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CLIMATE CHANGES AND THE FUTURE OF ENDEMIC FLORA OF SOUTH-WESTERN ALPS: IMPACT ASSESSMENT AND CONSERVATION STRATEGIES

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Un sincero ringraziamento a Gabriele Casazza,
senza il cui aiuto, supporto e simpatia
questo mio lavoro non avrebbe potuto
concretizzarsi in nulla di sensato.

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1 - INTRODUCTION

1.1 - Biodiversity in a changing world: the climate threat

In the last decades, the world climate has experienced deep change, which probably will continue in the next century (Solomon et al., 2007) and it will produce a serious biodiversity crisis (Thomas et al., 2004). Despite it is difficult to verify a direct link between climate change and recent species extinctions, several studies suggested that climate change will be the greatest threat to biodiversity in the next future, surpassing habitat destruction (Leadley et al., 2010). In fact, climate change can act on all organization levels of biodiversity, from organism to biome, affecting genetic patterns, physiological responses, phenological behavior, population dynamics, distribution of species and habitats, structure and productivity of biotic communities, ecosystem services and biome's integrity (Bellard et al., 2012).

Endemic species are disproportionally threatened by climate change, as they are often confined to very narrow geographical areas and/or specific environments (Thuiller et al., 2005). Moreover, most of endemisms shows poor dispersal capabilities and they consequently are less able to track the shifting of their habitat induced by climate change (Hu & Jiang, 2011). Furthermore, because of the features that make them unique, these species often play a key role in the maintenance of ecosystem integrity (Mouillot et al., 2013). For all these reasons, the conservation of endemic species in the face of climate change represents a major task for biologists.

Forecasting the potential effects of climate change on biodiversity is currently a major challenge in the field of nature conservation and it play a key role in the elaboration of management plans and conservation strategies aimed to mitigate the impact of climate change on biodiversity (Pereira et al., 2010; Parmesan et al., 2011).

1.2 - Species distribution models and niche analysis

Species Distribution Models (hereafter SDM) are the most important tool to forecast the effects of climate change on biodiversity; they combine species occurrences and environmental (mostly climatic) data in order to obtain the spatial projection of the potential niche of species (Guisan & Zimmermann, 2000). Despite several caveats still persist in the methodology (Jarnevich et al., 2015), the statistical analysis of SDMs represent an important connection between habitat field study and the recent development of GIS technology (Elith & Leathwick, 2009). Hence, SDMs are currently employed in several fields of biology (Guisan & Thuiller, 2005; Raxworthy et al., 2007). In particular, in recent years, there has been a growing number of publications that used SDMs to forecast the effects of climate change on biodiversity (e.g., Loarie et al., 2008; Barbet-Massin et al., 2012; Broennimann et al., 2012; Maiorano et al., 2011).

1.3 - South western Alps as a center of endemism

In the Mediterranean Basin, which constitute a global biodiversity hotspot, South western Alps (hereafter SW Alps) are recognized as an important centre of endemism (Médail & Quézel, 1997; Casazza et al., 2008). SW Alps have been a place of contemporary speciation and long-term persistence because of their crossroad position between Mediterranean and Alpine eco-regions, and their complex geological and climatic history since the mid Tertiary (Médail & Diadema, 2009), as demonstrated by the presence of several neo- and paleo-endemisms (Casazza et al., 2005). Moreover, the importance of SW Alps as long-term refuge is supported by phylogeographical studies on both endemic and widely distributed species occurring in this area (Diadema et al., 2005; Minuto et al., 2006; Cheddadi et al., 2006; Szövényi et al., 2009; Grassi et al., 2009; Guerrina et al., 2015; Patsiou et al, 2014).

Several studies based on SDMs showed that in the next future mountainous regions will be more exposed to climate change (Thuiller et al., 2005), and that most mountain species will experience upward shifts of their range (Lenoir et al., 2008). Moreover, in Europe, not all mountainous regions will be equally threatened by climate change: the major impacts will be manifested in mountain chains where the increase in temperature will be accompanied by a decrease of precipitations (Engler et al., 2011). Unfortunately, this chance is expected in SW Alps. For these reasons, the assessment of the climate impact on the endemic flora of SW Alps is very urgent, and it is a useful tool to develop effective conservation strategies.

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2 - CLIMATE CHANGE AND ENDEMISMS: THE FUTURE OF ENDEMIC FLORA OF SW ALPS

2.1 - Introduction

Drawing on evidence from species distribution models, I assessed the effects of climate change on potential range of 100 plant taxa endemic or subendemic of South Western Alps. My research provides an original contribution to understand the effects of climate change on endemic taxa, which are often less used than widely distributed species in studies aimed to investigate climate-induced range dynamics. Moreover, because SW Alps are a very heterogeneous area from environmental point of view, ranging from mediterranean to alpine climate, we investigate whether the relationship between projected range loss and niche properties is different depending on the vegetation belt where species grow.

I found that the distribution pattern of plants endemic to South Western Alps will deeply change in the future, despite the overall species composition of the endemic flora will be little affected by climate change. In particular, those species that currently occupy environmental conditions toward which the climate of the study area is expected to move in the future seem less prone to climate change.

Since our study area is one of the richest biodiversity hotspots of the Mediterranean Basin and the main centre of endemism in the Alps, knowing the effects of climate change on its endemic flora has also important implications for biodiversity conservation. In particular I stress that the urgency of conservation actions on endemics depends on both niche properties and climatic conditions currently experienced by them.

The results of this part of the PhD project were reported in a manuscript entitled “Climate change and the future of endemic flora: a case study from the centre of endemism of South Western Alps”, authored by Davide Dagnino, Luigi Minuto, Mauro Giorgio Mariotti, Frédéric Médail, Katia Diadema, Virgile Noble and Gabriele Casazza. The integral version of the manuscript, that is proposed in this chapter, was submitted to Climatic Change on 12 Febrary 2018.

2-2 - Climate change and the future of endemic flora: a case study from the centre of endemism of South Western Alps

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ABSTRACT

Climate change is a major threat to biodiversity, particularly in mountain ecosystems, which are often important centres of endemism. However, climate change effects are mainly studied on widely distributed taxa. Using species distribution model, we assessed the climate change impact on endemic flora of the richest centres of endemism in the Alps: South Western Alps. Assuming realistic dispersal abilities, we projected the species potential distributions (year 2070) using both an optimistic and a pessimistic scenario. Moreover, we explored the differences among vegetation belts and niche properties. Overall, high range loss and low range gain were predicted for all species, determining a strongly negative range change, mainly caused by dispersal limitation. Nevertheless, the predicted extinction rate was low. Mountain and subalpine species resulted more threatened by climate change than colline species, which are already experiencing dry and warm climate. Moreover, the relationship between range loss and niche properties vary among vegetation belts. The lowest range loss was predicted for specialist (termophilous) species in colline belt and for generalist species in mountain and subalpine belts. Altogether, these results suggest that the distribution pattern of this endemic flora will deeply change in the future, despite its overall species composition will be little affected by climate change. Particularly, those species that currently occupy environmental conditions toward which the climate of the study area is expected to move in the future seem less prone to climate change. These result underline the urgency of elaborating conservation strategies focused on mountain and subalpine taxa.

INTRODUCTION

It is widely accepted that global warming is inducing one of the greatest threats to biodiversity (Bellard et al. 2012; Cahill et al. 2012; Moritz & Agudo 2013; Sax et al. 2013). In particular, mountain ecosystems, that are important centres of biodiversity where species and ecosystems at risk persist (Nogués-Bravo et al. 2007), are particularly exposed to climate change effects, even if their vulnerability is highly variable among mountain systems (Engler et al. 2011). In Europe, the strongest effects of climate change were predicted for Southern European mountain systems, where the increase of temperature will be associated with a decrease of precipitation (Thuiller et al. 2005; Engler et al. 2011; Pauli et al. 2012).

Unfortunately, these predictions were mainly based on widely distributed taxa, whereas knowledge on rare and narrow endemic species are still incomplete (but see Thuiller et al., 2006; Loarie et al., 2008; Dirnböck et al. 2011; Dullinger et al. 2012; Casazza et al. 2014; Cotto et al. 2017). Nevertheless, mountain endemic plant species are expected to be more susceptible to habitat modification induced by climate change (Dirnböck et al. 2011; Dullinger et al. 2012) because they often occur in narrow areas and in a particular habitat (Essl et al. 2009). Moreover, most of them are characterized by low dispersal ability, a feature that has strongly influenced their current distributional range (Essl et al. 2011) and that may decrease their capacity to shift their distributional range in new suitable areas in the future (Malcolm et al. 2002; Engler et al. 2009; Ozinga et al. 2009). For these reasons, to forecast the effects of climate change on mountain endemic plants is currently a primary importance task for conservationists and decision makers. In fact, the estimation of future potential range of species allows to identify the biogeographical changes resulting from climate change and to support the development of proactive strategies to mitigate impacts on biodiversity (Pereira et al. 2010; Parmesan et al. 2011).

South Western Alps (hereafter SW Alps) are located at the crossroads of the Mediterranean Basin and the Alps, and are one of the most relevant biogeographical areas in Europe because of the high number of endemic taxa. In fact, they are the richest centres of endemism in the Alps (Aeschimann et al. 2011) and one of the most important hotspots of the Mediterranean Basin (Médail and Quézel, 1997). The high biodiversity of this area is primarily the result of particular climatic conditions, habitat heterogeneity and biogeographical history (Casazza et al, 2005, 2008). Unfortunately, SW Alps are also one of the European mountain systems that probably will be more prone by climate change.

In this study we use species distribution models (Guisan & Zimmermann 2000) to analyse the potential effects of climate change on 100 plants endemic or subendemic to SW Alps under different climate change scenarios, taking into account their dispersal abilities. Because it was found that the effects of climate change on species distribution are variable along the altitudinal gradient (Engler et al. 2011), we divided studied taxa according to the major vegetation belts characterizing the study area. Moreover, as the ecological characteristic of species can affect their sensitivity to climate change (Thuiller et al. 2005b), we explore the relation between potential range loss and niche properties. More specifically, we are asking the following questions: i) How and how much climate change will affect the distributional range of endemic taxa? ii) Are there predictors related to the extinction risk of endemic species?

METHODS

Study area and taxa

The study area includes SW Alps (sensu SOIUSA; Marazzi 2005) and surrounding area (Online Resource 1), to take into account the entire distributional range of sub-endemic taxa (i.e., taxa in which at least 75% of the populations occur in the SW Alps). According to data availability, we selected 100 plants endemic (68 taxa) or subendemic (32 taxa) of SW Alps, representing the 56% and the 80% of the endemic and subendemic flora of this area, respectively (Online Resource 2).

Environmental layers

Nineteen bioclimatic variables representative of current (1960-1990) and future (2070) conditions were downloaded from the WorldClim dataset website (version 1.4; http://www.worldclim.org) at about 1x1 km spatial resolution (Hijmans et al. 2005). To reduce collinearity and to minimize model overfitting, pairwise Pearson correlation between current bioclimatic predictors was calculated and only seven predictors, that were not highly correlated ($r \leq |0.70|$), were retained (Fig. 1). For future conditions, two Representative Concentration Pathways, representing moderate and extreme possible future emission trajectories, were selected: RCP2.6 and RCP8.5 (hereafter optimistic and pessimistic scenario, respectively). For each RCP we used projections from four international recognized circulation models (GCMs), which represent physical processes in the atmosphere, ocean, cryosphere and land surface (Fig. 1). In addition, a layer reporting substrates was obtained from lithological map data set GLiM (Hartmann & Moosdorf 2012). We considered ten lithological categories, assigning each pixel to the most represented lithological category. Eventually, we obtained one environmental data set for the present and four environmental data sets for each future scenario (Fig. 1).

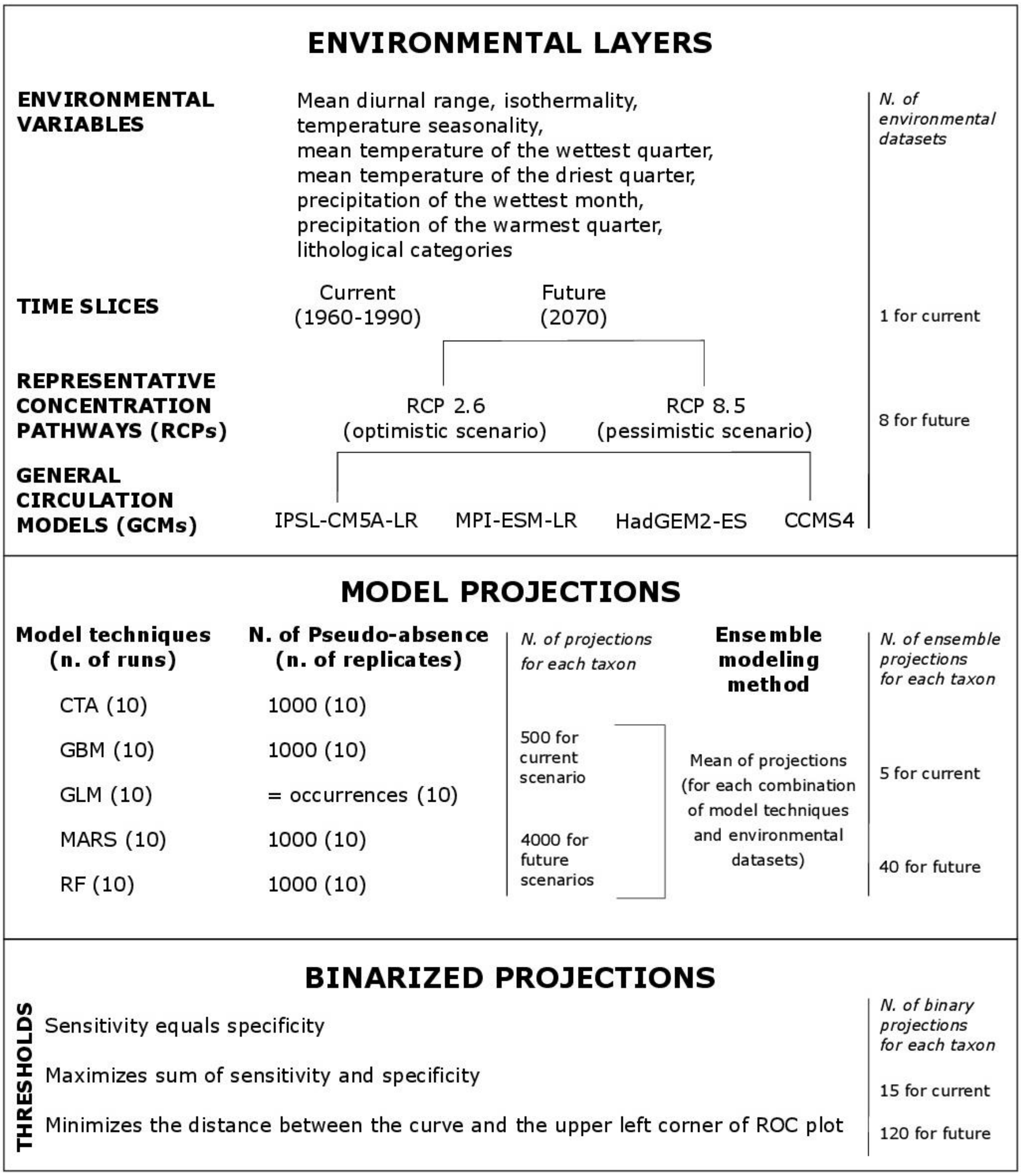


***Fig. 1 (previous page)** Environmental layers and model settings. RCP2.6 and RCP8.5 are two representative concentration pathways named according to two possible range of radiative forcing values in the year 2100 relative to preindustrial values (+2.6 and +8.5 W/m^2, respectively). GCMs are general circulation models provided by Institut Pierre-Simon Laplace (IPSL-CM5A-LR), Max Planck Institute for Meteorology (MPI-ESM-LR), Met Office Unified Model (HadGEM2-ES) and Community Earth System Model (CCMS4). Optimistic and pessimistic scenarios are the mean value of the four GCMs for RCP2.6 and RCP8.5, respectively. Model techniques: CTA, Classification Tree Analysis (Breiman et al. 1984); GBM, Generalised Boosted Models (Ridgeway 1999); GLM, Generalized Linear Models (McCullagh & Nelder 1989); MARS, Multivariate Adaptive Regression Splines (Friedman 1991); RF, Random Forest (Breiman 2001).*

Species Distribution Models

To account for model-based uncertainties in the modelling process (Araújo & New 2007; Petchey et al. 2015), five SDM techniques included in the R package (R Development Core Team, 2008) BIOMOD2 v 3.3.7 (Thuiller et al. 2009) were used (Fig.1). For each taxon we generated 10 replicate sets of pseudo-absences, setting the number of pseudo-absences according to Barbet-Massin et al (2012). To taking into account the environmental heterogeneity of the study area, pseudoabsences were selected using the spatial exclusion criterion, setting the minimum and maximum distance from occurrences equals to 5 and 50 km, respectively. For each pseudo-absence set, a split-sample cross-validation was repeated 10 times, using a random subset (30%) of the initial data set (Fig. 1). Model performance was evaluated using three different measures implemented in BIOMOD2: AUC (Hanley & McNaeil 1982), KAPPA (Monserud & Leemans 1992) and TSS (Allouche et al. 2006). Finally, for each taxon we obtained 5 current and 40 future projections calculating the mean value of runs and pseudo-absence sets per combination of modelling techniques and environmental datasets (Fig. 1). The suitability maps obtained from ensemble projections were converted into binary distribution maps. Because the choice of threshold is critical by increasing or decreasing prediction bias, three different thresholds implemented in the R package PresenceAbsence (Freeman & Moisen, 2008) were selected (Fig. 1) according to Cao et al. (2013) and Liu et al. (2005). We then considered species as occurring in a cell if at least 50% of models predict its occurrence there (i.e., a majority consensus rule).

Spatial indices for distribution under future climates and dispersal scenario

The percentage of predicted future range change (RC) was estimated using the formula RC=100x(RG-RL)/PR, where range gain (RG) is the number of grid cells projected to be not suitable under current condition but suitable under future climate, range loss (RL) is the number of grid cells projected to be suitable under current climate but unsuitable under future climate and present range

(PR) is the number of grid cells projected suitable under current climate. A positive RC value indicates a forecasted increase in range size, while a negative value indicates a forecasted decrease in range size. To avoid that currently suitable areas that are too far from occurrences might affect the analysis, the calculation of PR was restricted to grid cells that are no more than 5 km away from species occurrences.

To forecast the effects of climate change on species distribution, a key role is played by dispersal ability of species, affecting their capability to track the geographical shift in suitable environments (Malcolm et al. 2002). In order to take into account dispersal ability of species, we assigned each species to one of the seven dispersal categories defined by Vittoz and Engler (2007) based on dispersal vector and plant traits. To obtain the maximum distance that each species could reach in 2070, the upper limit of the distances within which 99% of seeds of each species are dispersed was multiplied for 55 years (Online Resource 2). Then, the maximum dispersal distance for each species was used to buffering future distribution to a buffer zones around PR of the species. Then, we calculated the average and the standard deviation of RC, RG and RL values for both optimistic and pessimistic scenarios.

To analyse the potential impact of climate change per vegetation belt, we assigned each taxa to one of the three belts defined using both altitude and mean annual temperature according to Engler et al. (2011): colline (C); mountain (M); subalpine (S). Each species was assigned to the vegetation belt in which the highest frequency of occurrences was recorded (Online Resource 2). To test whether the optimistic scenario differed significantly from pessimistic one in all spatial indices (RL, RG and RC), we used a Kruskal–Wallis test. The analysis was performed considering both all species together and species occurring into each vegetation belt.

Correlates of extinction risk

To understand which niche properties are more useful to explain the degree of RL variation among taxa, we performed a hierarchical partitioning analysis using the R package HIER.PART (Walsh & Mac Nally 2013). Analyses were carried out for each vegetation belt. We considered niche marginality and breadth (*sensu* Dolédec et al. 2000), altitudinal range, and PR. Niche marginality is calculated using the OMI index which is the distance between the mean habitat conditions used by species and the mean habitat conditions of the study area. Niche breadth is calculated using the tolerance index, which is the variance of habitat conditions used by the species. Altitudinal range is calculated as the standard deviation of the altitude of species occurrences and it could be considered as a proxy of niche breadth (Essl et al. 2009). We used linear regression to test correlation between RL and niche properties.

