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Knowing the past to forecast the future: a case study on a relictual, endemic species of the SW Alps, *Berardia subacaulis*

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Abstract Future climate change may lead to a substantial loss of biodiversity, particularly affecting mountain regions, including the Alps. Range-size reduction in high mountain plant species is predicted to be more pronounced for endemic species. Investigating the broad temporal spectrum of range shifts is important for the conservation of biodiversity, since learning how species responded to climate change in the past provides useful insights on how they might react to warming trends in the present and future. Using species distribution models and an ensemble forecasting approach, we explored how the distribution of *Berardia subacaulis*, a monospecific genus endemic of the south-west Alps, may be affected by past and future projected climate change. During the last interglacial, the habitat suitability of *Berardia* was lower than present and a progressive increase was observed from the last glacial maximum until now. In the future, *Berardia* appears to lose more than 80 % of its range, becoming endangered by 2050. Our results suggest that *Berardia* probably survived past warmer periods in situ, expanding its distributional range during cooler periods. The severe future range contraction predicted for *Berardia* reflects similar results for other endemic species. As *Berardia* represents an interesting model species to evaluate the effects of climate warming on range size and shifts, demographic and precise range monitoring may be undertaken on this species.

Keywords Palaeoendemic plant species · Ecological niche modelling · Glaciations · Global warming · Past climate change

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Introduction

In the last decades, global climate has undergone dramatic changes, which are expected to continue into the twenty-first century (Solomon et al. 2007), inducing a substantial loss in biodiversity (McCann 2000). Predictions play a crucial role in alerting scientists and decision-makers to the potential future effects of global warming, with the possibility to develop proactive strategies aimed at mitigating these risks (Pereira et al. 2010; Bellard et al. 2012). Although the application of species distribution models (SDMs—Guisan and Zimmermann 2000; Guisan and Thuiller 2005) to climate change analyses has some limitations, major improvements have been achieved, allowing the development of ever more accurate models (Elith et al. 2006; Guisan and Thuiller 2005; Wisz and Guisan 2009). Therefore, SDMs currently represent one of the main tools for assessing the impacts of predicted

climate change on species distribution (Guisan and Thuiller 2005).

According to SDMs, future climate change may lead to substantial losses of biodiversity (Thuiller et al. 2005b; Thomas et al. 2004), affecting especially mountain regions, including the Alps, Pyrenees, French Cevennes, Carpathians, ranges in central Spain and the Balkan peninsula (Thuiller et al. 2005b). The effects of ongoing global warming are already visible, for instance, in the significant upward shift of plant distributional ranges documented in the western European mountains for the last century (Lenoir et al. 2008).

Mountains often constitute centres of endemism for biodiversity, harbouring endangered species and ecosystems. It has long been assumed that the loss of endemic species will have limited impacts on ecosystem functioning in the short term and at local scales, due to their frequently low abundance in communities (Grime 1998). However, Mouillot et al. (2013) observed that species with restricted geographic distribution tend to support vulnerable functions and to increase the level of functional diversity within the communities, which in turn sustains local ecosystem processes. Additionally, species with restricted distribution, which usually occupy specialized habitats, are by definition more susceptible to changes in their habitats (Thuiller et al. 2005a). These species are also likely to be more dispersal-limited and less genetically variable and thus less able to rapidly adapt to climate change than species with broader distribution (Hu and Jiang 2011).

The SW Alps have been identified as the region with the highest diversity of plant species, specifically of endemics, in the entire Alpine mountain chain (Pawlowski 1970). This highest diversity of plants reflects the richness, topography and history of the SW Alps (Médail and Verlaque 1997), and it derives also from its situation as a biogeographical crossroad between the Mediterranean and Alpine regions (Médail and Verlaque 1997). In the SW Alps, the effects of glaciations were less severe, and this area served as a refugium where some species escaped extinction caused by Pleistocene glaciations (Diadema et al. 2005; Minuto et al. 2006; Casazza et al. 2008). Here, numerous endemic species survived (e.g. *Acanthoprasium frutescens*, *Acis nicaeensis*, *Berardia subacaulis*, *Moehringia lebrunii*, *Phyteuma cordatum*, *Potentilla saxifraga*, *Saxifraga florulenta*—Casazza et al. 2005).

