2001); (iii) classification tree analyses (Breiman et al. 1984); (iv) flexible discriminant analyses (Hastie et al. 1994); (v) Gaussian process SDMs using maximum a posteriori inference (Golding and Purse 2016); (vi) generalized additive models (Hastie and Tibshirani 1990); (vii) generalized linear models (McCullagh and Nelder 1989); (viii) factorial decomposition of Mahalanobis distances (Calenge et al. 2008); (ix) multivariate adaptive regression splines (Friedman 1991); (x) maximum entropy algorithm (MAXENT; Phillips et al. 2006), and (xi) random forests (Breiman 2001). SDMs were carried out through the packages ADEHABITAT (Calenge 2006), BIOMOD2 (Thuiller et al. 2016), and GRaF (Golding and Golding 2014) for the open-source software R (v. 3.1.2; http://www.R-project.org). We derived the sampling effort through a Gaussian kernel density analysis (given all the locations of the species). Then, we used the values of the resulting sampling effort map as a bias grid in the factorial decomposition of Mahalanobis distances, in the maximum entropy algorithm and as case weights in all the other SDMs (Elith et al. 2006; Fourcade et al. 2014; Stolar and Nielsen 2014; Milanesi et al. 2015, 2016b; Balestrieri et al. 2016). Thus, we generated 10,000 random points to serve as background data. We found evidence of spatial autocorrelation among residuals of models; therefore, we also included *X*- and *Y*-coordinates of species locations and their interaction in SDMs (Pasinelli et al. 2016). Thus, model residuals were no longer spatially autocorrelated (Pasinelli et al. 2016).

We carried out tenfold cross-validations (using a random subsample of 90% of the locations to calibrate the models and the remaining 10% to validate them: Thuiller et al. 2009) to evaluate the predictive accuracy of SDMs through (i) true skill statistics (TSS) and (ii) the continuous Boyce index (CBI: Supplementary Material 2). We converted the resulting ensemble prediction continuous map, representing the predicted probability of occurrence (%) of the crested porcupine, into a binary one (suitable/unsuitable) considering a threshold value estimated by maximizing the TSS (Allouche et al. 2006; Thuiller et al. 2016); values higher and lower than the threshold represented suitable and unsuitable areas, respectively. We computed these analyses through the R package BIOMOD2 (Thuiller et al. 2016) in R.

3 Results

We used a total of 1707 crested porcupine locations collected between 1969 and 2015. Seven out of 11 predictors showed VIF values higher than three (i.e., high multicollinearity), and thus, we considered only isothermality (i.e., the ratio between the mean diurnal and the annual temperature range), temperature seasonality (i.e., standard deviation of the mean monthly temperature), mean temperature of the wettest quarter (the continuous-wettest 3 months), and mean temperature of the driest quarter (the continuous-driest 3 months) in the development of the SDMs (Supplementary Material 1). Thus, we found that the probability of occurrence of the crested porcupine increased as isothermality did as well as the mean temperature of the driest quarter, while decreased as temperature seasonality and the mean temperature of the wettest quarter increased (Fig. 1). The tenfold cross-validations showed significant values for all the evaluation methods of all SDMs (Supplementary Material 2). Considering the resulting threshold value (36.4), ensemble prediction estimated the occurrence of the crested porcupine in a total of 135,177 km^2 (45.1% of the total study area; Fig. 2) under current climatic conditions. Future climate change scenarios showed a constant increment in the range of crested porcupines in Italy: in 2050, the distribution of the target species would increase (Table 1), ranging from 194,093 km^2 (64.7% of the total study area) when considering RCP 2.6, to 216,903 km^2 (72.3% of the total study area) when considering RCP 8.5 (Fig. 3; Fig. S1 in Supplementary Material 3). In 2070, the distribution of the crested porcupine would increase, ranging from 195,297 km^2 (65.1% of the total study area) when considering RCP 2.6, to 225,576 km^2 (75.2% of the total study area) when considering RCP 8.5 (Fig. 3; Fig. S1 in Supplementary Material 3).