RESULTS

Under current climate conditions, model evaluation indices mainly indicate a good model performance for all modelling techniques in the majority of species (Online Resource 3). Considering all species together, significant differences in spatial indices were detected between optimistic and pessimistic scenarios, with the exclusion of RG values (Fig.2). The average RL values were high (optimistic: 69.75 sd = 25.24, pessimistic: 89.28 sd = 13.89) and the RG values were low (optimistic: 7.09 sd = 6.82, pessimistic: 3.76 sd = 5.74) under future climatic conditions (Fig. 2, Online Resource 4). According with these results, the average values of the predicted RC were highly negative (optimistic: -62.66 sd = 31.71, pessimistic: -85.52 sd = 19.44) with few exceptions (four species under optimistic scenario and two species under pessimistic scenario have positive RC values - Fig. 2, Online Resource 4). In particular, a loose of potential range greater than 80% was forecasted for the 27% and for the 77% of species under optimistic and pessimistic scenarios, respectively. The 24% of species were projected to became extinct under pessimistic scenario while no species were predicted to became extinct under the optimistic one (Online Resource 4).

Considering vegetation belts, mountain species showed the highest RL, while colline species showed the lowest RL and the highest RG, both in optimistic and pessimistic scenario (Fig. 2, Online Resource 4). Both RL and RC were significantly different between emission scenarios in all vegetation belts (Fig. 2, Online Resource 4).

The relative importance and the total percentage of variance explained by niche properties considered in hierarchical partitioning analysis were variable among vegetation belts (Fig. 3). In colline species, niche marginality and altitudinal range were the two most likely causal factors explaining independent effects on RL in both scenarios (Fig. 3). In particular, niche marginality was significantly negatively correlated and altitudinal range was significantly positively correlated with RL. In mountain species, the most likely predictor was niche breadth, which was significantly negatively correlated with RL in optimistic scenario. In subalpine species, altitudinal range and niche breadth were the most likely predictors in optimistic and pessimistic scenario, respectively. Both predictors were significantly negatively correlated with RL. The relative importance of PR was very low and not significant in all vegetation belts.

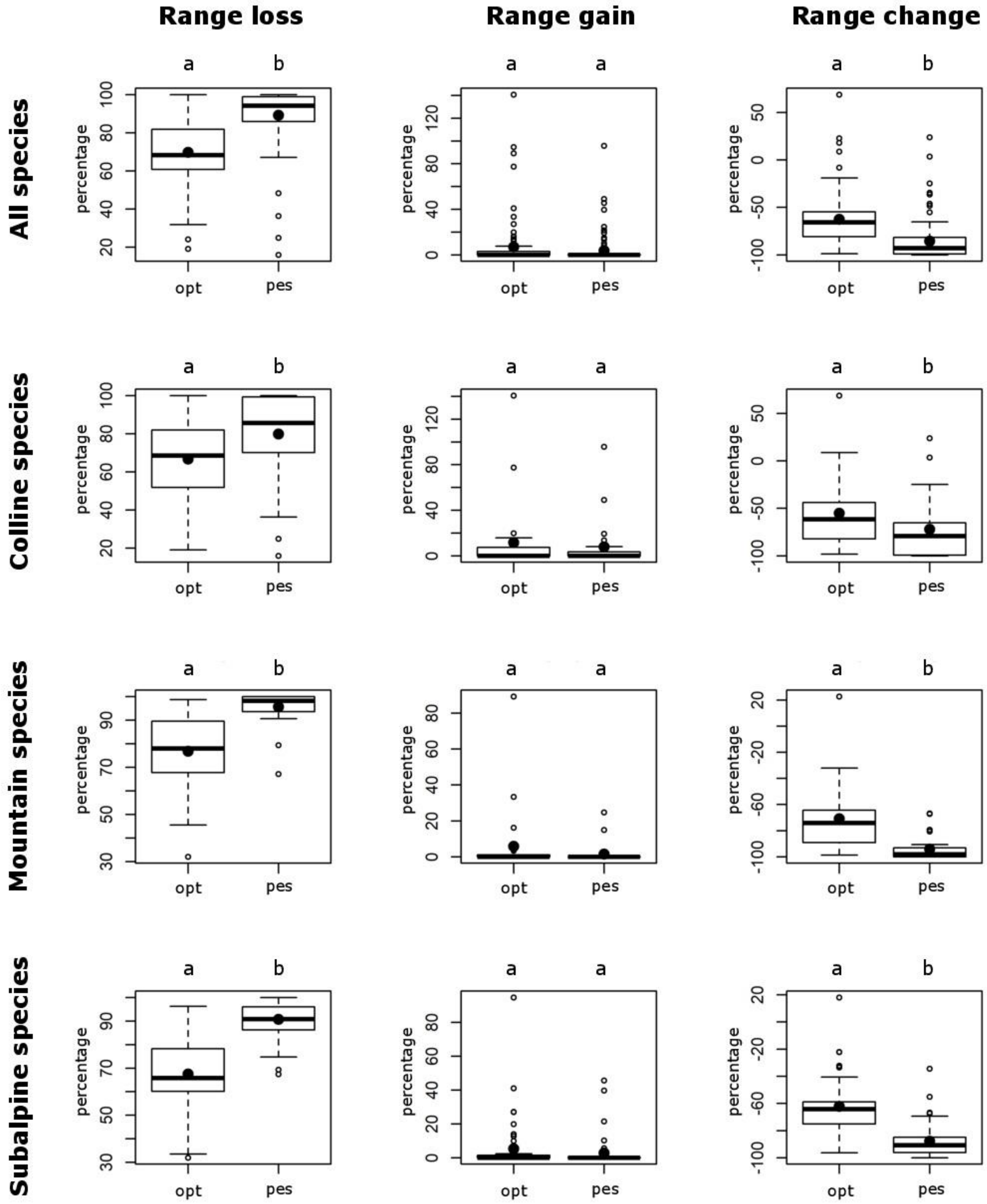
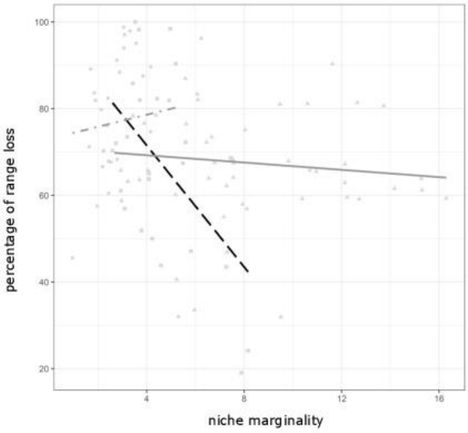
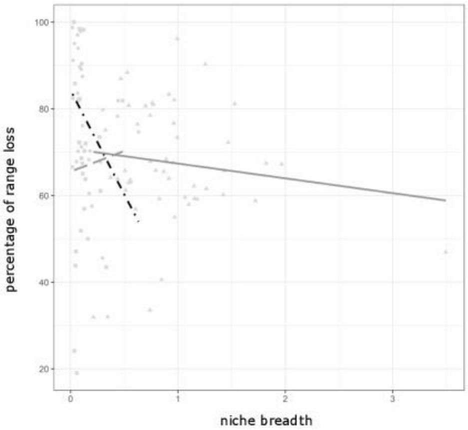


Fig. 2 *Projected impact of climate change on the distribution of the 100 studied taxa under future climate conditions. Opt: optimistic scenario; pes: pessimistic scenario. The values of range loss, range gain and range change are shown both for all species together and for species belonging to different vegetation belts (colline, mountain and subalpine). 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). The letters above the boxplots indicate the presence (same letters) or the absence (different letters) of a significant difference between the values of the two scenarios detected using the non-parametric Kruskal-Wallis test.*

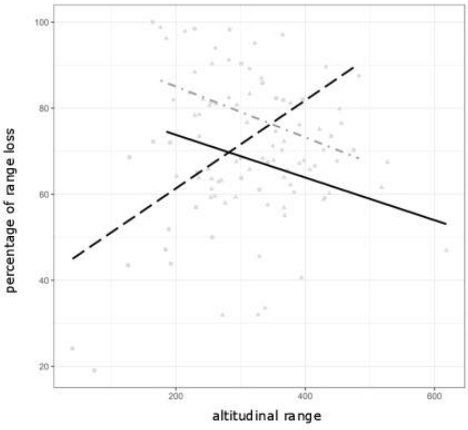
Optimistic scenario



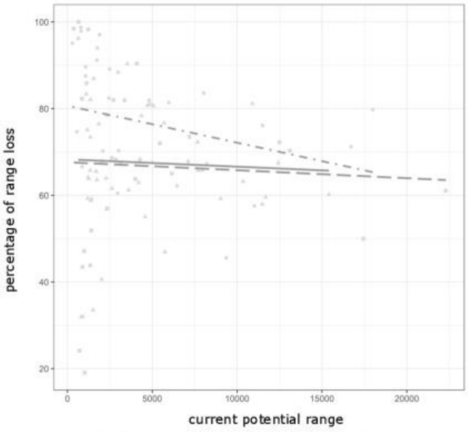
(colline: 43.67; mountain: 3.12; subalpine: 10.82)



(colline: 1.03; mountain: 59.83; subalpine: 11.28)

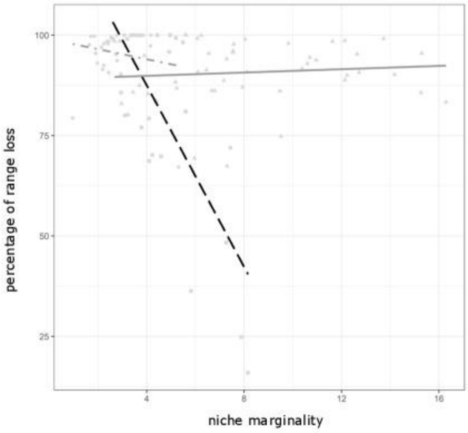


(colline: 44.4; mountain: 24.3; subalpine: 77.14)

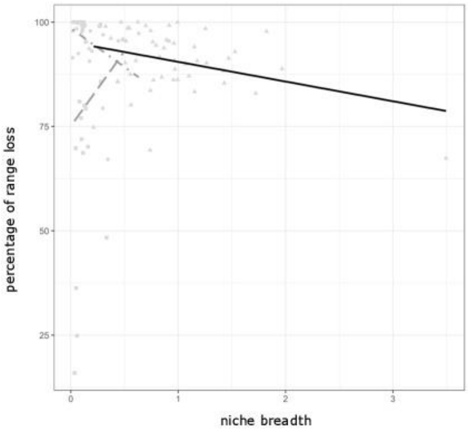


(colline: 10.9; mountain: 12.75; subalpine: 0.76)

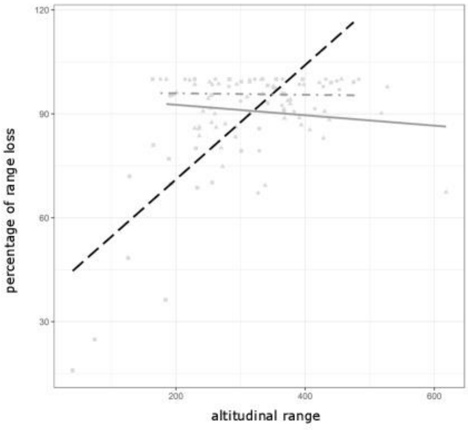
Pessimistic scenario



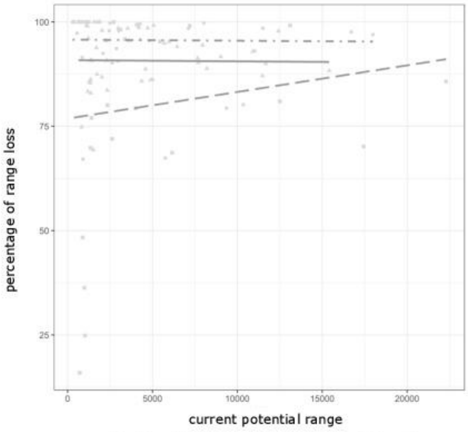
(colline: 47.56; mountain: 14.13; subalpine: 8.41)



(colline: 1.52; mountain: 83.06; subalpine: 74.63)



(colline: 48.03; mountain: 0.29; subalpine: 12.97)



(colline: 2.89; mountain: 2.52; subalpine: 4)

Fig. 3 (previous page). *Correlation between range loss and niche properties (niche marginality, niche breadth, altitudinal range, present range) for studied taxa belonging to each vegetation belt. Squares and dashed lines: colline species; circles and dot-dashed lines: mountain species; triangles and solid lines: subalpine species. Black lines indicate a statistically significant correlation (p value < 0.05); grey lines indicate a non-significant correlation (p value > 0.05). The relative importance of each niche property in different vegetation belts calculated with hierarchical partitioning analysis was reported in brackets. The total percentages of variance explained by all niche properties are: colline species: 41.49 (optimistic scenario), 67.33 (pessimistic scenario); mountain species: 28.74 (optimistic scenario), 15.25 (pessimistic scenario); subalpine species: 14.85 (optimistic scenario), 15.5 (pessimistic scenario)*

DISCUSSION

Our results indicate that in general plants endemic to SW Alps will be prone to high degree of range loss and low degree of range gain, resulting in highly negative degree of range change (Fig. 2, Online Resource 4). The projected change was different under the two analysed scenarios These results are in line with other studies on plants endemic to other biogeographical regions (Central-northern Mediterranean region: Casazza et al. 2014; California: Loarie et al. 2008; South Africa: Thuiller et al. 2006) and on widely distributed plants of Europe (Engler et al. 2011; Thuiller et al. 2005). However, differently to other studies (Casazza et al. 2014; Loarie et al. 2008; Thuiller et al. 2005a, 2006) the RG will not predicted to mitigate the RL. This difference may depend on the use of different dispersal scenarios (unlimited dispersal vs. realistic dispersal scenario). In fact, the unlimited dispersal scenario assumes that a species can colonize all locations without physiological, environmental or geographical limitations. This assumption allows to obtain high RG values but it is unrealistic. Most SW Alps endemic plants are mainly able to spread across a relatively short distance because of their dispersal strategies, primarily limited by the absence of specialized diaspores and by the short stem height. Nevertheless, species with weak dispersal abilities might be able to track their climatic requirements in highly environmental heterogeneous areas, like SW Alps, because species have to cover short distance to fully occupy climatically suitable areas (Engler et al. 2009; Loarie et al. 2009; Sandel et al. 2011). Indeed, short-distance altitudinal migrations seem to have favoured both genetic diversity and populations survival in some SW Alps endemic plants during Quaternary climate changes (Diadema et al. 2005; Patsiou et al. 2014; Guerrina et al. 2015; Casazza et al. 2016). However, the low degree of RG detected in our study suggests that the SW Alps endemic plants may not be able to keep up with future climate change and consequently will strongly reduce their distributional range.

Although species are predicted to lose most of their distributional range, a low number of them is expected to became extinct because of climate change (0% and 24% under optimistic and pessimistic scenario, respectively). This result suggests that the overall endemic species composition in SW Alps will be less affected by future climate change than distributional patterns of species. This observation is in line with the hypothesis that the rugged topography buffered the past climate changes and promoted the current endemism richness in this area minimising the extinction and favouring the diversification of species and genetic lineages (Medail & Diadema 2009; Casazza et al. 2016). Similarly, it was supposed that the same process will lead to low future extinction rate in centres of endemism (Harrison & Noss 2017). For these reasons, to understand how past climate has influenced the distributional pattern of endemics might enable us to detect future microrefugia within this centre of endemism, which will probably be disproportionally important for conservation purposes, particularly in the eventuality of pessimistic scenario of future climate (Graham et al. 2006, 2010; Svenning et al. 2011; Harrison & Noss 2017).

Moreover, we found a different effect of climate change among vegetation belts. The majority of subalpine and montane species will lose potentially suitable habitat without any gain. On the contrary, in colline species the potential loss of habitat will be partially mitigate by range gain (Fig. 2). These results are in line with previous findings according to which species growing at higher elevation are more exposed to loss of potentially suitable habitat than species growing at lower elevations (Engler et al. 2011; Gottfried et al. 2012). In fact, low elevation species are supposed to be less sensitive to climate change because they have more opportunity to upward their range shift (Engler et al. 2011). The lowest impact detected in species belonging to colline belt is in line with previous findings (Thuiller et al. 2005b) according to which in climates with large seasonal variations, such as the Mediterranean climate, the future climatic conditions will probably lie within those to which the species are already exposed (Thuiller et al. 2005b, 2006; Tielbörger et al. 2014). In fact, colline species that grow in Mediterranean condition are already experiencing a warm and dry season.

Niche properties are expected to strongly affect plant response to climate change because they are related to the degree of ecological specialization of species (Thuiller et al. 2005a, 2005b; Broennimann et al. 2006; Clavel et al. 2011; Casazza et al. 2014). In line with this general expectation, we found that niche marginality, niche breadth and altitudinal range were significantly correlated to RL, even if their importance changes among the vegetation belts (Fig. 3). In particular, the lowest values of RL in colline species were recorded in climatically restricted species (specialist species) showing high marginality and low altitudinal range, such as steno-Mediterranean species like *Senecio leucanthemifolius* subsp. *crassifolius*, *Limonium cordatum* and *Limonium pseudominutum*. These species are characterized by high levels of marginality because they grow in a Mediterranean climate within a mountain area mainly characterized by temperate conditions. Moreover, they show a low altitudinal range, because they are restricted to the lowest part of the colline belt. As previously discussed, these species are currently occupying environmental conditions toward which the climate of the study area is expected to move in the future. Differently, the lowest values of RL in mountain and subalpine species were recorded in species growing in a broad array of climate conditions (generalist species) showing wide niche breadth and altitudinal range (Fig. 3). This result is in line with the general expectation that generalist species are less sensitive to future climate change (Thuiller et al. 2005b; Clavel et al. 2011). However, despite their ability to survive in many environmental conditions, these species were not predicted to gain range because they grow in climatic conditions that are far from those forecasted in the future (Thuiller et al. 2005b). Our results suggest that even if a relationship exists between niche properties and plants sensitivity to climate change, this relationship is affected by the difference between the current climate where species grow and the forecasted climate. For this reason, specialist endemic species of SW Alps that grow in warm and arid conditions may be less affected by future climate change than generalist endemic species growing in cold conditions.

Taken together our results suggest that endemic plants of the SW Alps are threatened by climate change similarly to wide distributed taxa. Nevertheless, despite the high range loss forecasted, the number of species projected to became extinct is low. This support the idea of centres of endemism as areas of long-term persistence over past and future climate changes. Furthermore, even if niche properties are indictors of species sensitivity to climate change, an idiosyncratic response exists across different vegetation belts. Colline species climatically restricted to Mediterranean climate were predicted to lose proportionally less suitable habitat and gain more new habitats than mountain and subalpine species probably because they are already exposed to the warm and dry forecasted conditions. For these reasons, our results outline the urgency of conservation strategies focused on mountain and subalpine species characterized by narrow niche and low altitudinal range.

Online Resource

The following Online Resource are available online: detailed description of the study area (Online Resource 1), selection procedure and characteristics of the studied taxa (Online Resource 2), model performance (Online Resource 3), results of range analysis (Online Resource 4).