Pleistocene glaciations have strongly determined the distribution of narrow-ranging plants (Tribsch 2004). Climatic fluctuations have led to range restrictions, forcing species into refugia (Hewitt 1996; Tribsch and Schönswetter 2003), where climate conditions remained favourable during unfavourable periods (Araujo et al. 2008). Given this scenario of past range fluctuations in response to climatic cycles, investigating the broad temporal spectrum

of range shifts can provide useful information for the conservation of endemic species (Sillero and Carretero 2012).

Plants endemic to the Alps provide excellent models for such analyses, since they have experienced repeated cycles of Quaternary oscillations, often surviving in refugia when climate was adverse. *Berardia subacaulis* Vill. belongs to a monospecific genus endemic to the SW Alps (Fig. 1), grows exclusively on high-altitude calcareous screes and is viewed as an element of the palaeoflora, which was formed by a mosaic of tropical and subtropical plants mixed with temperate plants (Ozenda 2009). Contrary to the majority of palaeoendemic species that became extinct during Quaternary glaciations (Ozenda 2009), *B. subacaulis* probably survived in its peripheral refugium, located in the southern part of the SW Alps (Susanna and Garcia-Jacas 2009). The relictual nature of *B. subacaulis*, first proposed on the basis of its morphological features intermediate between Cardueae and Mutisieae tribes, of the monospecificity of the genus and of its position on an isolated long branch of the phylogenetic tree of the Cardueae (Susanna et al. 2006; Susanna and Garcia-Jacas 2009), was recently confirmed by molecular phylogenetic analyses that dated its origin in the early Oligocene about 33 Ma (95 % confidence interval 28.95–37.92 Ma) (Barres et al. 2013).

The present study is aimed at using *B. subacaulis* as a model to investigate how past climate change and future global warming are predicted to affect the survival of a palaeoendemic species restricted to the SW Alps. To achieve this goal, we used SDMs to infer the suitable habitats under a range of climate change scenarios for different time slices: last interglacial, last glacial maximum, current, 2050 and 2070. More specifically we asked three main questions: (1) How did past climate changes affect the distributional range of *B. subacaulis*? (2) Will projected climate change alter suitable habitat availability
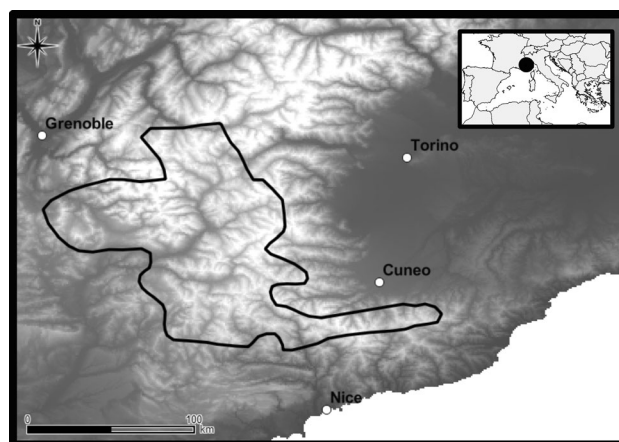
Fig. 1 Distributional range of *Berardia subacaulis* (*continuous black line*)

for *B. subacaulis*? (3) To what extent will *B. subacaulis* be threatened by future climate change? More broadly, this study contributes to ongoing debates on how species respond to climatic cycles, and, more specifically, whether ancient and narrowly distributed mountain species will go extinct or persist.

Materials and methods

Study species

Berardia subacaulis is a perennial herb growing on calcareous screes and stony slopes at high altitudes (between 1700 and 2700 m), and it is currently restricted to the SW Alps. Despite the species originated from a tropical and subtropical flora, it has some typical adaptations of plants to high mountains: acaulescence, dense wooly indument and stout woody rootstock (Garcia-Jacas et al. 2002). The flowers are protandrous, favouring the cross-fertilization, but self-fertilization is allowed (personal observations). The flowers are pollinated by a wide array of insects, but the visits are scarce (personal observations). The population size varies considerably from small population, with fewer than ten individuals, to very large population, with thousand of plants. Currently, *B. subacaulis* is not listed in the IUCN Red List at global scale. In Italy, at regional scale, *B. subacaulis* is listed as "critically endangered" (CR) (Conti et al. 1997). In France, the species has been included in Annex I of 92/43/EEC Directive (Council of European Communities 1992). Several populations are in conserved areas, such as SCIs in the Nature 2000 network or Natural Parks.