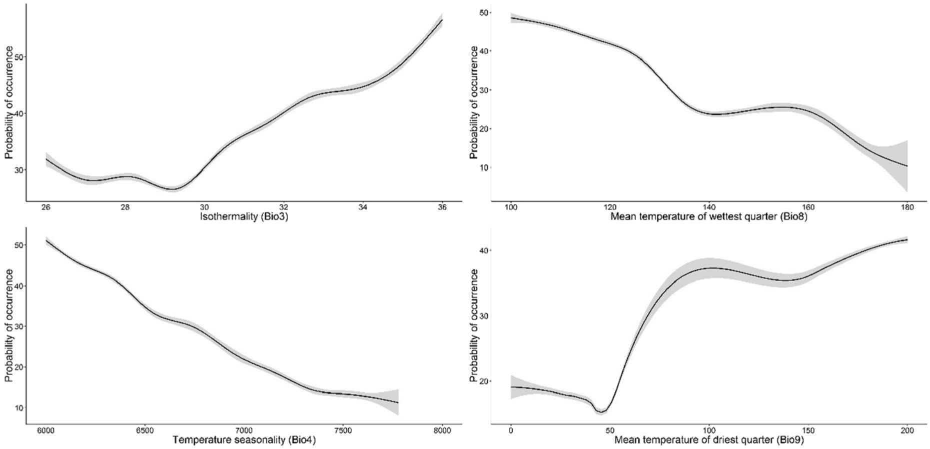

Fig. 1 Response curves and 95% confidence intervals (in gray) of the probability of occurrence of the crested porcupine derived by the ensemble prediction of the species distribution models in relation to predictor variables values

4 Discussion

The crested porcupine resulted to be a suitable model species to measure the effects of climate change on the distribution of animal species, given (i) the extent of the species range, which includes warm-to-hot areas, (ii) its remarkable ongoing expansion in Italy, and (iii) the availability of long-term, constantly updated occurrence data (cf. Parmesan and Matthews 2006).

All future climate change scenarios showed a further range expansion to the range of the crested porcupine in Italy, mainly towards areas where the species has never been present. Landscape features, climatic variability, and the distribution of suitable habitat play a pivotal role in shaping distribution ranges, along with species-specific dispersal abilities (Veech et al. 2011; Mori et al. 2013). However, all the studies carried out on habitat use by this species underline a high importance of deciduous woodland and shrublands to provide abundant food resources and shelter sites for the porcupines (Sonnino 1998; Mori et al. 2014a; Lovari et al. 2017).

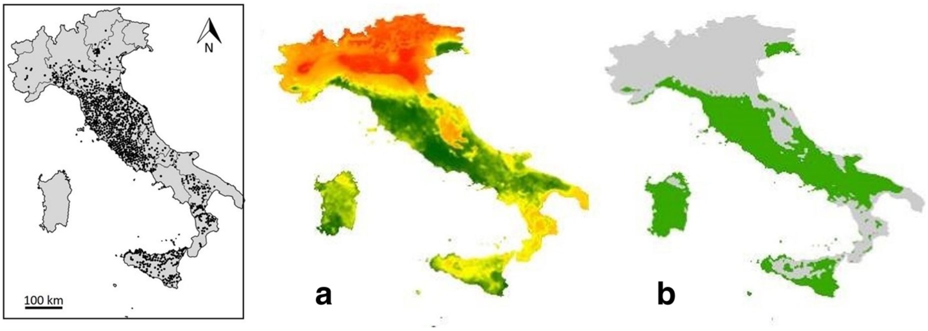

Fig. 2 **a** Probability of occurrence of the crested porcupine (green-red scale indicates higher-lower probability values, respectively) derived by the ensemble prediction of 11 species distribution models, **b** current distribution of the species (in green) in Italy estimated by the ensemble prediction using a threshold value (36.4). Inset (left): black points indicate crested porcupine locations

Table 1 Potential distribution (km^2) of crested porcupine in the years 2050 and 2070 derived by four Representative Concentration Pathways (RCP) of the Intergovernmental Panel on Climate Change 5th assessment—Coupled Model Intercomparison Project Phase 5