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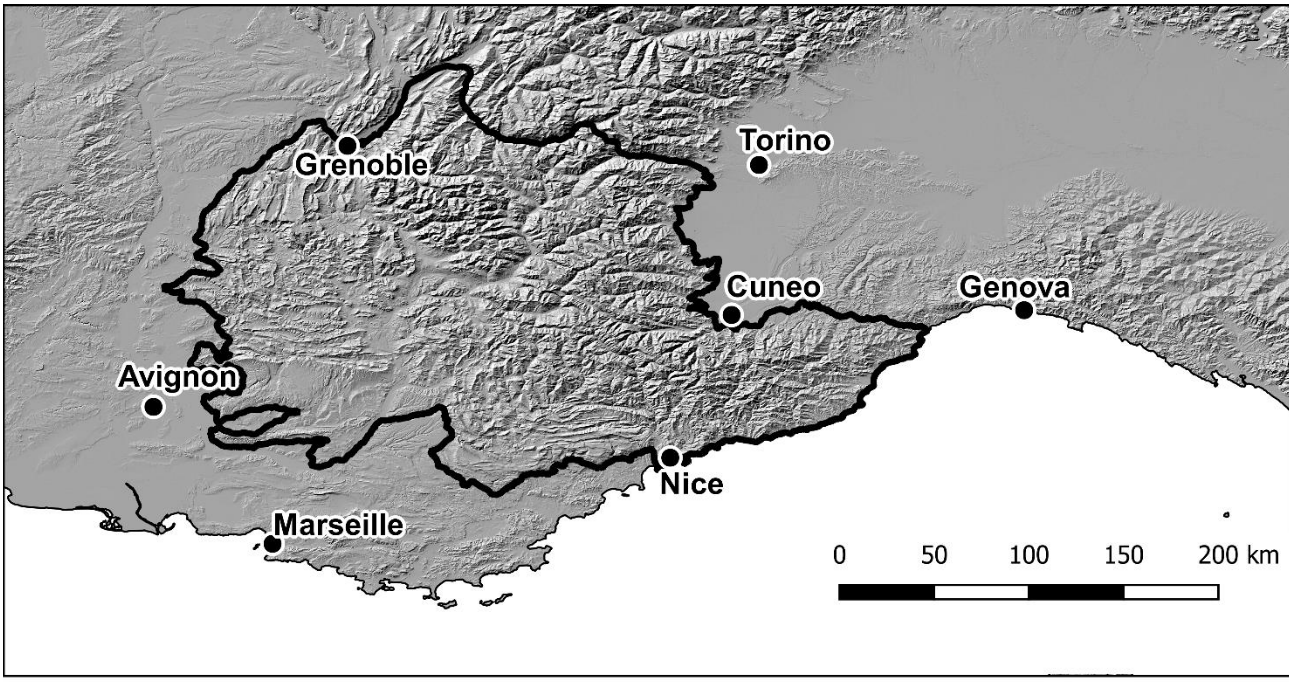
Online Resource 1 - detailed description of the study area

The area involved in this study is centred on the South-Western Alps (sensu SOIUSA; Marazzi 2005), harboring high levels of species richness and endemism rate (Aeschimann et al. 2011; Casazza et al. 2008; Casazza et al. 2005; Médail & Quézel 1997; Pawlowski 1970). However, to take into account the entire distributional range of sub-endemic species, the study area has been expanded to close biogeographical areas. The final study area (from 4.0° to 10.0° E; from 42.8° to 45.6° N) covers over 160.000 km^2, with an altitudinal range from sea level to 4800 m. This area exhibits a high environmental heterogeneity, both from a climatic (Rivas-Martinez et al. 2004) and lithological (Hartmann & Moosdorf 2012) point of view, but also a complex biogeographical and palaeoenvironmental history (e.g. Fauquette et al. 2017).



Study area, the area within the black line indicates the South Western Alps.

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Online Resource 2 – Studied taxa: selection procedure and characteristics

1.1 – Details on taxa selection procedure

In SW Alps total of 161 plant taxa endemic (i.e., all the populations within the SW Alps; 121 taxa) or subendemic (i.e., at least 75% of the populations within the SW Alps; 40 taxa) were detected. Nevertheless, because of different kinds of pitfalls some species were not considered in the following analyses: i) taxa very similar to each other or recently split in several subtaxa for which distributional data are of uncertain attribution (e.g., *Odontites luteus* subspecies and *Cotoneaster* spp.), ii) recently described taxa whose distribution range is still incompletely known (e.g., *Moehringia argenteria* Casazza & Minuto and *Viola laricicola* Marcussen), iii) taxa showing lacks in distributional data (e.g., *Sedum fragrans* 't Hart and *Primula cottia* Widmer), iv) species growing in very narrow and patchy habitats (e.g., *Pinguicula* spp.), and v) taxa with very narrow distributional range (occurring in less than 30 km^2; e.g., *Campanula albicans* (Buser) Engl. and *Acis fabrei* (Quézel & Girerd) Lledo et al.). Eventually, we selected 100 plant taxa both endemic (68 taxa, representing the 56% of the total endemic flora of SW Alps) and subendemic (32 taxa, representing the 80% of the total subendemic flora of SW Alps).

1.2 - Ecological, geographical and life-history traits of 100 studied taxa.

Legend: degree of endemicity respet of South-Western Alps (End.): E – endemic, S – subendemic; number of occurrences (Occ.); dispersal ability (DA): maximum distance that could be reached by the species in 2070 (km); vegetation belt (VB): C – colline, M – mountain, S – subalpine; growth form (GF): P – Phanerophytes, C – chamaephytes, H – hemicryptophytes, G – geophytes, T – therophytes; generation length (GL): A – annual, H – perennial herb, W – perennial woody; Grime's category (GC): S – stress tolerant, C – competitive-stress tolerant, R – ruderal-stress tolerant; range size (RS): number of grid cells occupied by the species; altitudinal range (AR): standard deviation of the altitude of species occurrences; marginality (OMI): distance between the mean habitat conditions used by species and the mean habitat conditions of the study area; niche breadth (Tolerance): variance of the habitat conditions used by a species.

Taxon	**Family**	**End.**	**Occ.**	**DA**	**VB**	**GF**	**GL**	**GC**	**RS**	**AR**	**OMI**	**Tolerance**
Acis nicaeensis (Ardoino) Lledo et al.	Amaryllidaceae	E	352	0.825	C	G	H	CS	83	229	4.9615	0.084551
Allium narcissiflorum Vill.	Alliaceae	S	1102	0.275	S	G	H	CS	574	377	7.278509	1.150056
Allium scaberrimum J.Serres	Alliaceae	E	140	0.275	C	G	H	CS	126	301	4.089979	0.13847
Androsace chaixii Gren.	Primulaceae	E	744	0.055	M	T	A	RS	500	221	1.848926	0.065432
Anthemis cretica L. subsp. *gerardiana* (Jord.) Greuter	Asteraceae	E	273	0.055	C	H	H	CS	184	366	4.9207	0.485667
Aquilegia reuteri Boiss.	Ranunculaceae	E	852	0.275	S	H	H	S	498	314	2.935909	0.506328
Arabis allionii DC.	Brassicaceae	E	49	0.055	S	H	A	CS	49	338	5.960416	0.738754
Arenaria cinerea DC.	Caryophyllaceae	E	107	0.055	M	C	H	CS	73	282	2.41085	0.020723
Arenaria provincialis Chater & G.Halliday	Caryophyllaceae	E	930	0.055	C	H	A	S	223	184	5.816142	0.049807
Asperula cynanchica subsp. *rupicola* (Jord.) Berher	Rubiaceae	E	389	0.055	S	H	H	S	224	229	3.435915	0.435983
Asperula hexaphylla All.	Rubiaceae	E	220	0.055	S	H	H	S	125	332	5.580736	0.467441
Asplenium jahandiezii (Litard.) Rouy	Aspleniaceae	E	101	27.5	C	H	H	S	49	164	3.533573	0.032337
Ballota frutescens (L.) J.Woods	Lamiaceae	E	180	0.825	C	C	W	S	87	189	3.784987	0.095845
Berardia subacaulis Vill.	Asteraceae	E	767	0.825	S	G	H	S	526	254	12.64321	0.762315
Brassica repanda (Willd.) DC. subsp. *repanda*	Brassicaceae	S	683	0.055	S	H	H	S	406	618	7.295532	3.494457
Campanula alpestris All.	Campanulaceae	S	2121	0.275	S	H	H	S	1294	377	10.60407	1.528878
Campanula elatines L.	Campanulaceae	E	111	0.275	M	H	H	S	100	383	2.437248	0.174795
Campanula fritschii Witasek	Campanulaceae	E	77	0.055	M	G	H	S	65	364	2.224609	0.070404
Campanula rotundifolia L. subsp. *macrorhiza* (J.Gay ex A.DC.) Bonnier & Layens	Campanulaceae	S	1746	0.275	C	C	H	S	1147	475	2.598344	0.129562
Campanula sabatia De Not.	Campanulaceae	E	240	0.055	C	H	H	RS	105	355	4.431604	0.085782
Campanula stenocodon Boiss. & Reut.	Campanulaceae	E	513	0.275	S	H	H	CS	383	367	6.453298	1.468772
Carex ferruginea subsp. *tenax* (H.Christ) K.Richt.	Cyperaceae	S	4672	82.5	S	H	H	CS	1311	437	5.179375	1.42297
Centaurea jordaniana Godr. & Gren.	Asteraceae	E	277	8.25	M	H	H	CS	97	415	2.188772	0.018097
Centaurea paniculata L. subsp. *polycephala* (Jord.) Nyman	Asteraceae	E	127	8.25	C	H	A	RS	106	301	5.195911	0.103344
Centaurea uniflora Turra subsp. *uniflora*	Asteraceae	S	2145	8.25	S	H	H	CS	1198	276	7.934577	1.10039

Coincya richeri (Vill.) Greuter & Burdet	Brassicaceae	S	1005	0.275	S	H	H	CS	363	256	11.6231	1.254566
Crocus ligusticus Mariotti	Iridaceae	S	300	0.055	C	G	H	CS	193	342	5.486938	0.109746
Crocus versicolor Ker Gawl.	Iridaceae	S	1205	0.055	M	G	H	CS	863	453	2.137858	0.300841
Cytisus ardoinii E.Fourn.	Fabaceae	E	215	0.275	M	C	W	CS	117	176	3.05809	0.01686
Cytisus sauzeanus Burnat & Briq.	Fabaceae	E	242	0.275	M	C	W	S	157	314	1.702383	0.09762
Dianthus furcatus Balb. subsp. *furcatus*	Caryophyllaceae	E	306	0.055	S	H	H	CS	229	368	7.166318	0.968946
Dianthus pavonius Tausch	Caryophyllaceae	S	2491	0.055	S	C	H	CS	1403	250	10.69753	0.793274
Dianthus subacaulis Vill.	Caryophyllaceae	E	330	0.055	S	C	H	S	169	255	3.696423	0.554949
Epipactis leptochila (Godfery) Godfery subsp. *provincialis* (Aubenas & Robatsch) J.M.Tison	Orchidaceae	E	106	0.825	C	H	H	CS	72	231	3.102156	0.127844
Eryngium spinalba Vill.	Apiaceae	E	1066	8.25	S	H	H	CS	414	229	2.887621	0.528563
Erysimum burnatii Vidal	Brassicaceae	E	73	0.055	S	H	H	CS	64	394	5.226364	0.845936
Euphorbia canutii Parl.	Euphorbiaceae	S	232	0.275	M	G	H	CS	149	300	2.782013	0.171126
Euphorbia graminifolia Vill.	Euphorbiaceae	S	120	0.275	C	H	H	CS	56	283	3.68169	0.121514
Euphorbia variabilis subsp. *valliniana* (Belli) Jauzein	Euphorbiaceae	E	72	0.055	M	G	H	S	44	354	4.154826	0.632065
Festuca scabriculmis (Hack.) K.Richt.	Poaceae	S	471	0.825	S	H	H	CS	328	266	12.13523	0.541549
Fritillaria involucrata All.	Liliaceae	E	1056	0.275	M	G	H	CS	680	391	2.371198	0.111148
Fritillaria tubaeformis Gren. & Godr. subsp. *moggridgei* (Baker) Rix	Liliaceae	E	118	0.055	S	G	H	CS	68	201	7.545923	0.371742
Fritillaria tubaeformis Gren. & Godr. subsp. *tubaeformis*	Liliaceae	E	323	0.055	S	G	H	CS	215	294	2.676556	0.541816
Galeopsis reuteri Rchb.f.	Lamiaceae	E	152	0.825	M	T	A	RS	125	428	2.242505	0.181723
Galium pseudohelveticum Ehrend.	Rubiaceae	S	1149	0.055	S	H	H	S	558	391	12.13955	1.965821
Galium saxosum (Chaix) Breistr.	Rubiaceae	E	283	0.055	S	H	H	S	134	242	6.098375	0.965402
Genista lobelii DC.	Fabaceae	E	397	0.275	C	C	W	S	156	192	4.58593	0.046152
Gentiana burseri Lapeyr. subsp. *actinocalyx* Polidori	Gentianaceae	E	48	0.825	S	H	H	CS	38	272	9.506245	0.212545
Gentiana burseri Lapeyr. subsp. *villarsii* (Griseb.) Rouy	Gentianaceae	S	454	0.825	S	H	H	CS	296	262	9.467913	0.770155
Gentiana rostanii Reut. ex Verl.	Gentianaceae	E	673	0.055	S	H	H	CS	434	252	13.72553	0.698258
Gymnadenia nigra (L.) Rchb.f. subsp. *corneliana* (Beauverd) J.M.Tison	Orchidaceae	S	984	27.5	S	G	H	CS	712	254	10.37722	0.827079
Hedysarum hedysaroides (L.) Schinz & Thell. subsp. *boutignyanum* (A.Camus) Jauzein	Fabaceae	E	839	0.825	S	H	H	CS	442	293	6.785159	0.955531
Helianthemum lunulatum (All.) DC.	Cistaceae	E	133	0.055	S	C	W	CS	90	422	8.033691	0.324433

Helictotrichon sempervirens (Vill.) Pilg.	Poaceae	E	1801	82.5	S	H	H	CS	1030	270	3.227878	0.560617
Helictotrichon setaceum (Vill.) Henrard	Poaceae	S	880	82.5	S	H	H	CS	448	310	3.89818	0.960793
Heracleum pumilum Vill.	Apiaceae	E	209	0.055	S	H	H	RS	96	236	6.663933	0.994087
Hesperis inodora L.	Brassicaceae	E	33	0.275	M	H	H	RS	27	327	5.308024	0.345379
Hormathophylla halimifolia (Boiss.) P.Küpfer	Brassicaceae	E	387	0.825	M	C	W	S	261	449	2.533152	0.278456
Hyacinthoides italica (L.) Rothm.	Hyacinthaceae	S	656	0.275	C	G	H	CS	460	440	3.199099	0.269589
Iberis aurosica Chaix	Brassicaceae	E	154	0.055	S	H	H	S	79	428	2.965409	1.721633
Iberis nana All.	Brassicaceae	E	141	0.055	S	H	H	S	69	314	6.073569	0.91633
Jovibarba allionii (Jord. & Fourr.) D.A.Webb	Crassulaceae	S	467	8.25	S	C	H	S	306	334	7.536358	0.890755
Leucanthemum burnatii Briq. & Cavill.	Asteraceae	E	170	0.055	M	H	H	CS	96	282	2.772544	0.024078
Leucanthemum virgatum (Desr.) Clos	Asteraceae	E	488	0.275	C	H	H	CS	311	396	3.717176	0.071815
Lilium pomponium L.	Liliaceae	E	809	0.275	M	G	H	CS	518	398	2.433854	0.054197
Limonium cordatum (L.) Mill.	Plumbaginaceae	E	327	0.055	C	H	H	S	79	126	7.265662	0.333074
Limonium pseudominutum Erben	Plumbaginaceae	E	661	0.055	C	H	H	S	166	74	7.885665	0.058008
Micromeria marginata (Sm.) Chater	Lamiaceae	E	239	0.055	S	C	W	S	147	456	5.617525	0.625028
Minuartia glomerata subsp. *burnatii* (Rouy & Foucaud) Favarger & F.Conti	Caryophyllaceae	E	110	0.055	M	C	H	S	84	261	3.06272	0.071564
Minuartia rupestris subsp. *clementei* (Huter) Greuter & Burdet	Caryophyllaceae	S	147	0.055	S	C	H	S	120	518	14.17269	1.264486
Moehringia intermedia Loisel. ex Panizzi	Caryophyllaceae	E	114	0.825	M	C	H	S	56	214	3.320291	0.09421
Moehringia sedoides (Pers.) Cumino ex Loisel.	Caryophyllaceae	E	156	0.825	M	C	H	S	93	483	3.849387	0.11161
Narcissus pseudonarcissus L. subsp. *provincialis* (Pugsley) J.M.Tison	Amaryllidaceae	E	165	0.055	M	G	H	CS	84	365	3.090919	0.065779
Ophrys bertolonii Moretti subsp. *saratoi* (E.G.Camus) R.Soca	Orchidaceae	S	460	27.5	C	G	H	CS	285	191	2.739086	0.139484
Ophrys exaltata subsp. *splendida* (Gölz & Reinhard) R.Soca	Orchidaceae	S	237	27.5	C	G	H	CS	144	128	7.438716	0.101316
Ophrys provincialis (Baumann & Künkele) Paulus	Orchidaceae	S	930	27.5	C	G	H	CS	576	165	5.597807	0.080712
Oreochloa seslerioides (All.) K.Richt.	Poaceae	E	384	0.055	S	H	H	CS	258	255	15.29751	0.513552
Potentilla delphinensis Gren. & Godr.	Rosaceae	S	269	0.275	S	H	H	CS	73	185	6.237611	0.993677
Potentilla saxifraga Ardoino ex De Not.	Rosaceae	E	186	0.055	C	C	W	S	101	334	3.432447	0.040622
Potentilla valderia L.	Rosaceae	E	426	0.825	S	C	H	CS	301	351	9.818939	0.743233
Primula allionii Loisel.	Primulaceae	E	145	0.055	M	H	H	S	51	322	3.564061	0.036454

Primula marginata Curtis	Primulaceae	S	3090	0.055	S	H	H	S	1805	527	7.567717	1.822247
Prunus brigantina Vill.	Rosaceae	S	1114	82.5	M	P	W	CS	529	196	1.896933	0.442742
Rhaponticum heleniifolium Godr. & Gren.	Asteraceae	E	215	0.825	S	H	H	CS	118	236	4.380508	0.741351
Santolina decumbens Mill.	Asteraceae	E	732	0.825	C	C	H	RS	426	233	4.102479	0.11422
Saxifraga cochlearis Rchb.	Saxifragaceae	S	352	8.25	M	C	H	S	173	432	4.167034	0.08524
Saxifraga exarata Vill. subsp. *delphinensis* (Ravaud) Kerguélen	Saxifragaceae	E	195	0.055	S	C	H	S	101	407	4.045687	1.429114
Saxifraga florulenta Moretti	Saxifragaceae	E	549	0.055	S	C	H	S	260	235	15.26225	0.437044
Saxifraga pedemontana All. subsp. *pedemontana*	Saxifragaceae	E	183	0.055	S	C	H	S	137	430	12.72223	1.179087
Saxifraga valdensis DC.	Saxifragaceae	S	64	0.055	S	C	H	S	46	292	16.29472	1.15371
Scrophularia provincialis Rouy	Scrophulariaceae	S	969	0.275	C	H	H	RS	807	329	2.939784	0.278276
Sempervivum calcareum Jord.	Crassulaceae	E	1393	0.275	M	C	H	S	928	350	1.640609	0.101247
Senecio leucanthemifolius Poir. subsp. *crassifolius* (Willd.) Ball	Asteraceae	E	280	0.825	C	T	A	S	69	40	8.160728	0.035601
Seseli annuum L. subsp. *carvifolium* (Vill.) P.Fourn.	Apiaceae	S	355	0.055	M	H	A	CS	287	329	0.953114	0.297113
Sideritis provincialis Jord. & Fourr.	Lamiaceae	S	1127	0.825	C	C	H	RS	882	256	4.227473	0.161226
Silene campanula Pers.	Caryophyllaceae	E	238	0.055	S	H	H	S	164	367	8.115277	0.605666
Silene cordifolia All.	Caryophyllaceae	E	373	0.055	S	H	H	S	269	373	10.95711	0.867144
Teucrium lucidum L.	Lamiaceae	E	1315	0.055	M	C	W	CS	932	342	1.969422	0.197365
Veronica allionii Vill.	Scrophulariaceae	S	2905	0.055	S	H	H	CS	1548	260	12.22578	1.066306
Viola valderia All.	Violaceae	E	256	0.825	S	H	H	CS	167	367	6.544913	0.914643

1.3 – Vegetation belts considered in this study

According to Engler et al. (2011) we divided the studied taxa into three ecological groups according to their occurrence within major vegetation belts, defined on the basis of both altitude and mean annual temperature; each species was assigned to the vegetation belt in which the highest frequency of occurrences was recorded. The vegetation belts are defined as follow.

Vegetation belt	**Altitudinal limit**	**Mean annual temperature**	**Vegetation structure**	**Vegetation period (days per year)**	**Number of studied taxa**
Colline (C; include planitial and mediterranean coastal environments)	< 800 m	> 10°C	Sclerophyllous communities in Thermo- and Meso-mediterranean conditions and deciduous forests dominated by *Quercus* sp. pl. in Supra-Mediterranean conditions.	> 250	25
Mountain (M)	800 – 1600 m	6 – 10 °C	Coniferous forest or mixed forests with deciduous tree (eg. *Fagus sylvatica*).	200 – 250	26
Subalpine (S; include alpine environments)	> 1600 m	< 6 °C	Coniferous forests and grasslands or small shrubs communities above the upper limit of the natural tree limit.	< 200	49

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Engler R, et al. 2011. 21st century climate change threatens mountain flora unequally across Europe. Global Change Biology **17**: 2330–2341.