Species occurrence data

We collected all occurrence data from the database "SILENE" of the Conservatoire Botanique National Méditerranéen de Porquerolles (CBNMED) and "FLORE" of the Conservatoire Botanique National Alpin de Gap (CBNA) and from our own field surveys (additional data are given in Online Resource 1). To perform detailed distribution models, we used only the data collected since 1995 with a GPS instrument from field surveys, which ensure enhanced geographic accuracy, for a final data set of 1184 records.

Environmental layers at different time slices

Climatic variables related to temperature and precipitation play a significant role, directly and indirectly, in plant physiology (Körner 2003). Nineteen bioclimatic variables for five time slices were downloaded from the WorldClim website (Hijmans et al. 2005; available at http://www.worldclim.org): last interglacial (LIG, ∼ 140–120 kyr BP), current, 2050 and 2070 at 30-s spatial resolution; last glacial maximum (LGM, ∼ 21.000 kyr BP) at 2.5-min spatial resolution.

For SDM analyses of current climatic layers, we performed a pairwise Pearson correlation among bioclimatic predictors aimed at reducing multicollinearity and minimizing model overfitting, retaining only predictors that were not highly correlated ($r \leq |0.80|$; see recommendation of Elith et al. 2006). Six bioclimatic variables were retained for the further analyses: BIO3, isothermality (monthly/annual temperature range); BIO8, mean temperature of wettest quarter; BIO10, mean temperature of warmest quarter; BIO15, precipitation seasonality; BIO17, precipitation of the coldest quarter; and BIO18, precipitation of the warmest quarter (additional information is given in Online Resource 2).

Because *B. subacaulis* grows only on specific calcareous substrates, for all the time slices we added a layer reporting the presence/absence of suitable substrate, based on the global lithological map data set, GLiM (Hartmann and Moosdorf 2012; in Online Resource 3).

Climate change scenarios

For SDM predictions in the LGM, we used data climate layers from both the Community Climate System Model (CCSM) and the Model for Interdisciplinary Research on Climate (MIROC).

For SDM predictions in the future, we chose three general circulation models (GCM): one provided by the Max Planck Institute (MPI-ESM-LR; Online Resource 4), one by the UK Met Office (HadGEM2-ES; Online Resource 4) and one developed by the Institut Pierre Simon Laplace (IPSL-CM5A-LR; Online Resource 4). For each GCM and each time slice, we applied two representative concentration pathways (RCP2.6 the low mitigation scenario and RCP8.5 the high emission scenario—Van Vuuren et al. 2011; Online Resource 4) adopted by the Intergovernmental Panel on Climate Change for its fifth Assessment Report (AR5).

Species distribution modelling

Species occurrence data and the seven selected variables (Online Resource 2) were used to construct distribution models using the BIOMOD2 package (Thuiller et al. 2009) implemented in R (R Development Core Team 2008). We applied six SDM techniques: multivariate adaptive regression splines (MARS—Friedman 1991), generalized linear models (GLM—McCullagh and Nelder 1989), classification tree analysis (CTA—Breiman et al. 1984),

flexible discriminant analysis (FDA—Hastie et al. 1994), random forest (RF—Breiman 2001) and Maxent (Phillips et al. 2006). These techniques belong to three different categories of models (i.e. regression methods—MARS and GLM; classification methods—CTA and FDA; and machine learning algorithms—RF and Maxent; Barbet-Massin et al. 2012).

For each SDM technique, the number of pseudo-absences was selected according to the recommendation of Barbet-Massin et al. (2012) (Online Resource 5). The predictive performance of the models was evaluated for each pseudo-absence run by repeating a split-sample cross-validation ten times, using a random subset (70 %) of the initial data set each time to calibrate the models, while the remaining 30 % were used to evaluate the models. The models predicted suitability values between 0 and 1000 at each site and were downscaled at 0–1 range. Two different measures for the evaluation of the models were calculated: the area under the curve (AUC) of a receiver operating characteristic (ROC) plot and the true skill statistic (TSS) (Thuiller et al. 2009). To transform the inferred continuous probability values to binary presence–absence form, we used the TSS. For the final ensemble projections, we considered the average among all the models for the same time slices.