RCP	2050	2070
2.6	194,093	195,297
4.5	207,132	214,208
6	211,363	216,256
8.5	216,903	225,576

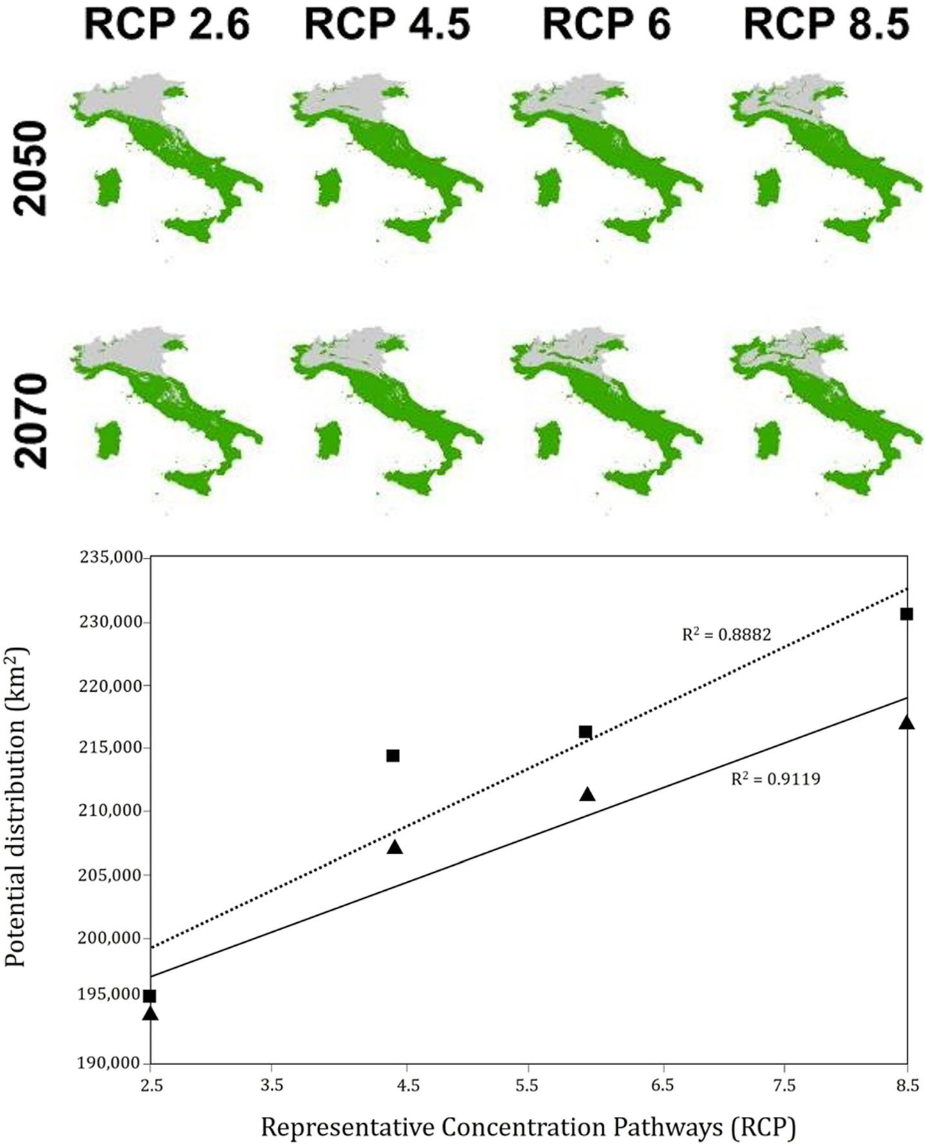

Fig. 3 Crested porcupine predicted distribution in 2050 and 2070 (in green), according to four RCPs of the Intergovernmental Panel on Climate Change 5th assessment—Coupled Model Intercomparison Project Phase 5. We used the same threshold value used for the current distribution of the species (36.4). Below, increase in the predicted distribution in 2050 and 2070 (in km^2), according to the RCP

High mountainous areas (i.e., > 1500 m a.s.l.) are reported to be unsuitable habitats for the crested porcupine, as they are covered by ice for some periods of the year (Mori et al. 2013). In fact, the species mainly feeds on underground storage vegetal organs (Bruno and Riccardi 1995) and it needs food resources throughout the year (Alkon and Saltz 1988), as it does not hibernate (Corsini et al. 1995). However, the crested porcupine may locally exploit, at low population density, areas covered by snow in some periods of the year, both in Central Italy (> 1700 m a.s.l.: Mori et al. 2013) and in the Moroccan Anti-Atlas (up to 2550 m a.s.l.: Cuzin 2003). In these areas, cold temperatures and snow cover alters the spatial behavior of this large rodent, although they do not prevent its survival, where snow covers last for less than 1 month (Corsini et al. 1995; Mori 2017).