Online Resource 3 – Model performance

Model performance measured using three evaluation methods:

- Area under the curve (AUC) of relative operating characteristic curve - Hanley, J.A., McNeil, B.J., 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143, 29–36. doi:10.1148/radiology.143.1.7063747
- Cohen's K - Monserud, R.A., Leemans, R., 1992. Comparing global vegetation maps with the Kappa statistic. Ecol. Model. 62, 275–293. doi:10.1016/0304-3800(92)90003-W
- True skill statistic (TSS) - Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232. doi:10.1111/j.1365-2664.2006.01214.x

Under current climate conditions, model evaluation indices indicate a good model performance for all modelling techniques in the majority of species, with the exception of ten taxa (*Arabis allionii* DC., *Brassica repanda* (Willd.) DC. subsp. *repanda*, *Campanula fritschii* Witasek, *Erysimum burnati* Vidal, *Euphorbia graminifolia* Vill., *Euphorbia variabilis* subsp. *valliniana* (Belli) Jauzein, *Galeopsis reuteri* Rchb.f., *Hesperis inodora* L., *Iberis aurosica* Chaix and *Moehringia sedoides* (Pers.) Cumino ex Loisel.). In particular, at least two evaluation indices indicate a poor model performance for CTA in five species, Kappa indicated a poor model performance for GLM in eight species, and for MARS in one species.

The shown values represent the mean values of ten evaluation runs for each algorithm; values in brackets indicate standard deviation. Values marked with an asterisk indicate a poor model performance, according to the following indications:

- AUC) 1>excellent>0.9>good>0.8>fair>0.7>poor>0.6>fail;
- TSS and KAPPA) 1>excellent>0.8>good>0.6>fair>0.4>poor>0.2>fail.

Species	**Algorithm**	**TSS**	**AUC**	**KAPPA**
Acis nicaeensis	CTA	0.906 (0.031)	0.961 (0.017)	0.907 (0.031)
	GBM	0.956 (0.017)	0.993 (0.005)	0.955 (0.017)
	GLM	0.933 (0.059)	0.974 (0.033)	0.913 (0.068)
	MARS	0.892 (0.06)	0.951 (0.034)	0.908 (0.044)
	RF	0.966 (0.02)	0.998 (0.002)	0.966 (0.02)
Allium narcissiflorum	CTA	0.884 (0.023)	0.961 (0.01)	0.884 (0.023)
	GBM	0.892 (0.016)	0.981 (0.006)	0.892 (0.016)
	GLM	0.891 (0.016)	0.979 (0.006)	0.891 (0.016)

	MARS	0.856 (0.065)	0.955 (0.032)	0.81 (0.056)
	RF	0.916 (0.014)	0.989 (0.004)	0.917 (0.014)
Allium scaberrimum	CTA	0.676 (0.09)	0.859 (0.051)	0.676 (0.09)
	GBM	0.801 (0.054)	0.948 (0.02)	0.799 (0.055)
	GLM	0.734 (0.057)	0.922 (0.036)	0.662 (0.075)
	MARS	0.753 (0.078)	0.915 (0.041)	0.753 (0.078)
	RF	0.79 (0.057)	0.947 (0.022)	0.789 (0.057)
Androsace chaixii	CTA	0.848 (0.027)	0.943 (0.017)	0.848 (0.027)
	GBM	0.862 (0.023)	0.975 (0.007)	0.862 (0.023)
	GLM	0.847 (0.016)	0.971 (0.006)	0.843 (0.017)
	MARS	0.829 (0.058)	0.95 (0.031)	0.806 (0.06)
	RF	0.89 (0.021)	0.984 (0.005)	0.891 (0.021)
Anthemis cretica subsp. *gerardiana*	CTA	0.755 (0.064)	0.916 (0.03)	0.755 (0.064)
	GBM	0.824 (0.042)	0.965 (0.012)	0.824 (0.042)
	GLM	0.717 (0.043)	0.93 (0.019)	0.673 (0.048)
	MARS	0.702 (0.067)	0.906 (0.033)	0.694 (0.074)
	RF	0.866 (0.037)	0.976 (0.011)	0.865 (0.037)
Aquilegia reuteri	CTA	0.838 (0.023)	0.945 (0.013)	0.838 (0.023)
	GBM	0.855 (0.019)	0.974 (0.005)	0.855 (0.019)
	GLM	0.839 (0.019)	0.969 (0.006)	0.837 (0.019)
	MARS	0.793 (0.061)	0.937 (0.029)	0.754 (0.063)
	RF	0.893 (0.02)	0.983 (0.005)	0.893 (0.02)
Arabis allionii	CTA	0.463 (0.133)*	0.737 (0.076)*	0.458 (0.132)*
	GBM	0.655 (0.091)	0.856 (0.055)	0.644 (0.095)
	GLM	0.659 (0.073)	0.858 (0.047)	0.51 (0.067)*
	MARS	0.651 (0.106)	0.849 (0.061)	0.654 (0.106)
	RF	0.693 (0.091)	0.887 (0.048)	0.687 (0.093)
Arenaria cinerea	CTA	0.71 (0.094)	0.865 (0.051)	0.712 (0.093)
	GBM	0.849 (0.055)	0.966 (0.018)	0.847 (0.055)
	GLM	0.844 (0.073)	0.948 (0.046)	0.747 (0.088)
	MARS	0.809 (0.082)	0.93 (0.045)	0.812 (0.08)
	RF	0.834 (0.056)	0.959 (0.021)	0.83 (0.058)
Arenaria provincialis	CTA	0.952 (0.014)	0.985 (0.007)	0.952 (0.014)
	GBM	0.963 (0.012)	0.997 (0.002)	0.963 (0.012)
	GLM	0.945 (0.03)	0.981 (0.019)	0.944 (0.03)
	MARS	0.916 (0.055)	0.96 (0.028)	0.921 (0.055)
	RF	0.977 (0.009)	0.999 (0.001)	0.977 (0.009)
Asperula cynanchica subsp. *rupicola*	CTA	0.818 (0.032)	0.925 (0.019)	0.819 (0.032)
	GBM	0.851 (0.03)	0.968 (0.011)	0.852 (0.03)
	GLM	0.84 (0.03)	0.958 (0.017)	0.801 (0.034)
	MARS	0.801 (0.069)	0.917 (0.043)	0.823 (0.058)
	RF	0.859 (0.035)	0.972 (0.01)	0.859 (0.034)
Asperula hexaphylla	CTA	0.779 (0.067)	0.911 (0.035)	0.78 (0.067)
	GBM	0.897 (0.043)	0.982 (0.011)	0.897 (0.043)
	GLM	0.913 (0.025)	0.984 (0.012)	0.87 (0.031)
	MARS	0.82 (0.07)	0.932 (0.037)	0.831 (0.069)
	RF	0.915 (0.039)	0.988 (0.008)	0.916 (0.039)

Asplenium jahandiezii	CTA	0.85 (0.07)	0.935 (0.038)	0.85 (0.069)
	GBM	0.937 (0.046)	0.99 (0.012)	0.937 (0.045)
	GLM	0.912 (0.073)	0.964 (0.04)	0.862 (0.086)
	MARS	0.872 (0.069)	0.942 (0.038)	0.876 (0.067)
	RF	0.949 (0.038)	0.994 (0.007)	0.949 (0.038)
Ballota frutescens	CTA	0.801 (0.06)	0.912 (0.033)	0.801 (0.06)
	GBM	0.89 (0.041)	0.973 (0.015)	0.889 (0.041)
	GLM	0.891 (0.061)	0.959 (0.034)	0.817 (0.075)
	MARS	0.828 (0.069)	0.939 (0.039)	0.832 (0.065)
	RF	0.91 (0.038)	0.979 (0.012)	0.91 (0.038)
Berardia subacaulis	CTA	0.905 (0.017)	0.968 (0.01)	0.905 (0.017)
	GBM	0.926 (0.017)	0.991 (0.004)	0.926 (0.017)
	GLM	0.923 (0.015)	0.991 (0.003)	0.924 (0.015)
	MARS	0.892 (0.056)	0.963 (0.032)	0.875 (0.056)
	RF	0.931 (0.015)	0.992 (0.003)	0.931 (0.015)
Brassica repanda subsp. *repanda*	CTA	0.734 (0.035)	0.896 (0.025)	0.733 (0.035)
	GBM	0.771 (0.027)	0.947 (0.01)	0.771 (0.027)
	GLM	0.667 (0.03)	0.894 (0.014)	0.673 (0.028)
	MARS	0.694 (0.076)	0.885 (0.042)	0.594 (0.068)*
	RF	0.811 (0.024)	0.961 (0.008)	0.81 (0.024)
Campanula alpestris	CTA	0.905 (0.01)	0.972 (0.007)	0.905 (0.01)
	GBM	0.909 (0.011)	0.988 (0.002)	0.909 (0.011)
	GLM	0.896 (0.027)	0.981 (0.019)	0.892 (0.027)
	MARS	0.859 (0.06)	0.952 (0.036)	0.783 (0.055)
	RF	0.931 (0.009)	0.993 (0.002)	0.931 (0.009)
Campanula elatines	CTA	0.733 (0.08)	0.877 (0.044)	0.734 (0.08)
	GBM	0.824 (0.06)	0.95 (0.027)	0.826 (0.058)
	GLM	0.862 (0.032)	0.965 (0.012)	0.772 (0.041)
	MARS	0.801 (0.073)	0.923 (0.041)	0.802 (0.07)
	RF	0.853 (0.06)	0.961 (0.023)	0.852 (0.06)
Campanula fritschii	CTA	0.513 (0.12)*	0.767 (0.068)*	0.519 (0.119)*
	GBM	0.643 (0.097)	0.86 (0.052)	0.649 (0.097)
	GLM	0.715 (0.083)	0.88 (0.041)	0.456 (0.083)*
	MARS	0.623 (0.095)	0.846 (0.05)	0.622 (0.095)
	RF	0.701 (0.081)	0.893 (0.043)	0.706 (0.08)
Campanula rotundifolia subsp. *macrorhiza*	CTA	0.848 (0.017)	0.951 (0.009)	0.848 (0.017)
	GBM	0.837 (0.015)	0.973 (0.004)	0.837 (0.015)
	GLM	0.747 (0.025)	0.944 (0.008)	0.744 (0.027)
	MARS	0.723 (0.07)	0.909 (0.041)	0.619 (0.083)
	RF	0.909 (0.012)	0.99 (0.002)	0.909 (0.012)
Campanula sabatia	CTA	0.913 (0.036)	0.965 (0.019)	0.913 (0.036)
	GBM	0.959 (0.023)	0.996 (0.004)	0.958 (0.023)
	GLM	0.959 (0.022)	0.989 (0.011)	0.949 (0.024)
	MARS	0.908 (0.056)	0.96 (0.031)	0.914 (0.044)
	RF	0.964 (0.018)	0.997 (0.003)	0.963 (0.018)
Campanula stenocodon	CTA	0.779 (0.037)	0.919 (0.018)	0.779 (0.038)
	GBM	0.824 (0.03)	0.96 (0.01)	0.825 (0.03)

	GLM	0.818 (0.027)	0.956 (0.009)	0.795 (0.029)
	MARS	0.766 (0.061)	0.922 (0.034)	0.761 (0.061)
	RF	0.84 (0.036)	0.966 (0.012)	0.84 (0.036)
Carex ferruginea subsp. *tenax*	CTA	0.889 (0.009)	0.972 (0.004)	0.889 (0.009)
	GBM	0.869 (0.009)	0.982 (0.002)	0.869 (0.009)
	GLM	0.847 (0.017)	0.972 (0.005)	0.842 (0.018)
	MARS	0.808 (0.067)	0.939 (0.041)	0.682 (0.074)
	RF	0.938 (0.007)	0.995 (0.001)	0.938 (0.007)
Centaurea jordaniana	CTA	0.78 (0.051)	0.912 (0.029)	0.782 (0.051)
	GBM	0.862 (0.038)	0.967 (0.013)	0.864 (0.038)
	GLM	0.791 (0.07)	0.922 (0.042)	0.696 (0.074)
	MARS	0.709 (0.075)	0.877 (0.05)	0.741 (0.076)
	RF	0.901 (0.034)	0.984 (0.009)	0.901 (0.034)
Centaurea paniculata subsp. *polycephala*	CTA	0.692 (0.081)	0.861 (0.046)	0.692 (0.081)
	GBM	0.789 (0.049)	0.944 (0.02)	0.787 (0.049)
	GLM	0.775 (0.053)	0.94 (0.03)	0.706 (0.057)
	MARS	0.757 (0.068)	0.915 (0.031)	0.755 (0.066)
	RF	0.795 (0.059)	0.944 (0.024)	0.792 (0.059)
Centaurea uniflora subsp. *uniflora*	CTA	0.883 (0.013)	0.959 (0.007)	0.883 (0.013)
	GBM	0.891 (0.011)	0.977 (0.004)	0.891 (0.011)
	GLM	0.877 (0.015)	0.97 (0.007)	0.877 (0.015)
	MARS	0.846 (0.052)	0.945 (0.034)	0.75 (0.05)
	RF	0.914 (0.011)	0.989 (0.003)	0.914 (0.011)
Coincya richeri	CTA	0.827 (0.024)	0.942 (0.015)	0.827 (0.024)
	GBM	0.841 (0.022)	0.97 (0.006)	0.841 (0.022)
	GLM	0.806 (0.033)	0.956 (0.01)	0.807 (0.032)
	MARS	0.801 (0.059)	0.916 (0.042)	0.803 (0.058)
	RF	0.878 (0.017)	0.982 (0.004)	0.878 (0.017)
Crocus ligusticus	CTA	0.802 (0.048)	0.913 (0.029)	0.802 (0.049)
	GBM	0.872 (0.039)	0.974 (0.011)	0.872 (0.039)
	GLM	0.89 (0.02)	0.974 (0.008)	0.855 (0.025)
	MARS	0.833 (0.066)	0.944 (0.033)	0.843 (0.058)
	RF	0.891 (0.033)	0.981 (0.01)	0.891 (0.034)
Crocus versicolor	CTA	0.742 (0.026)	0.907 (0.015)	0.743 (0.026)
	GBM	0.753 (0.025)	0.943 (0.008)	0.754 (0.025)
	GLM	0.741 (0.024)	0.926 (0.011)	0.745 (0.024)
	MARS	0.704 (0.07)	0.891 (0.037)	0.632 (0.071)
	RF	0.801 (0.019)	0.965 (0.005)	0.801 (0.019)
Cytisus ardoinii	CTA	0.895 (0.037)	0.957 (0.019)	0.896 (0.037)
	GBM	0.945 (0.026)	0.992 (0.006)	0.945 (0.026)
	GLM	0.938 (0.033)	0.984 (0.019)	0.905 (0.035)
	MARS	0.89 (0.062)	0.956 (0.033)	0.903 (0.058)
	RF	0.951 (0.026)	0.993 (0.006)	0.952 (0.026)
Cytisus sauzeanus	CTA	0.765 (0.066)	0.898 (0.039)	0.766 (0.066)
	GBM	0.826 (0.046)	0.964 (0.013)	0.826 (0.046)
	GLM	0.805 (0.027)	0.96 (0.009)	0.774 (0.03)
	MARS	0.745 (0.08)	0.911 (0.043)	0.739 (0.075)

	RF	0.843 (0.04)	0.971 (0.01)	0.844 (0.04)
Dianthus furcatus subsp. *furcatus*	CTA	0.762 (0.057)	0.9 (0.032)	0.762 (0.057)
	GBM	0.806 (0.043)	0.956 (0.014)	0.806 (0.043)
	GLM	0.815 (0.028)	0.956 (0.009)	0.759 (0.031)
	MARS	0.791 (0.057)	0.932 (0.032)	0.797 (0.057)
	RF	0.821 (0.04)	0.962 (0.012)	0.821 (0.04)
Dianthus pavonius	CTA	0.901 (0.011)	0.964 (0.006)	0.901 (0.011)
	GBM	0.896 (0.011)	0.981 (0.004)	0.896 (0.011)
	GLM	0.894 (0.015)	0.978 (0.006)	0.893 (0.015)
	MARS	0.876 (0.046)	0.961 (0.027)	0.796 (0.055)
	RF	0.929 (0.01)	0.991 (0.002)	0.929 (0.01)
Dianthus subacaulis	CTA	0.857 (0.033)	0.943 (0.019)	0.858 (0.032)
	GBM	0.89 (0.03)	0.98 (0.009)	0.89 (0.03)
	GLM	0.871 (0.025)	0.974 (0.007)	0.842 (0.028)
	MARS	0.845 (0.056)	0.954 (0.028)	0.832 (0.051)
	RF	0.897 (0.028)	0.984 (0.007)	0.896 (0.028)
Epipactis leptochila subsp. *provincialis*	CTA	0.632 (0.099)	0.829 (0.052)	0.633 (0.099)
	GBM	0.785 (0.066)	0.927 (0.031)	0.776 (0.067)
	GLM	0.703 (0.09)	0.889 (0.057)	0.625 (0.098)
	MARS	0.709 (0.084)	0.879 (0.049)	0.707 (0.084)
	RF	0.801 (0.069)	0.941 (0.024)	0.794 (0.069)
Eryngium spinalba	CTA	0.857 (0.019)	0.946 (0.013)	0.858 (0.019)
	GBM	0.866 (0.017)	0.97 (0.006)	0.866 (0.017)
	GLM	0.857 (0.021)	0.962 (0.011)	0.86 (0.021)
	MARS	0.832 (0.057)	0.936 (0.035)	0.798 (0.061)
	RF	0.909 (0.014)	0.988 (0.003)	0.909 (0.014)
Erysimum burnati	CTA	0.556 (0.109)*	0.791 (0.064)*	0.553 (0.11)*
	GBM	0.68 (0.081)	0.878 (0.043)	0.673 (0.083)
	GLM	0.69 (0.055)	0.891 (0.03)	0.564 (0.061)*
	MARS	0.638 (0.076)	0.856 (0.044)	0.638 (0.077)
	RF	0.721 (0.081)	0.907 (0.038)	0.718 (0.083)
Euphorbia canutii	CTA	0.726 (0.059)	0.892 (0.031)	0.726 (0.059)
	GBM	0.82 (0.043)	0.96 (0.014)	0.82 (0.042)
	GLM	0.798 (0.036)	0.953 (0.012)	0.75 (0.038)
	MARS	0.766 (0.074)	0.922 (0.039)	0.764 (0.064)
	RF	0.846 (0.041)	0.968 (0.012)	0.846 (0.041)
Euphorbia graminifolia	CTA	0.699 (0.09)	0.875 (0.05)	0.701 (0.09)
	GBM	0.863 (0.063)	0.959 (0.024)	0.86 (0.062)
	GLM	0.73 (0.046)	0.889 (0.022)	0.499 (0.045)*
	MARS	0.78 (0.072)	0.912 (0.036)	0.783 (0.071)
	RF	0.896 (0.051)	0.974 (0.015)	0.892 (0.051)
Euphorbia variabilis subsp. *valliniana*	CTA	0.553 (0.131)*	0.787 (0.074)*	0.554 (0.131)*
	GBM	0.735 (0.09)	0.908 (0.04)	0.735 (0.089)
	GLM	0.834 (0.055)	0.943 (0.029)	0.683 (0.054)
	MARS	0.731 (0.09)	0.889 (0.059)	0.73 (0.091)
	RF	0.748 (0.085)	0.925 (0.038)	0.746 (0.086)
Festuca scabriculmis	CTA	0.908 (0.028)	0.966 (0.015)	0.908 (0.028)