Species extinction risks

The following thresholds were used to assign the species to different threat categories for future SDM projections, according to the IUCN Red List criterion A3 (IUCN 2012): projected range loss of 100 %, extinct (EX); projected range loss of >80 %, critically endangered (CR); projected range loss of >50 %, endangered (EN); and projected range loss of >30 %, vulnerable (VU). Although this Red Listing approach is simplistic because it considers only the role of climatic variables on species survival, it provides a synthetic overview of biotic threats driven specifically by climate change (Thuiller et al. 2005b).

Spatial index for potential impacts of climate change

Following Hu and Jiang (2011), we used two approaches to assess the impact of climate change on potential habitat range. First, we estimated the percentage of predicted future range change (C) by cell using $C = 100(\text{RG-RL})/\text{PR}$, where RG is the range gain by cell, RL is the range loss by cell and PR is the predicted present range by cell. A negative C value indicates a loss in overall range, whereas a positive value indicates an increase in overall range size. The future range turnover (T) by cell of the climate envelope range was estimated using $T = 100(\text{RL} + \text{RG})/(\text{PR} + \text{RG})$. A T value of 0 indicates no shift in range, whereas a value of 100 indicates a complete range shift

when compared with the predicted range under current conditions. The full-dispersal scenario assumes that a species could reach all geographical areas that are predicted to be suitable in future climate projections (i.e. $RG \geq 0$). On the contrary, the no-dispersal scenario assumes no dispersion from current to future suitable sites (i.e. $RG = 0$), implying that future sites that might become suitable for a species remain unoccupied. The no-dispersal scenario was calculated as the percentage of range lost (percentage of RL), while the full-dispersal scenario was calculated as percentage of range changed (C), as the result of the difference between RG and RL related to the present range (PR). The full-dispersal scenario is likely to be unrealistic because it assumes that a species can colonize all locations without physiological, environmental or geographical limitations, while the no-dispersal scenario is likely to be more appropriate for poor dispersers as endemic species frequently are.

Second, we extracted the probability of occupancy for known localities of *B. subacaulis* for the past and future time slices considered. We then characterized the trends in the projected probability of occurrences using raster packages for R (R Development Core Team 2008).

Results

Under current climate conditions, AUC and TSS, interpreted using the classification of the BIOMOD manual (Thuiller et al. 2008), indicated excellent model performance for all modelling techniques, making them suitable for deriving past and future projections (additional information are given in Online Resources 6 and 7).

The potential range of *B. subacaulis* changed substantially among the five investigated time slices. During the LIG, the model identified habitat suitability in the area of SW Alps (Fig. 2a). During the LGM, the model highlighted an overall increase in habitat suitability in the study area, with higher values of habitat suitability mainly found in the southern part of SW Alps (Fig. 2b). Under climatic current conditions, the highest suitability values were detected in the entire area of the SW Alps (Fig. 2c). For the future projections, a progressive decrease in suitability values was observed in the SW Alps (Fig. 2d, e). According to these results, the probability of occurrence for known localities of *B. subacaulis* increased from the past to the present time, varying from 0.5 by LIG to 0.7 by LGM and 0.99 at present, and is predicted to decrease to 0.5 by 2050 and 0.4 by 2070 (Fig. 3).

The potential range of *B. subacaulis* was discernibly impacted by projected climate change. Across the GCMs and the two RCP scenarios, it was clear that the strength of the impacts increased with time. In the RCP2.6, the average