On mountains, along with traditional land use abandonment, ongoing global warming is currently altering habitat composition (Grace et al. 2002; Beniston 2003; Walther et al. 2005; Gottfried et al. 2012). As a response, although climatic suitability is just one of the factors which make habitat suitability, several animal species, including birds, butterflies, and woodland rodents, are shifting their distribution towards high altitudes (e.g., Ching-Cheng et al. 2011; Wilson and Gutierrez 2012; Roth et al. 2014; Rowe et al. 2015; Bertolino et al. 2016).

The duration of snow and ice cover at the ground level has significantly decreased over the Alps since the 1970s (9 days per decade, on average; Klein et al. 2016), and as a result, the photosynthetic activity of the local vegetation is maintained throughout the winter (resulting in an earlier spring; Zeeman et al. 2017). The progressive decrease of snow cover may allow porcupines to dig their burrows in suitable areas (i.e., steep, compact soils covered with dense canopies: Monetti et al. 2005), and to search for food throughout the year in mountainous areas (Alkon and Saltz 1988; Mori 2017). Therefore, global warming would promote a further range expansion of the crested porcupine, possibly even over the Alps. Conversely, the similar North American porcupine *Erethizon dorsatum* is declining throughout the USA possibly because of climate change, which increased fire frequency and severity (E. Beever, personal communication, 2018). Differently from the crested porcupine, the North American species is linked to forests and produce a small number of cubs per year (Roze 2009), which may increase the sharpness of its decline.

Despite this positive trend in range expansion, the crested porcupine is still widely poached both for its meat (Cerri et al. 2017; Lovari et al. 2017) and for being considered a crop raider (Bertolino et al. 2015; Laurenzi et al. 2016) in Central and Southern Italy. Therefore, the crested porcupine may represent a severe problem for traded grape varieties (e.g., Prosecco di Conegliano and Valdobbiadene) and for riverbanks (Bertolino et al. 2015) in the range expansion area.

A continuous and standardized monitoring activity of crested porcupines should be required to develop effective management strategies, particularly if this species will overpass the Italian borders. Accordingly, the global climate change is currently increasing the success of biological invaders (Ching-Cheng et al. 2011; Hulme 2017), and new colonized areas seem to be more vulnerable to the impact of alien species with respect to previously occupied ones (Parmesan and Matthews 2006; Bertolino et al. 2014). Immediate detection and quantification of the range expansion of an alien species is indeed recommended to prevent impacts on native species and ecosystems.

SDMs showed that many species have already shifted their geographic distributions toward higher latitudes and elevations due to climate change conditions (Rosenzweig 2007; Thomas 2010). Our predictions on the current potential distribution of crested porcupines agree with the Mori et al. (2013), revealing large areas with high probabilities of occurrence for this species. On the other hand, future projections on the probability of occurrence help to identify areas, which may become colonized by porcupines as a response to climate change. Considering all future scenarios for both 2050 and 2070, we found an overall expansion towards higher latitudes and altitudes. With an expected increase ranging between 19.6–27.2% in 2050 and 20.0–30.1% in 2070 (given as percentage of the study area), the overall magnitude of expected expansion appears to be high. Thus, compared to other mammal species in Italy (Mason et al. 2014), climate change would likely promote range expansion (and thus population growth) of the crested porcupine as representative concentration pathways increased (Moss et al. 2010). In addition, by facilitating the identification of areas of range expansion, our species distribution models will help in prioritizing management actions.

Global climate change represents a new challenge for the prevention and control of biological invasions. Reduced snow cover on the Alps will remove the most important barrier to the range expansion of the crested porcupine in Italy (Klein et al. 2016; Mori 2017). Given the importance of this large rodent, an integrated and constantly updated monitoring system, which sustains an addressed set of decision-making tools, should be recommended.

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