	GBM	0.935 (0.02)	0.989 (0.006)	0.935 (0.02)
	GLM	0.934 (0.016)	0.987 (0.005)	0.924 (0.019)
	MARS	0.881 (0.064)	0.958 (0.036)	0.877 (0.056)
	RF	0.935 (0.022)	0.988 (0.006)	0.935 (0.022)
Fritillaria involucrata	CTA	0.82 (0.025)	0.94 (0.013)	0.82 (0.025)
	GBM	0.83 (0.018)	0.965 (0.006)	0.83 (0.018)
	GLM	0.74 (0.026)	0.935 (0.009)	0.741 (0.026)
	MARS	0.728 (0.074)	0.904 (0.041)	0.671 (0.075)
	RF	0.893 (0.018)	0.983 (0.004)	0.894 (0.018)
Fritillaria tubiformis subsp. *moggridgei*	CTA	0.795 (0.086)	0.905 (0.045)	0.796 (0.086)
	GBM	0.866 (0.052)	0.959 (0.02)	0.867 (0.052)
	GLM	0.85 (0.036)	0.952 (0.017)	0.71 (0.052)
	MARS	0.834 (0.072)	0.939 (0.039)	0.839 (0.07)
	RF	0.87 (0.056)	0.968 (0.017)	0.871 (0.056)
Fritillaria tubiformis subsp. *tubiformis*	CTA	0.786 (0.046)	0.906 (0.024)	0.787 (0.045)
	GBM	0.84 (0.038)	0.959 (0.014)	0.84 (0.037)
	GLM	0.828 (0.029)	0.959 (0.01)	0.784 (0.032)
	MARS	0.78 (0.075)	0.925 (0.04)	0.788 (0.067)
	RF	0.846 (0.035)	0.963 (0.011)	0.847 (0.035)
Galeopsis reuteri	CTA	0.579 (0.081)*	0.808 (0.048)	0.583 (0.08)*
	GBM	0.69 (0.066)	0.896 (0.032)	0.692 (0.065)
	GLM	0.603 (0.047)	0.838 (0.021)	0.415 (0.046)*
	MARS	0.616 (0.087)	0.824 (0.057)	0.636 (0.083)
	RF	0.741 (0.058)	0.922 (0.024)	0.741 (0.058)
Galium pseudohelveticum	CTA	0.878 (0.02)	0.956 (0.011)	0.879 (0.02)
	GBM	0.897 (0.014)	0.984 (0.004)	0.897 (0.014)
	GLM	0.895 (0.016)	0.982 (0.004)	0.895 (0.015)
	MARS	0.859 (0.06)	0.953 (0.031)	0.821 (0.06)
	RF	0.92 (0.012)	0.99 (0.003)	0.92 (0.012)
Galium saxosum	CTA	0.825 (0.041)	0.918 (0.023)	0.826 (0.041)
	GBM	0.867 (0.034)	0.971 (0.011)	0.867 (0.034)
	GLM	0.873 (0.024)	0.973 (0.01)	0.835 (0.028)
	MARS	0.855 (0.058)	0.953 (0.029)	0.86 (0.055)
	RF	0.884 (0.031)	0.98 (0.008)	0.883 (0.031)
Genista lobelii	CTA	0.951 (0.025)	0.977 (0.013)	0.951 (0.025)
	GBM	0.967 (0.017)	0.994 (0.005)	0.967 (0.017)
	GLM	0.976 (0.014)	0.994 (0.008)	0.969 (0.016)
	MARS	0.914 (0.056)	0.96 (0.028)	0.924 (0.047)
	RF	0.975 (0.012)	0.997 (0.003)	0.975 (0.012)
Gentiana burseri subsp. *actinocalyx*	CTA	0.785 (0.084)	0.895 (0.044)	0.783 (0.084)
	GBM	0.889 (0.068)	0.968 (0.033)	0.888 (0.071)
	GLM	0.878 (0.081)	0.941 (0.042)	0.808 (0.081)
	MARS	0.865 (0.089)	0.937 (0.044)	0.86 (0.087)
	RF	0.91 (0.066)	0.979 (0.027)	0.908 (0.068)
Gentiana burseri subsp. *villarsii*	CTA	0.845 (0.036)	0.932 (0.02)	0.845 (0.036)
	GBM	0.88 (0.026)	0.97 (0.01)	0.88 (0.026)
	GLM	0.871 (0.02)	0.966 (0.013)	0.854 (0.022)

	MARS	0.843 (0.06)	0.938 (0.043)	0.836 (0.057)
	RF	0.884 (0.025)	0.974 (0.008)	0.884 (0.025)
Gentiana rostani	CTA	0.873 (0.023)	0.951 (0.012)	0.873 (0.023)
	GBM	0.903 (0.02)	0.982 (0.006)	0.903 (0.02)
	GLM	0.91 (0.017)	0.982 (0.007)	0.905 (0.018)
	MARS	0.891 (0.044)	0.96 (0.026)	0.879 (0.04)
	RF	0.905 (0.02)	0.986 (0.005)	0.905 (0.02)
Gymnadenia nigra subsp. *corneliana*	CTA	0.875 (0.021)	0.947 (0.012)	0.875 (0.021)
	GBM	0.892 (0.017)	0.978 (0.006)	0.892 (0.017)
	GLM	0.88 (0.02)	0.975 (0.006)	0.88 (0.02)
	MARS	0.841 (0.064)	0.944 (0.034)	0.816 (0.062)
	RF	0.9 (0.017)	0.98 (0.005)	0.9 (0.017)
Hedysarum hedysaroides subsp. *boutignyanum*	CTA	0.817 (0.029)	0.931 (0.016)	0.817 (0.029)
	GBM	0.84 (0.023)	0.962 (0.009)	0.84 (0.023)
	GLM	0.825 (0.024)	0.961 (0.008)	0.82 (0.024)
	MARS	0.784 (0.066)	0.917 (0.043)	0.789 (0.06)
	RF	0.874 (0.021)	0.978 (0.005)	0.874 (0.021)
Helianthemum lunulatum	CTA	0.851 (0.063)	0.933 (0.036)	0.854 (0.062)
	GBM	0.926 (0.045)	0.981 (0.018)	0.927 (0.044)
	GLM	0.905 (0.073)	0.962 (0.041)	0.833 (0.085)
	MARS	0.88 (0.061)	0.944 (0.034)	0.888 (0.058)
	RF	0.935 (0.041)	0.987 (0.013)	0.934 (0.041)
Helictotrichon sempervirens	CTA	0.901 (0.013)	0.965 (0.007)	0.901 (0.013)
	GBM	0.91 (0.012)	0.985 (0.003)	0.91 (0.012)
	GLM	0.918 (0.012)	0.988 (0.004)	0.917 (0.014)
	MARS	0.845 (0.062)	0.945 (0.034)	0.803 (0.068)
	RF	0.924 (0.011)	0.991 (0.002)	0.924 (0.011)
Helictotrichon setaceum	CTA	0.861 (0.022)	0.945 (0.014)	0.862 (0.022)
	GBM	0.878 (0.022)	0.975 (0.006)	0.879 (0.022)
	GLM	0.888 (0.016)	0.977 (0.006)	0.887 (0.017)
	MARS	0.834 (0.067)	0.936 (0.034)	0.82 (0.054)
	RF	0.901 (0.02)	0.985 (0.005)	0.901 (0.02)
Heracleum pumilum	CTA	0.838 (0.048)	0.926 (0.03)	0.841 (0.047)
	GBM	0.886 (0.032)	0.968 (0.015)	0.886 (0.032)
	GLM	0.882 (0.045)	0.966 (0.024)	0.81 (0.045)
	MARS	0.845 (0.061)	0.945 (0.032)	0.856 (0.059)
	RF	0.877 (0.043)	0.972 (0.015)	0.878 (0.042)
Hesperis inodora	CTA	0.606 (0.17)	0.801 (0.089)	0.612 (0.17)
	GBM	0.759 (0.1)	0.898 (0.054)	0.75 (0.103)
	GLM	0.718 (0.124)	0.87 (0.066)	0.536 (0.099)*
	MARS	0.634 (0.134)	0.827 (0.08)	0.63 (0.129)
	RF	0.724 (0.111)	0.894 (0.063)	0.715 (0.116)
Hormathophylla halimifolia	CTA	0.733 (0.047)	0.894 (0.025)	0.734 (0.047)
	GBM	0.781 (0.038)	0.943 (0.013)	0.782 (0.038)
	GLM	0.698 (0.037)	0.905 (0.016)	0.65 (0.038)
	MARS	0.685 (0.071)	0.875 (0.047)	0.692 (0.068)
	RF	0.833 (0.03)	0.967 (0.01)	0.833 (0.03)

Hyacinthoides italica	CTA	0.815 (0.032)	0.925 (0.02)	0.815 (0.032)
	GBM	0.848 (0.021)	0.973 (0.007)	0.848 (0.02)
	GLM	0.819 (0.023)	0.955 (0.01)	0.819 (0.024)
	MARS	0.787 (0.065)	0.926 (0.032)	0.742 (0.059)
	RF	0.891 (0.022)	0.985 (0.006)	0.891 (0.023)
Iberis aurosica	CTA	0.639 (0.079)	0.845 (0.04)	0.643 (0.079)
	GBM	0.744 (0.063)	0.918 (0.032)	0.747 (0.061)
	GLM	0.724 (0.037)	0.891 (0.017)	0.523 (0.044)*
	MARS	0.69 (0.093)	0.87 (0.058)	0.707 (0.09)
	RF	0.778 (0.053)	0.936 (0.025)	0.779 (0.053)
Iberis nana	CTA	0.756 (0.076)	0.883 (0.042)	0.758 (0.074)
	GBM	0.838 (0.046)	0.963 (0.016)	0.838 (0.046)
	GLM	0.838 (0.035)	0.959 (0.014)	0.743 (0.042)
	MARS	0.807 (0.065)	0.93 (0.038)	0.812 (0.061)
	RF	0.842 (0.049)	0.966 (0.015)	0.843 (0.049)
Jovibarba allionii	CTA	0.849 (0.037)	0.94 (0.022)	0.849 (0.037)
	GBM	0.889 (0.023)	0.981 (0.007)	0.889 (0.023)
	GLM	0.887 (0.019)	0.976 (0.007)	0.875 (0.021)
	MARS	0.862 (0.054)	0.957 (0.026)	0.842 (0.051)
	RF	0.905 (0.018)	0.984 (0.006)	0.905 (0.018)
Leucanthemum burnatii	CTA	0.886 (0.049)	0.951 (0.027)	0.887 (0.048)
	GBM	0.934 (0.034)	0.986 (0.01)	0.934 (0.034)
	GLM	0.9 (0.048)	0.966 (0.029)	0.83 (0.072)
	MARS	0.87 (0.061)	0.948 (0.034)	0.874 (0.059)
	RF	0.934 (0.029)	0.988 (0.008)	0.934 (0.029)
Leucanthemum virgatum	CTA	0.833 (0.034)	0.943 (0.019)	0.833 (0.034)
	GBM	0.88 (0.027)	0.983 (0.006)	0.88 (0.027)
	GLM	0.848 (0.024)	0.967 (0.008)	0.819 (0.027)
	MARS	0.825 (0.062)	0.944 (0.031)	0.831 (0.055)
	RF	0.922 (0.021)	0.992 (0.004)	0.922 (0.021)
Lilium pomponium	CTA	0.855 (0.023)	0.947 (0.013)	0.855 (0.022)
	GBM	0.882 (0.018)	0.981 (0.005)	0.883 (0.018)
	GLM	0.849 (0.019)	0.972 (0.006)	0.842 (0.02)
	MARS	0.835 (0.062)	0.952 (0.03)	0.814 (0.065)
	RF	0.914 (0.022)	0.989 (0.004)	0.914 (0.022)
Limonium cordatum	CTA	0.93 (0.034)	0.969 (0.019)	0.929 (0.034)
	GBM	0.955 (0.023)	0.994 (0.005)	0.955 (0.023)
	GLM	0.887 (0.029)	0.975 (0.017)	0.846 (0.033)
	MARS	0.884 (0.053)	0.947 (0.029)	0.902 (0.048)
	RF	0.966 (0.019)	0.996 (0.004)	0.966 (0.019)
Limonium pseudominutum	CTA	0.924 (0.023)	0.971 (0.011)	0.924 (0.023)
	GBM	0.951 (0.017)	0.996 (0.002)	0.951 (0.017)
	GLM	0.943 (0.014)	0.993 (0.003)	0.937 (0.016)
	MARS	0.893 (0.057)	0.959 (0.033)	0.9 (0.047)
	RF	0.975 (0.011)	0.998 (0.002)	0.975 (0.011)
Micromeria marginata	CTA	0.778 (0.059)	0.914 (0.032)	0.777 (0.059)
	GBM	0.864 (0.033)	0.973 (0.01)	0.864 (0.034)

	GLM	0.813 (0.03)	0.953 (0.012)	0.798 (0.037)
	MARS	0.79 (0.07)	0.93 (0.036)	0.778 (0.072)
	RF	0.884 (0.039)	0.979 (0.012)	0.884 (0.039)
Minuartia glomerata subsp. *burnatii*	CTA	0.813 (0.064)	0.913 (0.035)	0.811 (0.064)
	GBM	0.893 (0.048)	0.978 (0.014)	0.892 (0.048)
	GLM	0.877 (0.047)	0.964 (0.031)	0.806 (0.082)
	MARS	0.853 (0.068)	0.956 (0.034)	0.854 (0.069)
	RF	0.89 (0.054)	0.978 (0.014)	0.89 (0.053)
Minuartia rupestris subsp. *clementei*	CTA	0.641 (0.074)	0.841 (0.042)	0.642 (0.074)
	GBM	0.759 (0.058)	0.931 (0.025)	0.758 (0.058)
	GLM	0.787 (0.038)	0.941 (0.017)	0.687 (0.041)
	MARS	0.745 (0.07)	0.905 (0.037)	0.75 (0.068)
	RF	0.777 (0.058)	0.941 (0.021)	0.777 (0.058)
Moehringia intermedia	CTA	0.722 (0.076)	0.886 (0.044)	0.721 (0.075)
	GBM	0.863 (0.051)	0.972 (0.017)	0.861 (0.051)
	GLM	0.858 (0.073)	0.952 (0.047)	0.753 (0.12)
	MARS	0.818 (0.073)	0.945 (0.037)	0.822 (0.07)
	RF	0.876 (0.055)	0.975 (0.019)	0.873 (0.056)
Moehringia sedoides	CTA	0.724 (0.079)	0.9 (0.037)	0.723 (0.08)
	GBM	0.835 (0.05)	0.963 (0.018)	0.833 (0.051)
	GLM	0.7 (0.038)	0.88 (0.017)	0.496 (0.039)*
	MARS	0.759 (0.086)	0.914 (0.052)	0.762 (0.081)
	RF	0.857 (0.053)	0.972 (0.015)	0.854 (0.054)
Narcissus pseudonarcissus subsp. *provincialis*	CTA	0.815 (0.063)	0.915 (0.035)	0.814 (0.063)
	GBM	0.884 (0.045)	0.974 (0.013)	0.883 (0.045)
	GLM	0.889 (0.04)	0.97 (0.021)	0.838 (0.053)
	MARS	0.846 (0.066)	0.943 (0.039)	0.849 (0.064)
	RF	0.896 (0.038)	0.977 (0.011)	0.894 (0.038)
Ophrys bertolonii subsp. *saratoi*	CTA	0.763 (0.041)	0.905 (0.025)	0.763 (0.041)
	GBM	0.802 (0.034)	0.959 (0.011)	0.802 (0.034)
	GLM	0.69 (0.061)	0.908 (0.042)	0.66 (0.06)
	MARS	0.735 (0.066)	0.908 (0.037)	0.706 (0.064)
	RF	0.854 (0.027)	0.971 (0.008)	0.853 (0.027)
Ophrys exaltata subsp. *splendida*	CTA	0.822 (0.047)	0.92 (0.026)	0.822 (0.047)
	GBM	0.886 (0.034)	0.973 (0.013)	0.885 (0.034)
	GLM	0.847 (0.027)	0.958 (0.011)	0.782 (0.033)
	MARS	0.859 (0.054)	0.95 (0.032)	0.854 (0.05)
	RF	0.905 (0.031)	0.98 (0.01)	0.905 (0.031)
Ophrys provincialis	CTA	0.861 (0.021)	0.95 (0.012)	0.861 (0.021)
	GBM	0.879 (0.018)	0.978 (0.006)	0.879 (0.018)
	GLM	0.824 (0.084)	0.935 (0.052)	0.823 (0.084)
	MARS	0.834 (0.056)	0.94 (0.031)	0.809 (0.058)
	RF	0.912 (0.016)	0.987 (0.004)	0.912 (0.016)
Oreochloa seslerioides	CTA	0.873 (0.035)	0.948 (0.021)	0.873 (0.035)
	GBM	0.914 (0.027)	0.985 (0.008)	0.914 (0.027)
	GLM	0.921 (0.017)	0.987 (0.005)	0.918 (0.017)
	MARS	0.892 (0.051)	0.968 (0.028)	0.878 (0.047)

	RF	0.921 (0.025)	0.987 (0.006)	0.921 (0.025)
Potentilla delphinensis	CTA	0.797 (0.044)	0.916 (0.025)	0.798 (0.044)
	GBM	0.853 (0.039)	0.966 (0.014)	0.853 (0.038)
	GLM	0.833 (0.029)	0.951 (0.01)	0.768 (0.037)
	MARS	0.801 (0.066)	0.93 (0.032)	0.803 (0.061)
	RF	0.869 (0.035)	0.972 (0.011)	0.868 (0.036)
Potentilla saxifraga	CTA	0.776 (0.063)	0.901 (0.036)	0.776 (0.063)
	GBM	0.846 (0.043)	0.967 (0.015)	0.844 (0.043)
	GLM	0.785 (0.05)	0.926 (0.028)	0.678 (0.066)
	MARS	0.766 (0.073)	0.916 (0.039)	0.761 (0.068)
	RF	0.884 (0.039)	0.976 (0.015)	0.882 (0.04)
Potentilla valderia	CTA	0.863 (0.037)	0.948 (0.021)	0.863 (0.037)
	GBM	0.9 (0.029)	0.983 (0.007)	0.9 (0.029)
	GLM	0.899 (0.019)	0.984 (0.005)	0.895 (0.021)
	MARS	0.863 (0.068)	0.957 (0.038)	0.858 (0.061)
	RF	0.916 (0.024)	0.989 (0.005)	0.916 (0.024)
Primula allionii	CTA	0.824 (0.061)	0.922 (0.031)	0.821 (0.061)
	GBM	0.91 (0.047)	0.98 (0.015)	0.906 (0.048)
	GLM	0.877 (0.056)	0.964 (0.034)	0.799 (0.079)
	MARS	0.84 (0.066)	0.934 (0.041)	0.846 (0.058)
	RF	0.922 (0.041)	0.983 (0.013)	0.919 (0.042)
Primula marginata	CTA	0.894 (0.011)	0.971 (0.005)	0.894 (0.011)
	GBM	0.881 (0.012)	0.983 (0.002)	0.881 (0.012)
	GLM	0.879 (0.016)	0.98 (0.004)	0.851 (0.016)
	MARS	0.848 (0.046)	0.952 (0.026)	0.683 (0.061)
	RF	0.94 (0.009)	0.995 (0.001)	0.94 (0.009)
Prunus brigantina	CTA	0.825 (0.025)	0.942 (0.014)	0.825 (0.025)
	GBM	0.836 (0.023)	0.969 (0.007)	0.836 (0.023)
	GLM	0.783 (0.023)	0.948 (0.008)	0.784 (0.023)
	MARS	0.767 (0.063)	0.92 (0.033)	0.714 (0.058)
	RF	0.882 (0.017)	0.984 (0.003)	0.883 (0.017)
Rhaponticum heleniifolium	CTA	0.744 (0.054)	0.887 (0.032)	0.745 (0.053)
	GBM	0.779 (0.046)	0.933 (0.019)	0.78 (0.046)
	GLM	0.776 (0.028)	0.935 (0.01)	0.674 (0.034)
	MARS	0.767 (0.071)	0.905 (0.039)	0.778 (0.067)
	RF	0.804 (0.046)	0.946 (0.017)	0.804 (0.045)
Santolina decumbens	CTA	0.863 (0.024)	0.956 (0.013)	0.863 (0.024)
	GBM	0.89 (0.024)	0.981 (0.006)	0.89 (0.024)
	GLM	0.859 (0.02)	0.971 (0.006)	0.858 (0.02)
	MARS	0.81 (0.064)	0.937 (0.035)	0.755 (0.062)
	RF	0.919 (0.016)	0.988 (0.005)	0.919 (0.016)
Saxifraga cochlearis	CTA	0.823 (0.039)	0.929 (0.025)	0.824 (0.039)
	GBM	0.878 (0.031)	0.981 (0.008)	0.878 (0.031)
	GLM	0.86 (0.022)	0.956 (0.011)	0.819 (0.031)
	MARS	0.844 (0.061)	0.94 (0.038)	0.84 (0.062)
	RF	0.926 (0.026)	0.992 (0.005)	0.925 (0.026)
	CTA	0.794 (0.055)	0.907 (0.033)	0.794 (0.055)