(a) LIG

(b) LGM

(c) CURRENT

(d) 2050

(e) 2070
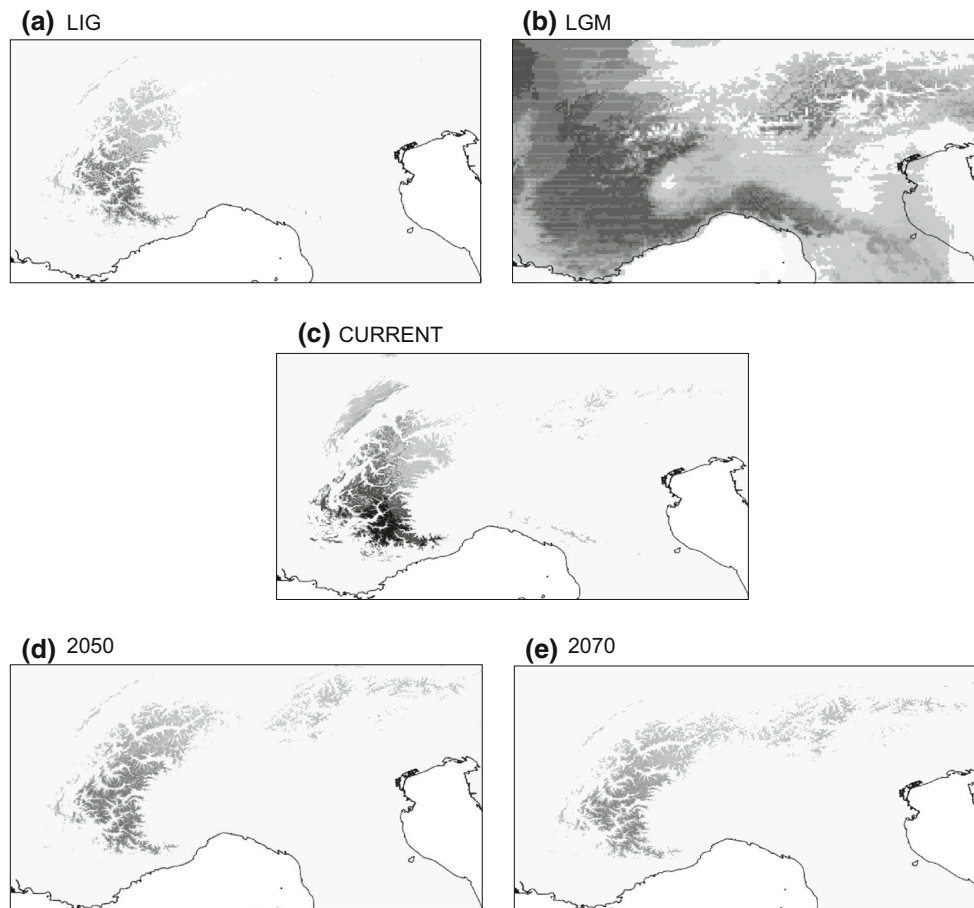
Fig. 2 Predicted distribution of *Berardia subacaulis* for five time slices: LIG (**a** ~120 years BP), LGM (**b** ~21 years BP), current (**c**), 2050 (**d**) and 2070 (**e**). LGM model is obtained with an ensemble forecasting approach across two palaeoclimate models (MIROC and CCSM). Future models are obtained with an ensemble forecasting approach across three general circulation models (MPI-ESM, HadGEM2-ES and IPSL-CM5A-LR) and two representative concentration pathways (RCP2.6 and RCP8.5). The values of habitat suitability are represented in a *grey* scale. The current coastal line is added to all the projections. The *black colour* represents the highest value of habitat suitability

percentage of range loss was 75.74 and 75.76 %, while in the RCP8.5, it was 90.79 and 97.55 %, for the years 2050 and 2070, respectively (Fig. 4a, b). The average percentage of range gain was 8.69 and 8.35 % in RCP2.6, while in the RCP8.5, it was 17.58 and 14.81 %, for the years 2050 and 2070, respectively. The high range loss and the low range gain values resulted in high range change values (Fig. 4c). This predicted a strong turnover (Fig. 4d) in range, and small range increases were projected for all future time slices. Under the full migration assumption, *B. subacaulis* becomes endangered (>50 % range loss) by 2050 and critically endangered (>80 % range loss) starting from 2070.

Discussion

In this study, we present an analysis of the potential effects of past and future climate change on the distributional range of *B. subacaulis*. Our results should be considered with caution