Saxifraga exarata subsp. *delphinensis*	GBM	0.861 (0.042)	0.967 (0.016)	0.861 (0.042)
	GLM	0.86 (0.027)	0.97 (0.008)	0.797 (0.035)
	MARS	0.816 (0.067)	0.942 (0.033)	0.815 (0.062)
	RF	0.872 (0.044)	0.972 (0.014)	0.873 (0.045)
Saxifraga florulenta	CTA	0.913 (0.023)	0.969 (0.014)	0.913 (0.023)
	GBM	0.952 (0.019)	0.995 (0.003)	0.952 (0.019)
	GLM	0.954 (0.016)	0.991 (0.009)	0.948 (0.02)
	MARS	0.913 (0.051)	0.968 (0.027)	0.917 (0.045)
	RF	0.955 (0.018)	0.996 (0.002)	0.955 (0.018)
Saxifraga pedemontana subsp. *pedemontana*	CTA	0.833 (0.053)	0.93 (0.028)	0.832 (0.053)
	GBM	0.891 (0.045)	0.981 (0.012)	0.891 (0.045)
	GLM	0.926 (0.024)	0.989 (0.007)	0.896 (0.028)
	MARS	0.874 (0.064)	0.96 (0.034)	0.877 (0.06)
	RF	0.911 (0.039)	0.987 (0.01)	0.911 (0.039)
Saxifraga valdensis	CTA	0.629 (0.107)	0.825 (0.062)	0.633 (0.105)
	GBM	0.758 (0.085)	0.919 (0.043)	0.758 (0.088)
	GLM	0.821 (0.055)	0.944 (0.03)	0.656 (0.059)
	MARS	0.735 (0.102)	0.891 (0.059)	0.732 (0.101)
	RF	0.799 (0.086)	0.943 (0.037)	0.793 (0.088)
Scrophularia provincialis	CTA	0.751 (0.028)	0.912 (0.015)	0.751 (0.028)
	GBM	0.766 (0.024)	0.946 (0.009)	0.766 (0.024)
	GLM	0.735 (0.024)	0.928 (0.01)	0.735 (0.024)
	MARS	0.707 (0.059)	0.891 (0.035)	0.622 (0.058)
	RF	0.835 (0.024)	0.969 (0.007)	0.835 (0.024)
Sempervivum calcareum	CTA	0.859 (0.019)	0.951 (0.011)	0.859 (0.019)
	GBM	0.868 (0.015)	0.974 (0.004)	0.868 (0.015)
	GLM	0.857 (0.018)	0.973 (0.006)	0.857 (0.016)
	MARS	0.804 (0.064)	0.937 (0.038)	0.723 (0.062)
	RF	0.897 (0.014)	0.985 (0.004)	0.897 (0.014)
Senecio leucanthemifolius subsp. *crassifolius*	CTA	0.912 (0.035)	0.962 (0.018)	0.912 (0.035)
	GBM	0.949 (0.025)	0.994 (0.004)	0.949 (0.025)
	GLM	0.942 (0.019)	0.987 (0.009)	0.921 (0.021)
	MARS	0.898 (0.058)	0.952 (0.032)	0.91 (0.049)
	RF	0.966 (0.017)	0.997 (0.002)	0.966 (0.017)
Seseli annuum carvifolium	CTA	0.677 (0.046)	0.857 (0.027)	0.678 (0.046)
	GBM	0.739 (0.047)	0.922 (0.021)	0.739 (0.047)
	GLM	0.681 (0.029)	0.901 (0.012)	0.643 (0.031)
	MARS	0.683 (0.069)	0.875 (0.04)	0.66 (0.062)
	RF	0.765 (0.04)	0.933 (0.016)	0.765 (0.04)
Sideritis provincialis	CTA	0.856 (0.02)	0.949 (0.01)	0.856 (0.02)
	GBM	0.88 (0.019)	0.976 (0.006)	0.88 (0.019)
	GLM	0.813 (0.038)	0.957 (0.025)	0.815 (0.038)
	MARS	0.842 (0.049)	0.956 (0.027)	0.746 (0.06)
	RF	0.907 (0.016)	0.986 (0.004)	0.907 (0.016)
Silene campanula	CTA	0.837 (0.048)	0.933 (0.027)	0.837 (0.048)
	GBM	0.909 (0.032)	0.981 (0.01)	0.909 (0.032)
	GLM	0.921 (0.027)	0.982 (0.01)	0.9 (0.028)

	MARS	0.868 (0.068)	0.956 (0.037)	0.864 (0.06)
	RF	0.923 (0.031)	0.984 (0.008)	0.922 (0.031)
Silene cordifolia	CTA	0.861 (0.037)	0.946 (0.025)	0.861 (0.038)
	GBM	0.914 (0.026)	0.988 (0.006)	0.914 (0.026)
	GLM	0.926 (0.017)	0.988 (0.005)	0.919 (0.017)
	MARS	0.882 (0.054)	0.967 (0.031)	0.868 (0.045)
	RF	0.924 (0.023)	0.99 (0.004)	0.924 (0.023)
Teucrium lucidum	CTA	0.846 (0.022)	0.944 (0.012)	0.846 (0.022)
	GBM	0.859 (0.018)	0.971 (0.006)	0.859 (0.018)
	GLM	0.828 (0.021)	0.962 (0.007)	0.832 (0.02)
	MARS	0.811 (0.06)	0.946 (0.026)	0.745 (0.055)
	RF	0.897 (0.016)	0.986 (0.003)	0.897 (0.016)
Veronica allionii	CTA	0.927 (0.009)	0.973 (0.005)	0.927 (0.009)
	GBM	0.929 (0.009)	0.987 (0.003)	0.929 (0.009)
	GLM	0.92 (0.015)	0.984 (0.007)	0.915 (0.015)
	MARS	0.898 (0.048)	0.97 (0.022)	0.806 (0.06)
	RF	0.947 (0.007)	0.993 (0.002)	0.946 (0.007)
Viola valderia	CTA	0.781 (0.058)	0.912 (0.028)	0.781 (0.058)
	GBM	0.871 (0.039)	0.976 (0.011)	0.871 (0.039)
	GLM	0.852 (0.031)	0.967 (0.011)	0.813 (0.033)
	MARS	0.819 (0.064)	0.945 (0.034)	0.81 (0.065)
	RF	0.884 (0.033)	0.977 (0.009)	0.884 (0.033)

Online Resource 4 – Results of range analysis for the 100 studied taxa.

Percentage of range gain (RG), range loss (RL) and range change (RC) under two future scenarios (optimistic and pessimistic) for the 100 studied taxa. The reported values are the mean values of model obtained using five different model techniques; the values in bracket indicate standard deviation. For each species the vegetation belt (VB) is reported: C, colline; M, mountain; S, subalpine.

TAXON	VB	optimistic			pessimistic		
		RG	RL	RC	RG	RL	RC
Acis nicaeensis	C	98.44 (3.76)	0.38 (1.07)	-98.06 (4.67)	100 (0)	0 (0)	-100 (0)
Allium narcissiflorum	S	62.16 (27.93)	0 (0)	-62.16 (27.93)	94.09 (12.54)	0 (0)	-94.09 (12.54)
Allium scaberrimum	C	63.74 (28.97)	0 (0)	-63.74 (28.97)	79.29 (24.15)	0 (0)	-79.29 (24.15)
Androsace chaixii	M	83.59 (21.96)	0 (0)	-83.59 (21.96)	99.74 (0.86)	0 (0)	-99.74 (0.86)
Anthemis cretica subsp. *gerardiana*	C	81.9 (14.91)	0 (0)	-81.9 (14.91)	95.84 (7.51)	0 (0)	-95.84 (7.51)
Aquilegia reuteri	S	65.75 (24.68)	0 (0)	-65.75 (24.68)	90.26 (12.84)	0 (0)	-90.26 (12.84)
Arabis allionii	S	33.53 (30.47)	0 (0)	-33.53 (30.47)	69.34 (31.69)	0 (0)	-69.34 (31.69)
Arenaria cinerea	M	82.41 (24.69)	0 (0)	-82.41 (24.69)	97.87 (9.79)	0 (0)	-97.87 (9.79)
Arenaria provincialis	C	47.13 (40.04)	0 (0)	-47.13 (40.04)	36.3 (45.5)	0 (0)	-36.3 (45.5)
Asperula cynanchica subsp. *rupicola*	S	78.31 (25.43)	0 (0)	-78.31 (25.43)	85.81 (24.83)	0 (0)	-85.81 (24.83)
Asperula hexaphylla	S	86.95 (25.56)	0 (0)	-86.95 (25.56)	100 (0)	0 (0)	-100 (0)
Asplenium jahandiezii	C	100 (0)	4.13 (13.26)	-95.87 (13.26)	100 (0)	0.1 (0.56)	-99.9 (0.56)
Ballota frutescens	C	51.88 (34.99)	13.73 (10.11)	-38.15 (44.8)	77.01 (38.75)	8.24 (11.32)	-68.77 (49.68)
Berardia subacaulis	S	81.4 (27.33)	0.72 (1.43)	-80.68 (28.52)	95.28 (14.54)	0.35 (0.82)	-94.93 (15.26)
Brassica repanda subsp. *repanda*	S	46.9 (23.29)	0 (0)	-46.9 (23.29)	67.38 (27.93)	0 (0)	-67.38 (27.93)
Campanula alpestris	S	81.15 (24.66)	0 (0)	-81.15 (24.66)	92.9 (19.83)	0 (0)	-92.9 (19.83)
Campanula elatines	M	60.49 (20.27)	0 (0)	-60.49 (20.27)	90.65 (14.04)	0 (0)	-90.65 (14.04)
Campanula fritschii	M	70.2 (27.93)	0 (0)	-70.2 (27.93)	92.46 (11.64)	0 (0)	-92.46 (11.64)
Campanula rotundifolia subsp. *macrorhiza*	C	70.27 (28.94)	0 (0)	-70.27 (28.94)	99.14 (1.78)	0 (0)	-99.14 (1.78)
Campanula sabatia	C	82.29 (21.96)	0 (0)	-82.29 (21.96)	100 (0)	0 (0)	-100 (0)
Campanula stenocodon	S	72.26 (23.92)	0 (0)	-72.26 (23.92)	91.34 (19.31)	0 (0)	-91.34 (19.31)

Carex ferruginea subsp. *tenax*	S	60.18 (29.34)	27.1 (28.04)	-33.07 (53.34)	88.33 (17.81)	21.5 (39.45)	-66.83 (53.01)
Centaurea jordaniana	M	66.59 (33.87)	89.18 (82.73)	22.59 (116.14)	91.46 (24.65)	24.73 (64.23)	-66.73 (88.72)
Centaurea paniculata subsp. *polycephala*	C	90.36 (17.56)	7.76 (14.68)	-82.6 (32.1)	99.29 (3.11)	0.42 (1.88)	-98.88 (4.98)
Centaurea uniflora subsp. *uniflora*	S	57.94 (28.66)	12.75 (9.86)	-45.19 (38.31)	87.08 (25.93)	5.55 (9.32)	-81.53 (35.12)
Coincya richeri	S	90.3 (14.61)	0 (0)	-90.3 (14.61)	98.44 (4.28)	0 (0)	-98.44 (4.28)
Crocus ligusticus	C	67.4 (32.04)	0 (0)	-67.4 (32.04)	98.2 (3.82)	0 (0)	-98.2 (3.82)
Crocus versicolor	M	79.79 (21.16)	0 (0)	-79.79 (21.16)	96.97 (7.33)	0 (0)	-96.97 (7.33)
Cytisus ardoinii	M	98.74 (6.09)	0 (0)	-98.74 (6.09)	100 (0)	0 (0)	-100 (0)
Cytisus sauzeanus	M	89.15 (20.21)	0 (0)	-89.15 (20.21)	99.74 (0.87)	0 (0)	-99.74 (0.87)
Dianthus furcatus subsp. *furcatus*	S	55.04 (33.79)	0 (0)	-55.04 (33.79)	88.72 (18.84)	0 (0)	-88.72 (18.84)
Dianthus pavonius	S	65.81 (26.03)	0 (0)	-65.81 (26.03)	94.46 (13.87)	0 (0)	-94.46 (13.87)
Dianthus subacaulis	S	63.58 (28.38)	0 (0)	-63.58 (28.38)	87.49 (15.47)	0 (0)	-87.49 (15.47)
Epipactis leptochila subsp. *provincialis*	C	56.93 (34.66)	7.39 (5.42)	-49.55 (39.65)	80.04 (38.35)	3.81 (6.82)	-76.24 (45.09)
Eryngium spinalba	S	88.39 (16.97)	19.77 (19.16)	-68.62 (35.08)	98.49 (6.39)	2.38 (7.9)	-96.11 (14.12)
Erysimum burnati	S	40.59 (25.48)	0 (0)	-40.59 (25.48)	86.8 (15.86)	0 (0)	-86.8 (15.86)
Euphorbia canutii	M	68.29 (26)	0 (0)	-68.29 (26)	93.64 (8.11)	0 (0)	-93.64 (8.11)
Euphorbia graminifolia	C	98.25 (3.03)	0 (0)	-98.25 (3.03)	99.95 (0.4)	0 (0)	-99.95 (0.4)
Euphorbia variabilis subsp. *valliniana*	M	74.64 (20.84)	0 (0)	-74.64 (20.84)	97.29 (7.67)	0 (0)	-97.29 (7.67)
Festuca scabriculmis	S	62.92 (29.97)	1.55 (1.86)	-61.37 (31.57)	98.66 (3.27)	0.22 (0.66)	-98.45 (3.72)
Fritillaria involucrata	M	76.11 (24.07)	0 (0)	-76.11 (24.07)	98.49 (4.53)	0 (0)	-98.49 (4.53)
Fritillaria tubaeformis subsp. *moggridgei*	S	64.15 (30.67)	0 (0)	-64.15 (30.67)	96.11 (10.88)	0 (0)	-96.11 (10.88)
Fritillaria tubaeformis subsp. *tubaeformis*	S	80.76 (23.45)	0 (0)	-80.76 (23.45)	98.51 (4.02)	0 (0)	-98.51 (4.02)
Galeopsis reuteri	M	70.27 (30.85)	5.54 (5.42)	-64.73 (36.05)	97.88 (8.77)	0.6 (2.32)	-97.27 (11.08)
Galium pseudohelveticum	S	67.19 (30.11)	0 (0)	-67.19 (30.11)	88.84 (18.95)	0 (0)	-88.84 (18.95)
Galium saxosum	S	82.06 (23.51)	0 (0)	-82.06 (23.51)	90.79 (18.19)	0 (0)	-90.79 (18.19)
Genista lobelii	C	43.83 (34.56)	0 (0)	-43.83 (34.56)	69.81 (40.6)	0 (0)	-69.81 (40.6)
Gentiana burseri subsp. *actinocalyx*	S	31.91 (30.78)	9.87 (10.83)	-22.04 (39.01)	74.79 (28.83)	1.87 (2.47)	-72.92 (30.74)
Gentiana burseri subsp. *villarsii*	S	81.01 (23.56)	1.46 (1.97)	-79.55 (25.43)	86.09 (26.73)	1.25 (2.37)	-84.84 (28.96)
Gentiana rostani	S	80.64 (25.65)	0 (0)	-80.64 (25.65)	99.16 (2.91)	0 (0)	-99.16 (2.91)
Gymnadenia nigra subsp. *corneliana*	S	59.23 (33.65)	26.99 (27.89)	-32.24 (60.5)	91.67 (20.26)	10.2 (23.42)	-81.47 (43.51)

Hedysarum hedysaroides subsp. *boutignyanum*	S	67.55 (29.51)	5.1 (5.08)	-62.45 (34.19)	86.15 (23.16)	3.12 (4.19)	-83.03 (27.04)
Helianthemum lunulatum	S	75.09 (33.69)	0 (0)	-75.09 (33.69)	98.99 (5.7)	0 (0)	-98.99 (5.7)
Helictotrichon sempervirens	S	63.18 (24.44)	40.98 (41.59)	-22.2 (61.74)	80.15 (27.13)	45.64 (56.68)	-34.51 (82.04)
Helictotrichon setaceum	S	76.65 (20.49)	94.6 (89.3)	17.95 (107.35)	94.89 (11.1)	39.67 (66.88)	-55.22 (76.24)
Heracleum pumilum	S	73.42 (24.9)	0 (0)	-73.42 (24.9)	86.21 (20.62)	0 (0)	-86.21 (20.62)
Hesperis inodora	M	32 (28.79)	0 (0)	-32 (28.79)	67.13 (32.14)	0 (0)	-67.13 (32.14)
Hormathophylla halimifolia	M	67.71 (23.02)	3.39 (2.71)	-64.32 (25.49)	99.5 (1.01)	0.33 (0.82)	-99.17 (1.74)
Hyacinthoides italica	C	73.48 (26.92)	0 (0)	-73.48 (26.92)	99.03 (2.13)	0 (0)	-99.03 (2.13)
Iberis aurosica	S	58.77 (25.12)	0 (0)	-58.77 (25.12)	82.97 (27.95)	0 (0)	-82.97 (27.95)
Iberis nana	S	83.33 (22.65)	0 (0)	-83.33 (22.65)	99.22 (2.21)	0 (0)	-99.22 (2.21)
Jovibarba allionii	S	68.32 (32.05)	13.89 (16.21)	-54.42 (47.73)	95.72 (9.27)	3.48 (6.9)	-92.25 (15.11)
Leucanthemum burnatii	M	91.18 (19.36)	0 (0)	-91.18 (19.36)	99.99 (0.06)	0 (0)	-99.99 (0.06)
Leucanthemum virgatum	C	81.99 (21.24)	0 (0)	-81.99 (21.24)	99.97 (0.1)	0 (0)	-99.97 (0.1)
Lilium pomponium	M	67.8 (31.32)	0 (0)	-67.8 (31.32)	98.43 (3.99)	0 (0)	-98.43 (3.99)
Limonium cordatum	C	43.48 (28.21)	0 (0)	-43.48 (28.21)	48.36 (34.4)	0 (0)	-48.36 (34.4)
Limonium pseudominutum	C	19.06 (21.35)	0 (0)	-19.06 (21.35)	24.86 (28.06)	0 (0)	-24.86 (28.06)
Micromeria marginata	S	76.47 (32.12)	0 (0)	-76.47 (32.12)	100 (0)	0 (0)	-100 (0)
Minuartia glomerata subsp. *burnatii*	M	93.97 (14.05)	0 (0)	-93.97 (14.05)	100 (0)	0 (0)	-100 (0)
Minuartia rupestris subsp. *clementei*	S	61.57 (35.69)	0 (0)	-61.57 (35.69)	90.19 (20.9)	0 (0)	-90.19 (20.9)
Moehringia intermedia	M	97.87 (5.48)	1.12 (2.5)	-96.75 (7.59)	99.96 (0.17)	0.01 (0.04)	-99.95 (0.21)
Moehringia sedoides	M	87.5 (23.65)	4.09 (6.6)	-83.41 (29.31)	100 (0.03)	0.01 (0.06)	-99.98 (0.09)
Narcissus pseudonarcissus subsp. provincialis	M	97.04 (9.04)	0 (0)	-97.04 (9.04)	100 (0)	0 (0)	-100 (0)
Ophrys bertolonii subsp. *saratoi*	C	72 (22.16)	140.6 (95.66)	68.59 (114.47)	95.28 (8.06)	49.05 (79.9)	-46.22 (84.84)
Ophrys exaltata subsp. *splendida*	C	68.6 (23.95)	77.41 (69.47)	8.81 (88.82)	71.96 (33.15)	95.81 (109.67)	23.84 (140.85)
Ophrys provincialis	C	72.21 (25.97)	19.86 (22.27)	-52.36 (45.9)	80.96 (24.72)	13.63 (17.45)	-67.33 (41.6)
Oreochloa seslerioides	S	61.21 (30.02)	0 (0)	-61.21 (30.02)	95.48 (7.85)	0 (0)	-95.48 (7.85)
Potentilla delphinensis	S	96.23 (8.71)	0 (0)	-96.23 (8.71)	99.95 (0.2)	0 (0)	-99.95 (0.2)
Potentilla saxifraga	C	85.84 (18.89)	0 (0)	-85.84 (18.89)	100 (0)	0 (0)	-100 (0)
Potentilla valderia	S	67.89 (30.69)	1.39 (2.25)	-66.5 (32.35)	97.95 (6.01)	0.11 (0.36)	-97.83 (6.21)
Primula allionii	M	95.07 (21.29)	0 (0)	-95.07 (21.29)	100 (0)	0 (0)	-100 (0)
Primula marginata	S	67.45 (32.01)	0 (0)	-67.45 (32.01)	97.77 (5.1)	0 (0)	-97.77 (5.1)

Prunus brigantina	M	81.9 (20.55)	33.4 (42.96)	-48.51 (62.86)	95.49 (11.43)	14.91 (38.75)	-80.59 (50.07)
Rhaponticum heleniifolium	S	78.51 (22.58)	4.25 (4.62)	-74.26 (26.7)	83.61 (25.07)	3.79 (5.58)	-79.81 (30.23)
Santolina decumbens	C	65.01 (36.32)	3.57 (4.42)	-61.44 (40.62)	68.65 (35.69)	3.46 (4.4)	-65.19 (40.01)
Saxifraga cochlearis	M	89.61 (23.38)	16.19 (32.91)	-73.42 (55.66)	100 (0)	0.09 (0.4)	-99.91 (0.4)
Saxifraga exarata subsp. *delphinensis*	S	65.73 (35.03)	0 (0)	-65.73 (35.03)	85.39 (24.19)	0 (0)	-85.39 (24.19)
Saxifraga florulenta	S	63.84 (32.16)	0 (0)	-63.84 (32.16)	85.68 (22.96)	0 (0)	-85.68 (22.96)
Saxifraga pedemontana subsp. *pedemontana*	S	59.15 (32.5)	0 (0)	-59.15 (32.5)	90.72 (18.88)	0 (0)	-90.72 (18.88)
Saxifraga valdensis	S	59.31 (36.59)	0 (0)	-59.31 (36.59)	83.33 (26.82)	0 (0)	-83.33 (26.82)
Scrophularia provincialis	C	61.04 (20.91)	0 (0)	-61.04 (20.91)	85.7 (21.35)	0 (0)	-85.7 (21.35)
Sempervivum calcareum	M	71.22 (27.99)	0 (0)	-71.22 (27.99)	97.59 (6.15)	0 (0)	-97.59 (6.15)
Senecio leucanthemifolius subsp. *crassifolius*	C	24.16 (24.36)	15.87 (6.06)	-8.29 (29.7)	15.95 (16.74)	19.33 (5.72)	3.38 (21.11)
Seseli annuum subsp. *carvifolium*	M	45.56 (24.41)	0 (0)	-45.56 (24.41)	79.35 (28.12)	0 (0)	-79.35 (28.12)
Sideritis provincialis	C	49.98 (22.58)	2.86 (1.53)	-47.12 (23.87)	70.16 (34.11)	1.92 (2.11)	-68.24 (36.14)
Silene campanula	S	56.88 (30.38)	0 (0)	-56.88 (30.38)	90.76 (13.28)	0 (0)	-90.76 (13.28)
Silene cordifolia	S	65.49 (32.15)	0 (0)	-65.49 (32.15)	93.78 (11.27)	0 (0)	-93.78 (11.27)
Teucrium lucidum	M	57.54 (29.67)	0 (0)	-57.54 (29.67)	93.03 (9.14)	0 (0)	-93.03 (9.14)
Veronica allionii	S	59.57 (32.2)	0 (0)	-59.57 (32.2)	90.01 (21.9)	0 (0)	-90.01 (21.9)
Viola valderia	S	63.93 (32.17)	2.37 (2.62)	-61.56 (34.51)	95.42 (8.6)	0.37 (0.74)	-95.05 (9.07)

3 - THE LEGACY OF PAST CLIMATE

3.1 - Introduction

Climate change is not a prerogative of contemporary ages; climate is periodically changed during the Earth's history. Despite some regions experienced weaker past climate changes than others (and then they acted as refugia for biodiversity), no truly stable areas exist on Earth. Therefore, species have always faced the challenges of climate change: adapting, migrating, extinguishing or persisting *in situ* despite changes of climate. The combination of these processes over time has determined the current patterns of species distribution and richness. To predict the effect of future climate change means to analyze only a half of the history, preventing the possibility of a fully understand of how the species will react to it.