due to some limitations of the approach we adopted. First, climate is only one of several determinants of species distribution (Nogués-Bravo 2009; Thuiller et al. 2009; Chuine 2010; Swab et al. 2012). For example, a restricted distribution may result from dispersal limitation, competition with established vegetation, effects of past, large-scale events and human impacts (Normand et al. 2011; Nogués-Bravo 2009, Svenning and Skov 2004). Nevertheless, the predictive power of climatic distribution models is high for species with small geographic ranges and limited environmental tolerance (Brotons et al. 2004; Elith et al. 2006; Hernandez et al. 2006; Rebelo and Jones 2010), such as *B. subacaulis*. Moreover, models of species with a restricted geographical distribution usually obtain higher values of model evaluation compare to species with wider distribution, because the former species, occupying a smaller part of the environmental space, have a stronger contrast between presence and pseudo-absences in that space (Jimeméz-Valverde et al. 2008; Stokland et al. 2011). According to this statement, we found high values of
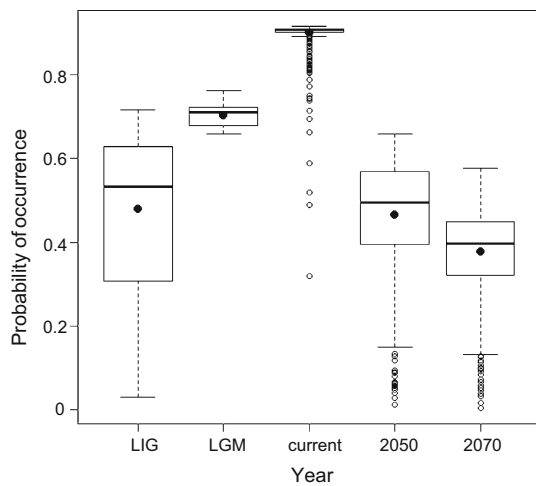
Fig. 3 Predicted probability of occurrence for known localities of *Berardia subacaulis* at different time slices. The probability of occurrence is extracted on the base of predicted distributions from an ensemble forecast approach. The *black line* represents the median, *black circle* represents the mean, *edge box* corresponds to the first and third quartiles (the 25th and 75th percentiles), *whiskers* are 1.5 * IQR (where IQR is the inter-quartile range), and *circles* are outliers

both AUC and TSS. Second, coarse-scale models might underestimate the presence of microrefugia (Randin et al. 2009; Ashcroft 2010; Franklin et al. 2013; Patsiou et al. 2014). However, we produced our models at roughly 1 km^2 of resolution to avoid the problem of hidden local refugia, as suggested by Maiorano et al. (2011) and Franklin et al. (2013). Consequently, we can be reasonably confident that our models for the distribution of *B. subacaulis* are as accurate as currently possible.

Past and future models

According to our results, *B. subacaulis* experienced cycles of severe reduction of habitat suitability, followed by expansion, during the Pleistocene climatic oscillations (Fig. 2). In particular, during the LGM ($\sim$21,000 years BP, Fig. 2b), SDMs exhibited a suitable area wider than during the LIG ($\sim$120,000 years BP, Fig. 2a). The low habitat suitability inferred for the warmer interglacial period and the higher values inferred for the colder glacial period (Figs. 2, 3) may explain the survival

Fig. 4 Projected impacts of climate change on the distribution of *Berardia subacaulis*. Percentage of range loss (**a**), range gain (**b**), range change (**c**) and range turnover (**d**) as predicted using three general circulation models (MPI-ESM, HadGEM2-ES and IPSL-CM5A-LR) and two representative concentration pathways (RCP2.6 and RCP8.5), for two time slices (2050 and 2070). The *black line* represents the median, *black circle* represents the mean, *edge box* corresponds to the first and third quartiles (the 25th and 75th percentiles), *whiskers* are 1.5 * IQR (where IQR is the inter-quartile range), and *circles* are outliers
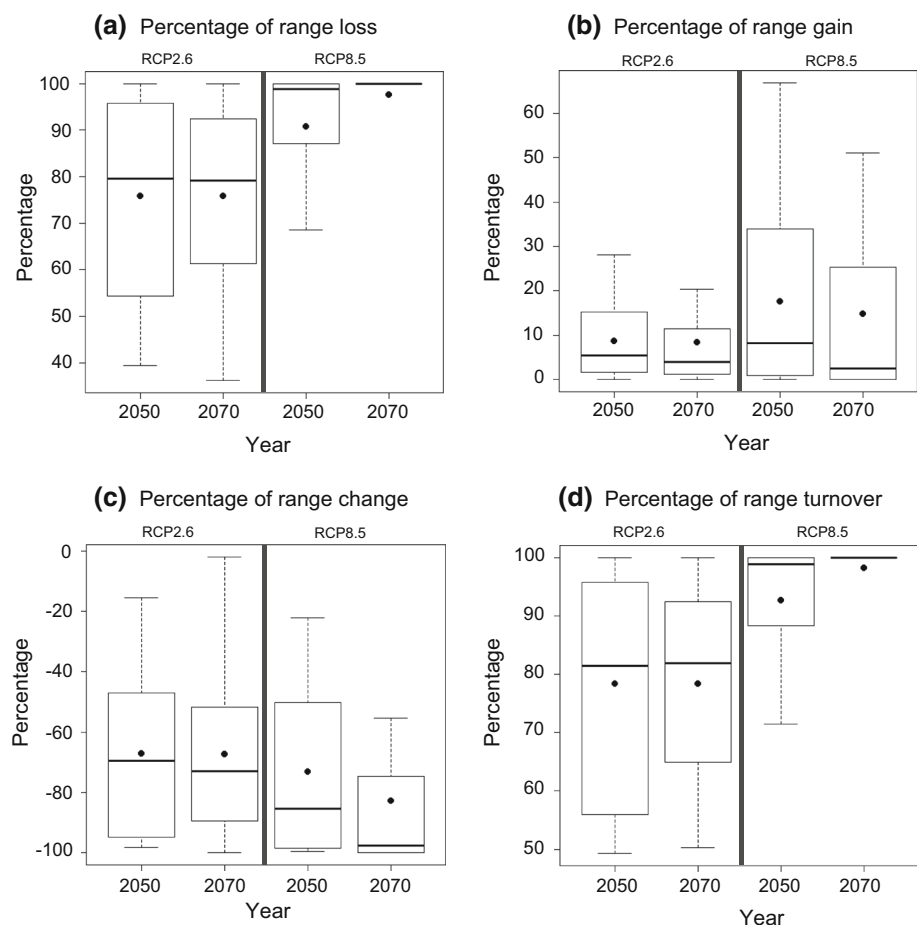
of this species, suggesting that *B. subacaulis* is a cold-loving plant. Contrarily, on the basis of fossil evidence and molecular analyses, range contraction during the glacial period is recorded for other species belonging to the same flora, such as *Ramonda myconi* (Dubreuil et al. 2008), *Frangula alnus* (Hampe et al. 2003), *Tetraclinis articulata* (Médail and Diadema 2009) and *Zelkova sicula* (Di Pasquale et al. 1992). The pattern observed in *B. subacaulis* seems to be more similar to the one recorded for low temperature adapted species, such as *Juniperus thurifera* (Terrab et al. 2008), belonging to the flora differentiated at the end of the Miocene epoch, when the global cooling occurred. This observation is congruent with the morphological adaptations to high mountains conditions detected in *B. subacaulis*. In addition, the pattern observed in *B. subacaulis* fits with the 'displacement refugia model' (Kropf et al. 2003) predicting that European high-elevation plants faced range fragmentation mostly during the warmer, short interglacial periods. A survival in refugia during interglacial periods, such as *B. subacaulis*, has been inferred also for other plant (*Dryas octopetala* and *Betula nana*—Stewart et al. 2009; *Potentilla matsumurae*—Ikeda et al. 2006) and animal species (*Spermophilus citellus*—Musil 1985; *Stenobothrus cotticus*—Berger et al. 2010) on the basis of multidisciplinary analyses. According to Theurillat and Guisan (2001), cold-loving Tertiary relictual species and cold-resistant species probably survived in situ uninterruptedly since the late Tertiary. This hypothesis seems to be likely for *B. subacaulis*, which probably survived the interglacial periods in refugia situated at high altitude in the SW Alps, as shown in the LIG projection (Fig. 2a). As observed by Patsiou et al. (2014) in *Saxifraga florulenta*, *B. subacaulis* could have contracted in microrefugia during adverse periods. During glacial maxima, *B. subacaulis* probably expanded its putative distributional range within SW Alps due to more favourable climatic conditions and to the less severe ice effect in this part of the Alps (Médail and Diadema 2009). In the future, phylogeographical studies will be useful to clarify the history of the species and to confirm the results of the SDMs, since for *B. subacaulis*, as for most of the herbaceous taxa, there are no fossil records. In general, species such as *B. subacaulis* that prefer cooler conditions are of most immediate concern as they face increased threat with further rises in global temperatures (Skov and Svenning 2004). Phylogeographical studies on *B. subacaulis* will elucidate its genetic structure and diversity, two elements that are thought to be important factors for persistence of populations against changing environments (Barret and Kohn 1991). Moreover, genetic studies can improve conservation activities by identifying the populations that have very low genetic diversity. They can also provide information

regarding the extent of gene flow among fragmented populations (Frankham et al. 2010).