Fortunately, the same methodology (i.e., SDMs) used to forecast the effects of future climate change can be used to investigate species response to past climate changes (e.g., the Quaternary glaciations). In other words, we can test whether plant species endemic to SW Alps survived in the same areas where they currently occur (*in situ* persistence) or if they had periodically migrated tracking the shift of their niches. Moreover, we can verify the possible link between endemic richness and the distribution of local climatically stable areas. From a conservation point of view, the comprehension of past dynamics may help us to identify the key areas for the preservation of the endemic flora in the future and to elaborate both proactive conservation strategies for specific areas and transplantation experiments (i.e., artificially facilitated migration).

The results of this part of the PhD project were reported in a manuscript entitled “Historical and ecological factors affecting species distribution and richness of plant endemic to South Western Alps”, authored by Davide Dagnino, Luigi Minuto, Frédéric Médail, Katia Diadema, Virgile Noble and Gabriele Casazza. The manuscript is still in preparation, and it will soon be submitted to an appropriate journal of conservation biology; a proof of the manuscript is proposed in the next section of this chapter.

3.2 - Historical and ecological factors affecting species distribution and richness of plant endemic to South Western Alps

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INTRODUCTION

Species and endemics are not uniformly distributed across the world but some areas are richer than others (Myers et al., 2000; Hobohm, 2003). This trend span across different spatial scales with narrow rich areas nested within wider rich one (Cañadas et al., 2014). Because of their irreplaceability, endemic species represent a global conservation priority (Brooks et al., 2006). Unfortunately, particularly in mountain ecosystems, endemic species seem to be disproportionately exposed to climate change effects (Dirnböck et al., 2011), because they are generally characterized by small range size and specific ecological requirements.

In general, it is widely recognized that past climate change strongly affected species and endemics richness and distribution (Jansson, 2003; Graham et al., 2006; Svenning and Skov, 2007, Casazza et al., 2008; Feng et al., 2016). In fact, during past climate changes species survived adverse periods in so-called refugia and expanded their range during favourable periods (i.e., expansion-contraction model; Taberlet et al., 1998; Hewitt, 2004). Refugia are, then, areas characterized by low values of climate change velocity, that is a measure of the minimum dispersal rate that a species must attain to follow a particular climatic condition (Loarie et al., 2009; Sandel et al., 2011, 2016). The relative habitat stability of these areas within a shifting landscape enabled the persistence of species over time, and therefore the accumulation of species and endemics (Graham et al. 2010; Sandel et al., 2011). In addition, poor dispersal capabilities of endemic species may have strongly limited their range expansion after the recovering of favorable climatic conditions (Normand et al., 2011). As a result, endemic species probably survived in refugia during adverse period but, differently from other species, expanded little during favorable ones, because of dispersal limitations (Essl et al., 2011). Therefore, endemic species shifted little their distributional range over time, leading to their accumulation in the so-called areas of persistence because unable to persist in surrounding areas during adverse periods and to expand their range during favorable ones. According to this expectation, previous studies at global and regional scales suggested that paleoclimatic changes have been the main driver to endemism richness, that is higher in areas with low values of past climate change velocity (Crisp et al., 2001; Linder, 2001; Jansson, 2003; Sandel et al., 2011; Feng et al., 2016; Sandel et al., 2016). On the contrary, a strong relationship between endemism richness and modern climate was detected at local scale (Cañadas et al., 2014). Then, we are still far to understand how historically the patterns of endemism richness may have arisen and whether they changed over time. Nevertheless, understanding the climatic drivers that have contributed to the emergence of endemism rich areas is of outstanding importance to elucidate how and whether future climate changes may affect the patterns of endemism richness. This is an urgent and important issue because conservation planners must face up to the challenge of preserving richest areas in a changing world.

The South-Western Alps (hereafter SW Alps) are characterized by a particularly rich endemic flora which shows an inhomogeneous distribution across the region, allowing the identification of areas rich in endemics across all spatial scales (Casazza et al., 2008; Aeschimann et al., 2011). Furthermore, the presence of many Tertiary paleoendemics suggests that SW Alps are an area of long-term persistence (Casazza et al., 2016a). Nevertheless, despite the effect of past climate on the geographical patterns of genetic diversity in the SW Alps was widely investigated (Diadema et al., 2005; Minuto et al., 2006; Cheddadi et al., 2006; Szövényi et al., 2009; Grassi et al., 2009), to the best of our knowledge, the effects of past climate on endemic species distribution was explored only in few species (e.g. Guerrina et al., 2015; Patsiou et al., 2014).

Here, we used species distribution models and paleoclimatic data to explore (i) the relative importance of in situ persistence versus migration in explaining the current pattern of distribution and richness of endemic plants in SW Alps and (ii) the relationship between endemism richness and both past and current climate. More specifically, we are asking the following questions. (i) may long-term persistence explain the current distributional range of endemics? (ii) is current richness of endemics correlated to past richness and to stability in species composition? (iii) is current richness of endemics correlated to past climate change velocity and/or current climate conditions?

MATERIAL AND METHODS

Study area and taxa

The study area includes SW Alps (*sensu* SOIUSA; Marazzi 2005) and surrounding area (Figure 1), to take into account the entire distributional range of sub-endemic taxa (i.e., taxa in which at least 75% of the populations occur in the SW Alps). According to data availability, we selected 100 plants endemic (68 taxa) or subendemic (32 taxa) of SW Alps, representing the 56% and the 80% of the endemic and subendemic flora of this area, respectively (Appendix 1).

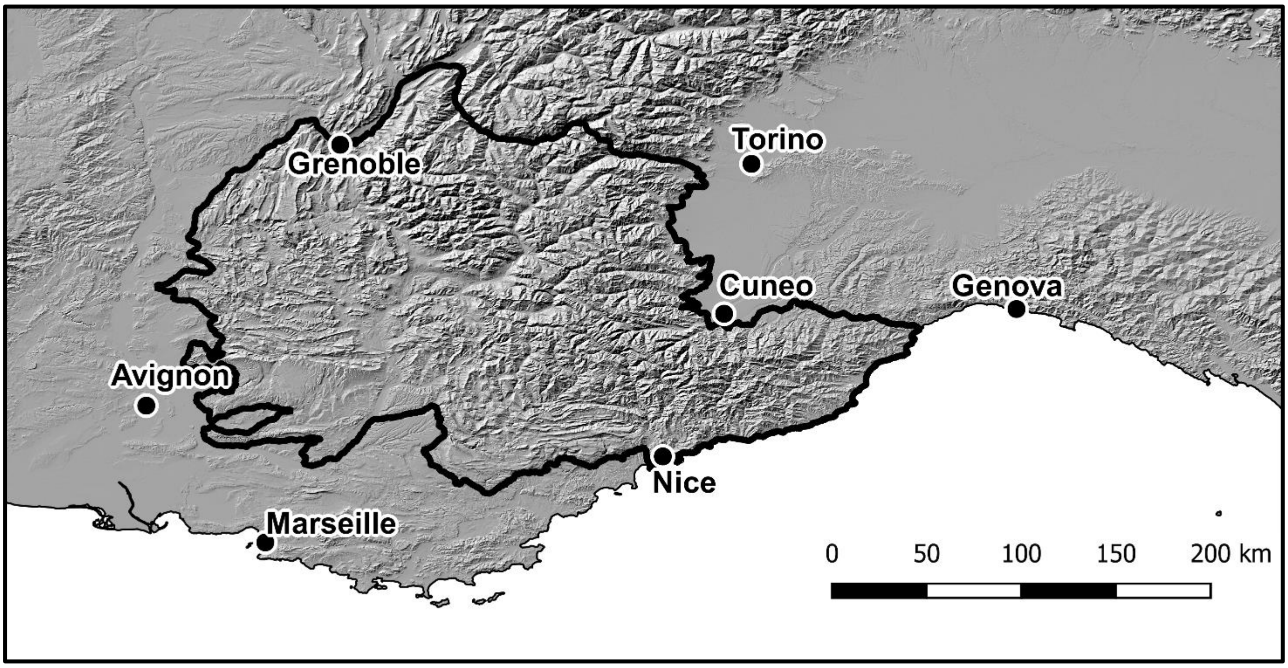

Fig. 1 - Study area, the area within the black line indicates the South Western Alps.

Environmental layers

Nineteen bioclimatic predictors representative of current (1960-1990) and past climate conditions were downloaded from the WorldClim dataset version 1.4 (Hijmans *et al.* 2005; http://www.worldclim.org) at 30-s spatial resolution (roughly 1x1 Km). To reduce collinearity and to minimize model overfitting were retained seven predictors not highly correlated (pairwise Pearson correlation ≤ |0.70|). We considered three past time slices: last interglacial (LIG, ~140–120 kyr BP), last glacial maximum (LGM, ~22 kyr BP), middle Holocene (MID, ~ 6 kyr BP). For LIG time slice we used data from Otto-Bliesner et al. (2006). For LGM and MID time slices we used three general circulation models (GCMs) provided by the Community Climate System Model (CCSM), the Model for Interdisciplinary Research on Climate (MIROC) and the Max Planck Institute for Meteorology

(MPI). Moreover we add to the analysis a lithological layer obtained from the lithological map dataset GLiM (Hartmann & Moosdorf , 2012), assuming the lithotype constancy through the considered time period. Each pixel was assigned to the most represented lithological category within its boundaries.

Species Distribution Models

To account for model-based uncertainties in the modelling process (Araújo & New 2007; Petchey et al. 2015), five SDM techniques included in the R package (R Development Core Team, 2008) BIOMOD2 v 3.3.7 (Thuiller et al. 2009) were used. For each taxon we generated 10 replicate sets of pseudo-absences, setting the number of pseudo-absences according to Barbet-Massin et al (2012). To account the environmental heterogeneity of the study area, pseudo-absences were selected using the spatial exclusion criterion, setting the minimum and maximum distance from occurrences equals to 5 and 50 km, respectively. For each pseudo-absence set, a split-sample cross-validation was repeated 10 times, using a random subset (30%) of the initial data set. Model performance was evaluated using three different measures implemented in BIOMOD2: AUC (Hanley & McNaeil 1982), KAPPA (Monserud & Leemans 1992) and TSS (Allouche et al. 2006). Finally, for each taxon we obtained 5 current and 35 past projections (5 for LIG, 15 for LGM and 15 for MID), calculating the mean value of runs and pseudo-absence sets per combination of modelling techniques and environmental datasets. The suitability maps obtained from ensemble projections were converted into binary distribution maps. Because the choice of threshold is critical by increasing or decreasing prediction bias, three different thresholds implemented in the R package PresenceAbsence (Freeman & Moisen, 2008) were selected according to Cao et al. (2013) and Liu et al. (2005). We then considered species as occurring in a cell if at least 50% of projections relative to a time slice predict its occurrence there (i.e., a majority consensus rule), obtaining for each species four majority consensus maps (one map for each time slice).

Extent of past potential range

For each species, we used the majority consensus maps of the three past time slices (i.e., LIG, LGM and MID) to assess the potential range in the past. We calculated the number of pixel belonging to the buffered zone of 10 km around occurrences that are predicted suitable in each past time slice. In each past time interval (i.e., from LIG to LGM and from LGM to MID) we classified the species potential range as stable (i.e., showing a percentage variation lower than 10%), increased (i.e., showing an increase higher than 10%) or decreased (i.e., showing a decrease higher than 10%). To avoid that time slices in which only a few pixels are predicted suitable could affect the analysis, we considered as zero (i.e., null habitat suitability) all time slices in which the pixels predicted suitable are lower than the 1% of the cells currently occupied by the species.

Persistence through time

We assessed persistence of species (i.e., in situ survival through time) modifying the approach of Graham et al. (2006). For each species, the majority consensus maps of the three past time slices were summed in a map of values of persistence over time, in which pixels range from 0 (i.e., occurrence was never predicted suitable in the past) to 3 (i.e., occurrence was predicted suitable in all past time slices). Finally, for each species we calculated the mean value of persistence over time. To test whether species with different past range dynamics (see above) have different mean persistence value we used the non-parametric Nemenyi–Damico–Wolfe–Dunn.

Pattern of species richness through time

We built a map of the currently know richness of endemics using the occurrences of all studied taxa. Known richness was compared to potential richness maps (for both current and past time) and to past species composition. To obtain the maps of the potential richness we summed the majority consensus maps of all species for both current and past time slices. Then, we averaged the number of species per cell of the three past time slices to obtain a mean value of past richness. To estimate the endemic species composition for each time interval (i.e., from LIG to LGM, from LGM to MID, and from MID to current), we calculated the pixel by pixel amount of species predicted to be stable (i.e., species that are predicted to be present in both time slice of the interval) and gained (i.e., species that were predicted to be absent in the first time slice and present in the second one). Then, we averaged these values, obtaining two maps of mean amount of stable and gained endemics. Finally, we calculated the pairwise Pearson correlation between known richness and (i) current potential richness, (ii) mean past richness, (iii) mean amount of stable and (iv) gained species.

Relation between endemism richness and climate

We explore the relationship between current endemism richness and both current and past climate. For current climate conditions we considered five widely used variables that describe the average and seasonal variation in temperature and precipitation (mean annual temperature – MAT; temperature seasonality – TS; mean annual precipitation – MAP; precipitation seasonality – PS) and the climate commonness (extent of analogous climate - EAC). We obtained MAT, TS, MAP and PS from the WorldClim dataset (Hijmans et al., 2005). The climate rarity measure of Ohlemüller et al. (2008) was used to calculate EAC: for each grid cell of the study area we calculated the number of surrounding cell within a 10 km radius where MAT was within 1°C and MAP was within 100 mm of the focal cell. It was expected that areas with locally unusual climates (i.e., low EAC values) are characterized by high levels of endemism richness (Sandel et al., 2016).

For past climate conditions we considered the climate change velocity as a measure of climate stability. We used the multivariate algorithm proposed by Hamann et al. (2015), considering as climatic variables the first two axes of a PCA based on MAT, TS, MAP and PS. For each pixel in each time slice we calculated the distance of the nearest pixel with analogous climate, using a single threshold value for all components that yielded approximately 120 unique values for the first principal component score. This distance divided by the number of years of the considered time interval correspond to the climate change velocity of such time interval. Finally, for each pixel we calculated the mean value of velocity considering all time slices.

Standard ordinary least squares (OLS) regression and simultaneous autoregressive models (SAR) were used to explore relationships between endemism richness and MAT, TS, MAP, PS, EAC and mean past velocity. Autoregressive model types (i.e., spatial error, lagged-response and lagged-mixed) were evaluated with different neighbourhood structures (increasing distances from 2 to 10 km) and the best model was selected based on the minimization of Akaike's Information Criterion (AIC) values. In addition, hierarchical partitioning (HP) was used to determine the relative importance of the variables most likely to affect variation in species richness.

RESULTS

Under current climate conditions, model evaluation indices mainly indicate a good model performance for all modelling techniques in almost all species (Appendix 2). This result makes our predictions on past time slice reliable.

The mean values of predicted persistence through time were very low (Appendix 3). The majority of species showed a mean value of persistence lower than 0.1 (55%) or between 0.1 and 1 (39%); only few species had a mean value between 1 and 2 (6%).

We found three different responses of species to past climate changes: species decreasing their range during glacial period and increasing it during interglacial period (i.e., species survived in glacial refugia, 10% of taxa – Appendix 3); species increasing their range during glacial period and decreasing it during interglacial periods (i.e., species survived in interglacial refugia, 57% of taxa – Appendix 3); species not showing a clear pattern (i.e.: same number of suitable cells over time, 28% of taxa; continuous increase from LIG to current, 1% of taxa; stable from LIG to LGM and increased from LGM to MID, 2% of taxa; decreased from LIG to LGM and stable from LGM to MID, 2% of taxa. Appendix 3). We found that species with glacial refugia showed significantly higher persistence values than species with interglacial refugia (Figure 2).

The currently known endemism richness was positively correlated both to current potential richness and gained species per cell, while the correlation with past mean richness and stable species was very low (Table I).

The lagged-mixed with neighbourhood distance equal to 5 km is resulted the best simultaneous autoregressive model type showing the lowest AIC value and the highest R2 (Table II), then it is retained for the following analysis. The variance of endemism richness explained by both current and past climatic conditions is higher when spatial autocorrelation is taken into account (Table III). The most important predictors of endemism richness are mean velocity, MAT and TS; considering spatial autocorrelation, endemism richness is positively correlated to mean velocity and MAT, and negatively correlated to TS (Table III – Appendix 4).

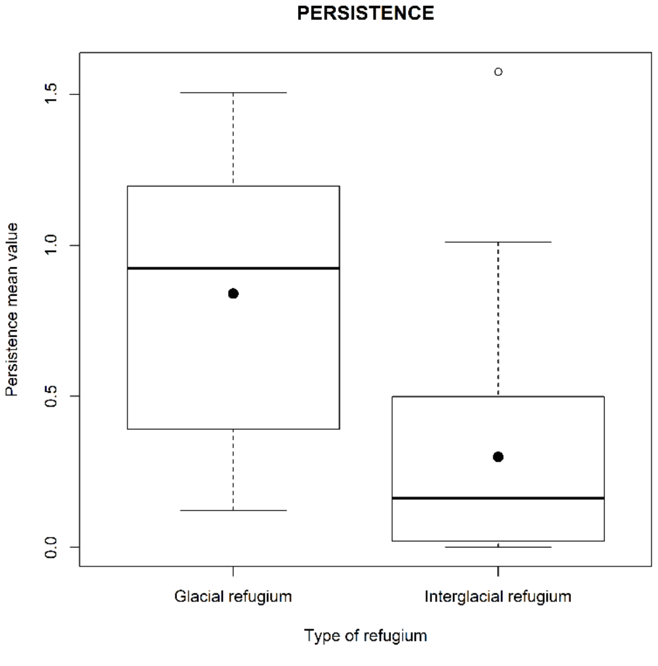

Fig. 2 – Persistence value according to type of refugium

	current known richness
current potential richness	0.40
past mean richness	0.18
stable species	0.16
gained species	0.39

Tab. I – Correlation values between current known richness and potential richness (current and past) and species composition.