Berardia subacaulis currently seems to be at its maximum range expansion, while a severe reduction in habitat suitability is projected for the next few decades (Figs. 2, 3, 4). Similarly, severe reductions have been predicted for both plant and animal species; in particular, 22 % of the European plant species are expected to lose more than 80 % of their range by 2080 (Thuiller et al. 2005b). Greater habitat loss is projected for higher- than lower-elevation species; depending on future climate scenarios, 36–55 % of alpine species will lose more than 80 % of their suitable habitat by 2070–2100, as compared to 31–51 % of subalpine species and 19–46 % of montane species (Engler et al. 2011). Range-size reductions in high mountain plant species are predicted to be more pronounced for endemic (72–76 %) than non-endemic (39–48 %) species (Dullinger et al. 2012). For example, the alpine species *Lilium pomponium*, endemic to the Maritime and Ligurian Alps, is expected to lose more than 80 % of their native range by 2050 (Casazza et al. 2014). Similar studies on vertebrates in the Mediterranean Basin show that endemic species will be severely threatened by global warming (Maiorano et al. 2011, 2013). Moreover, the projected future distribution of plant species may be strongly affected, and even hampered, by the dispersal capability of individual species, which influences their potential to reach new, suitable areas (Engler et al. 2009; Normand et al. 2011).

Conservation implications

Berardia subacaulis appears to lose more than 80 % of its range by 2070 (Fig. 4a) under the full-spread assumption (the possibility to reach all new potential habitat range). The range gain results very low and relatively stable through future time slices (Fig. 4b). Consequently, the increase in range turnover over the next few decades (Fig. 4d) is mainly due to the increase in habitat loss. Under the full-spread assumption, the species will become endangered by 2050. Our results corroborate those of previous, similar studies in the Alps. Using a range of climate change scenarios, Thuiller et al. (2005b) estimated that up to 48.5 % of mountain plant species in the European Alps are at risk of extinction. In general, global warming may result in a significant upward shift in species optimum elevation (Lenoir et al. 2008). However, marginal chains in the Alps have relatively low summit heights, making their alpine plant populations particularly vulnerable to mountaintop extinctions (Dullinger et al. 2012). Fitting this scenario, an altitudinal shift towards higher altitudinal areas does not appear to be a viable option for *B.*

subacaulis, for it has already reached the top of the mountains in the SW Alps (Theurillat and Guisan 2001). Additionally, the increase in competition due to upward shifts in species optimum elevations (Camenisch 2002; Burga et al. 2003; Lenoir et al. 2008; Engler et al. 2009, 2011) may strongly alter species interactions (Suttle et al. 2007; Engler et al. 2009), likely affecting species survival. This phenomenon, however, did not prevent *B. subacaulis* from surviving adverse climatic conditions since its estimated origin in the Oligocene (Barres et al. 2013), for it persisted in extreme habitats characterized by very limited, interspecific competition. Due to the severity and imminence of forecasted, climatic changes, *B. subacaulis* appears to be a useful species to study the direct and indirect effects of global warming on endemic species distribution and the ability of species to adapt to these changes.

Conclusions

As suggested by Schwartz (2012), SDMs are more useful to identify conservation opportunities in newly available habitats under changing climate than they are for asserting where current habitat will no longer exist under future climate conditions. Our results suggest that distinguishing the relative roles of present and past climates in determining species' distributions is not only of theoretical interest, but a key to understand species' responses to climate change, as already observed by Araújo and Pearson (2005). The paucity of local cold-climate refugia at high altitudes, combined with low mobility, exposes alpine endemics to extreme risks of extinction under climate warming (Dullinger et al. 2012). This seems to be the case of *B. subacaulis*: its preference for cool temperature conditions, the low likelihood of upward shift and its low-dispersal capability disproportionately increase extinction risk. Moreover, since *B. subacaulis* is on a long isolated branch on the phylogenetic tree (Susanna et al. 2006; Susanna and Garcia-Jacas 2009; Barres et al. 2013), its loss would represent a large loss of evolutionary history (Faith 2008). Due to its ancient origin and the high percentage of range loss forecasted, *B. subacaulis* seems to be an especially useful model species to study how cold-loving plants survived past warm periods and evaluate the effects of climate warming on their survival.

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