Autoregressive model type	**Distance**	**AIC**	**R2**
spatial error	2km	765.34	0.24099
	5km	560.04	0.25143
	8km	668.86	0.24592
	10km	761.67	0.24118
lagged-response	2km	542.27	0.25233
	5km	535.77	0.25265
	8km	780.11	0.24024
	10km	945.44	0.23172
lagged-mixed	2km	461.76	0.25697
	5km	**357.39**	**0.26218**
	8km	508.26	0.25464
	10km	624.59	0.24877

Tab. II - Akaike's Information Criterion (AIC) and R^2 *values for different combination of autoregressive model types (lagged-response, lagged-mixed, and spatial error) and neighborhood values. The best model (i.e., lowest AIC and highest* R^2*) is marked in bold.*

Variable	**OLS**	**SAR**	**HP**
intercept	3.1908^{***}	0.8893^{***}	
EAC	-0.0037^{***}	-0.0141^{***}	0.0017
MAT	-0.0003^{***}	0.0313^{**}	0.0458
MAP	-0.0601^{ns}	0.0036^{***}	0.0136
TS	-0.0031^{***}	-0.1004^{***}	0.0427
PS	-0.1272^{ns}	0.0065^{ns}	0.0097
Mean velocity	0.0019^{***}	0.0008^{***}	0.0480
R^2	0.1612	0.2514	0.1615

Tab. III - Results of ordinary least squares (OLS), simultaneous autoregressive model (SAR) and hierarchical partitioning (HP) for predictor variables and species richness of SW Alps endemic plants. $^{***}\ p<0.001$; $^{**}0.001<p<0.05$; $^{ns}\ p\geq0.05$

DISCUSSION

In our study, we analyzed the effect of past climate changes on endemic plant species distribution and richness in the SW Alps. Nevertheless, our results should be considered with attention to main limitations of the approach we adopted. First, SDMs assume that species-climate relationships remain unchanged through time. Even if niche stability has been demonstrated in many studies, species-climate relationships may change over time, potentially reducing predictive ability of SDMs (Williams & Jackson 2007; Gavin et al., 2014 and references therein). Second, SDM results may be strongly affected by spatial scale (Randin et al., 2009); nevertheless, we produced our models at about 1 km^2 of resolution, a scale widely used in other studies on endemic plant species (e.g., Casazza et al., 2014; Guerrina et al., 2015). Third, despite the use of an appropriate grid size, SDMs based on downscaled climatic data (such as those used in this study) may not be able to detect microrefugia because they do not consider factors driving unusual microclimatic conditions (Ashcroft, 2010; Gavin et al., 2014).

Endemic species are expected to show high values of *in situ* persistence through time because they are usually characterized by low dispersal ability (Malcolm et al. 2002; Engler et al. 2009; Ozinga et al. 2009). Conversely, the low persistence values found in all studied species (Appendix 3), suggest that species distributional ranges were deeply changed over time. The majority of species showed interglacial refugia (57%), a minority of species showed glacial refugia (10%) and the rest of species did not show a clear pattern (33%). Moreover, species having glacial refugia showed significantly higher values of persistence than the others (Figure 2), suggesting that they maintained part of their distributional range stable over time.

These results are consistent with phylogeographical evidences on both endemic and non-endemic plants occurring in the study area, suggesting that species shifted their geographical distribution in order to track climatic conditions (Diadema et al., 2005; Minuto et al., 2006; Cheddadi et al., 2006; Szövényi et al., 2009; Grassi et al., 2009). In mountain areas like SW Alps, genetic diversity and geographical distribution of species may be affected by recurrent short-distance altitudinal shift favoured by the rough topography (Gutiérrez Larena et al., 2002; Casazza et al., 2016b). However, our results suggest an idiosyncratic response of SW Alps endemics to past climate changes, as previously found in several studies (Williams et al., 2004; Magri et al., 2006; Bennet & Provan, 2008; Stewart, 2008; Médail & Diadema, 2009; Zecca et al., 2017). This is congruent with the concept that a single refugium is unlikely to be suitable for species having different environmental requirements (Stewart et al., 2010) or history (Soltis et al., 2006), as in the case of SW Alps endemics, that are ranging from steno-Mediterranean to alpine species. In particular, the majority of SW Alps endemics contracted their range during interglacial periods. This result is consistent with previous findings based on both SDMs and molecular analysis on plants occurring in SW Alps (Guerrina et al., 2016; Zecca et al., 2017) and with the expectation for species occurring in cold climate (Ravazzi, 2002; Stewart et al., 2003; 2010). In fact, these species are expected to increase their range during cold periods by spreading to lowland areas and experiencing distributional or demographical decline during warm interglacials (Stewart & Lister, 2001; Stewart et al., 2003; Dalén et al., 2005; Steweart & Dalén, 2008). Furthermore, the high rate of species showing interglacial refugia is consistent with the future range size reduction forecasted for the majority of species here considered (Dagnino et al., submitted). Nevertheless, not all species growing in cold climate are expected to expand their range during glacial periods and contract during warm periods. In fact, it was suggested that some alpine species may be adapted to a montane environment rather than a cold climate, and thus during glacial periods they may have not be able to expand their range into the surrounding lowlands, but would instead survived in glacial refugia (Holderegger & Thiel-Egenter, 2008; Stewart et al., 2010). In line with this observation, three out of teen species showing glacial refugia are alpine species (i.e., *Arabis allionii* DC., *Gentiana burseri* Lapeyr. subsp. *actinocalyx* Polidori and *Silene campanula* Pers.). The highest persistence values detected in species having glacial refugia may be because of glacial periods were generally much longer than interglacial ones (Hewitt, 1996; Rull, 2009). Consequently, these species spent long time in refugia and had short time to expand their range (Stewart et al., 2010), so many of their populations now occur in the glacial refugial areas. Altogether, our results suggest that species at different periods occupied different areas, supporting the view of refugia within a mountain range as temporally and spatially dynamic (Médail & Diadema, 2009; Graham et al., 2010).

The current pattern of endemics richness is correlated to current potential richness and mean amount of gained species in the different time slices (Table I). Furthermore, the endemics richness per cell is negatively correlated with seasonality of temperatures (TS) and positively correlated with mean annual temperature (MAT) and mean past climate change velocity (Table III – Appendix 4). The relation between current known richness and both gained species and current potential richness give further support to the idea that the species composition has been changed over time and suggests that current climate play an important role in affecting current pattern of endemics richness at local scale. This result is probably because of the idiosyncratic shift in geographic range of plants in response of climatic disturbance (Davis, 1981; Huntley & Birks, 1983; Huntley & Webb, 1988; Webb, 1988; Jackson et al., 2000; Williams et al., 2004; Graham et al., 2006). This idiosyncratic response to climate change is congruent with the repeated pattern of disaggregation and recombination of vegetal communities in response to past climate changes that was detected in several studies (Cushing, 1967; Overpeck et al., 1992; Jackson & Overpeck, 2000; Williams et al. 2001, 2004; Wing et al., 2005; Moritz & Agudo 2013) and that occurred particularly fast during the late-glacial period and early Holocene (16000-8000 yr BP) and after 500 yr BP (Williams et al., 2004).

Our results suggest that at local scale current climate (MAT and TS) and past climate velocity are the main factors determining the current pattern of endemics richness. In particular, the positive correlation between endemics richness and past climate velocity is in line with the high temporal and spatial range dynamic detected by SDMs and with the relationship between endemics richness and number of gained species. This result contrasts with several previous studies at regional scale that indicate past climate stability as the main determinant of endemics richness (Jansson, 2003; Graham et al., 2006; Araùjo et al., 2008; Sandel et al., 2011, 2016; Feng et al., 2016). Conversely, it is in line with the finding that at local scale endemics richness is strongly related to current climate conditions in Mediterranean region (Cañadas et al., 2014), confirming that the relation between endemics richness and explanatory variables is strongly scale-dependent (Foody, 2004). The discrepancy between our result and the previous ones may be because of the different scale used, regional vs local. In fact, the importance of past climate stability on current endemics richness depends on the dispersal ability of species, increasing from species having high dispersal ability to those having low dispersal ability (Sandel et al., 2011). For this reason, in SW Alps short-distance migrations may have weakened both the genetic signature of glaciations (Casazza et al., 2016b) and the importance of climate stability with respect to other factors, supporting the idea that dispersal ability of species may affect the relationship between local and regional species richness (Cornell & Lawton, 1992). Furthermore, as suggested by our previous results, current (warm) climate is an adverse period for the majority of studied taxa that are currently in refugia, a common condition for species that prefer cold climates (Ashcroft, 2010). As a result, current climate (in particular temperature-related variables) may have a strong influence on the current pattern of richness. Taken together, our results suggest that at local scale richest areas are not located in climatically stable areas, that may have acted as refugia for single species, but in changing areas, likely as a consequence of the co-occurrence of species colonizing these areas coming from separate refugia.

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SUPPORTING INFORMATION

Appendix 1 – Studied taxa

Taxon	**Family**
Acis nicaeensis (Ardoino) Lledo et al.	Amaryllidaceae
Allium narcissiflorum Vill.	Alliaceae
Allium scaberrimum J.Serres	Alliaceae
Androsace chaixii Gren.	Primulaceae
Anthemis cretica L. subsp. *gerardiana* (Jord.) Greuter	Asteraceae
Aquilegia reuteri Boiss.	Ranunculaceae
Arabis allionii DC.	Brassicaceae
Arenaria cinerea DC.	Caryophyllaceae
Arenaria provincialis Chater & G.Halliday	Caryophyllaceae
Asperula cynanchica subsp. *rupicola* (Jord.) Berher	Rubiaceae
Asperula hexaphylla All.	Rubiaceae
Asplenium jahandiezii (Litard.) Rouy	Aspleniaceae
Ballota frutescens (L.) J.Woods	Lamiaceae
Berardia subacaulis Vill.	Asteraceae
Brassica repanda (Willd.) DC. subsp. *repanda*	Brassicaceae
Campanula alpestris All.	Campanulaceae
Campanula elatines L.	Campanulaceae
Campanula fritschii Witasek	Campanulaceae
Campanula rotundifolia L. subsp. *macrorhiza* (J.Gay ex A.DC.) Bonnier & Layens	Campanulaceae
Campanula sabatia De Not.	Campanulaceae
Campanula stenocodon Boiss. & Reut.	Campanulaceae
Carex ferruginea subsp. *tenax* (H.Christ) K.Richt.	Cyperaceae
Centaurea jordaniana Godr. & Gren.	Asteraceae
Centaurea paniculata L. subsp. *polycephala* (Jord.) Nyman	Asteraceae
Centaurea uniflora Turra subsp. *uniflora*	Asteraceae
Coincya richeri (Vill.) Greuter & Burdet	Brassicaceae
Crocus ligusticus Mariotti	Iridaceae
Crocus versicolor Ker Gawl.	Iridaceae
Cytisus ardoinii E.Fourn.	Fabaceae

Cytisus sauzeanus Burnat & Briq.	Fabaceae
Dianthus furcatus Balb. subsp. *furcatus*	Caryophyllaceae
Dianthus pavonius Tausch	Caryophyllaceae
Dianthus subacaulis Vill.	Caryophyllaceae
Epipactis leptochila (Godfery) Godfery subsp. *provincialis* (Aubenas & Robatsch) J.M.Tison	Orchidaceae
Eryngium spinalba Vill.	Apiaceae
Erysimum burnatii Vidal	Brassicaceae
Euphorbia canutii Parl.	Euphorbiaceae
Euphorbia graminifolia Vill.	Euphorbiaceae
Euphorbia variabilis subsp. *valliniana* (Belli) Jauzein	Euphorbiaceae
Festuca scabriculmis (Hack.) K.Richt.	Poaceae
Fritillaria involucrata All.	Liliaceae
Fritillaria tubaeformis Gren. & Godr. subsp. *moggridgei* (Baker) Rix	Liliaceae
Fritillaria tubaeformis Gren. & Godr. subsp. *tubaeformis*	Liliaceae
Galeopsis reuteri Rchb.f.	Lamiaceae
Galium pseudohelveticum Ehrend.	Rubiaceae
Galium saxosum (Chaix) Breistr.	Rubiaceae
Genista lobelii DC.	Fabaceae
Gentiana burseri Lapeyr. subsp. *actinocalyx* Polidori	Gentianaceae
Gentiana burseri Lapeyr. subsp. *villarsii* (Griseb.) Rouy	Gentianaceae
Gentiana rostanii Reut. ex Verl.	Gentianaceae
Gymnadenia nigra (L.) Rchb.f. subsp. *corneliana* (Beauverd) J.M.Tison	Orchidaceae
Hedysarum hedysaroides (L.) Schinz & Thell. subsp. *boutignyanum* (A.Camus) Jauzein	Fabaceae
Helianthemum lunulatum (All.) DC.	Cistaceae
Helictotrichon sempervirens (Vill.) Pilg.	Poaceae
Helictotrichon setaceum (Vill.) Henrard	Poaceae
Heracleum pumilum Vill.	Apiaceae
Hesperis inodora L.	Brassicaceae
Hormathophylla halimifolia (Boiss.) P.Küpfer	Brassicaceae
Hyacinthoides italica (L.) Rothm.	Hyacinthaceae
Iberis aurosica Chaix	Brassicaceae
Iberis nana All.	Brassicaceae
Jovibarba allionii (Jord. & Fourr.) D.A.Webb	Crassulaceae
Leucanthemum burnatii Briq. & Cavill.	Asteraceae
Leucanthemum virgatum (Desr.) Clos	Asteraceae
Lilium pomponium L.	Liliaceae
Limonium cordatum (L.) Mill.	Plumbaginaceae
Limonium pseudominutum Erben	Plumbaginaceae
Micromeria marginata (Sm.) Chater	Lamiaceae
Minuartia glomerata subsp. *burnatii* (Rouy & Foucaud) Favarger & F.Conti	Caryophyllaceae
Minuartia rupestris subsp. *clementei* (Huter) Greuter & Burdet	Caryophyllaceae
Moehringia intermedia Loisel. ex Panizzi	Caryophyllaceae
Moehringia sedoides (Pers.) Cumino ex Loisel.	Caryophyllaceae
Narcissus pseudonarcissus L. subsp. *provincialis* (Pugsley) J.M.Tison	Amaryllidaceae
Ophrys bertolonii Moretti subsp. *saratoi* (E.G.Camus) R.Soca	Orchidaceae

Ophrys exaltata subsp. *splendida* (Gölz & Reinhard) R.Soca	Orchidaceae
Ophrys provincialis (Baumann & Künkele) Paulus	Orchidaceae
Oreochloa seslerioides (All.) K.Richt.	Poaceae
Potentilla delphinensis Gren. & Godr.	Rosaceae
Potentilla saxifraga Ardoino ex De Not.	Rosaceae
Potentilla valderia L.	Rosaceae
Primula allionii Loisel.	Primulaceae
Primula marginata Curtis	Primulaceae
Prunus brigantina Vill.	Rosaceae
Rhaponticum heleniifolium Godr. & Gren.	Asteraceae
Santolina decumbens Mill.	Asteraceae
Saxifraga cochlearis Rchb.	Saxifragaceae
Saxifraga exarata Vill. subsp. *delphinensis* (Ravaud) Kerguélen	Saxifragaceae
Saxifraga florulenta Moretti	Saxifragaceae
Saxifraga pedemontana All. subsp. *pedemontana*	Saxifragaceae
Saxifraga valdensis DC.	Saxifragaceae
Scrophularia provincialis Rouy	Scrophulariaceae
Sempervivum calcareum Jord.	Crassulaceae
Senecio leucanthemifolius Poir. subsp. *crassifolius* (Willd.) Ball	Asteraceae
Seseli annuum L. subsp. *carvifolium* (Vill.) P.Fourn.	Apiaceae
Sideritis provincialis Jord. & Fourr.	Lamiaceae
Silene campanula Pers.	Caryophyllaceae
Silene cordifolia All.	Caryophyllaceae
Teucrium lucidum L.	Lamiaceae
Veronica allionii Vill.	Scrophulariaceae
Viola valderia All.	Violaceae

Appendix 2 – Model performance

The shown values represent the mean values of ten evaluation runs for each algorithm; values in brackets indicate standard deviation. Values marked with an asterisk indicate a poor model performance, according to the following indications:

- AUC) 1>excellent>0.9>good>0.8>fair>0.7>poor>0.6>fail;
- TSS and KAPPA) 1>excellent>0.8>good>0.6>fair>0.4>poor>0.2>fail.

Species	**Algorithm**	**TSS**	**AUC**	**KAPPA**
Acis nicaeensis	CTA	0.906 (0.031)	0.961 (0.017)	0.907 (0.031)
	GBM	0.956 (0.017)	0.993 (0.005)	0.955 (0.017)
	GLM	0.933 (0.059)	0.974 (0.033)	0.913 (0.068)
	MARS	0.892 (0.06)	0.951 (0.034)	0.908 (0.044)
	RF	0.966 (0.02)	0.998 (0.002)	0.966 (0.02)

Allium narcissiflorum	CTA	0.884 (0.023)	0.961 (0.01)	0.884 (0.023)
	GBM	0.892 (0.016)	0.981 (0.006)	0.892 (0.016)
	GLM	0.891 (0.016)	0.979 (0.006)	0.891 (0.016)
	MARS	0.856 (0.065)	0.955 (0.032)	0.81 (0.056)
	RF	0.916 (0.014)	0.989 (0.004)	0.917 (0.014)
Allium scaberrimum	CTA	0.676 (0.09)	0.859 (0.051)	0.676 (0.09)
	GBM	0.801 (0.054)	0.948 (0.02)	0.799 (0.055)
	GLM	0.734 (0.057)	0.922 (0.036)	0.662 (0.075)
	MARS	0.753 (0.078)	0.915 (0.041)	0.753 (0.078)
	RF	0.79 (0.057)	0.947 (0.022)	0.789 (0.057)
Androsace chaixii	CTA	0.848 (0.027)	0.943 (0.017)	0.848 (0.027)
	GBM	0.862 (0.023)	0.975 (0.007)	0.862 (0.023)
	GLM	0.847 (0.016)	0.971 (0.006)	0.843 (0.017)
	MARS	0.829 (0.058)	0.95 (0.031)	0.806 (0.06)
	RF	0.89 (0.021)	0.984 (0.005)	0.891 (0.021)
Anthemis cretica subsp. *gerardiana*	CTA	0.755 (0.064)	0.916 (0.03)	0.755 (0.064)
	GBM	0.824 (0.042)	0.965 (0.012)	0.824 (0.042)
	GLM	0.717 (0.043)	0.93 (0.019)	0.673 (0.048)
	MARS	0.702 (0.067)	0.906 (0.033)	0.694 (0.074)
	RF	0.866 (0.037)	0.976 (0.011)	0.865 (0.037)
Aquilegia reuteri	CTA	0.838 (0.023)	0.945 (0.013)	0.838 (0.023)
	GBM	0.855 (0.019)	0.974 (0.005)	0.855 (0.019)
	GLM	0.839 (0.019)	0.969 (0.006)	0.837 (0.019)
	MARS	0.793 (0.061)	0.937 (0.029)	0.754 (0.063)
	RF	0.893 (0.02)	0.983 (0.005)	0.893 (0.02)
Arabis allionii	CTA	0.463 (0.133)*	0.737 (0.076)*	0.458 (0.132)*
	GBM	0.655 (0.091)	0.856 (0.055)	0.644 (0.095)
	GLM	0.659 (0.073)	0.858 (0.047)	0.51 (0.067)*
	MARS	0.651 (0.106)	0.849 (0.061)	0.654 (0.106)
	RF	0.693 (0.091)	0.887 (0.048)	0.687 (0.093)
Arenaria cinerea	CTA	0.71 (0.094)	0.865 (0.051)	0.712 (0.093)
	GBM	0.849 (0.055)	0.966 (0.018)	0.847 (0.055)
	GLM	0.844 (0.073)	0.948 (0.046)	0.747 (0.088)
	MARS	0.809 (0.082)	0.93 (0.045)	0.812 (0.08)
	RF	0.834 (0.056)	0.959 (0.021)	0.83 (0.058)
Arenaria provincialis	CTA	0.952 (0.014)	0.985 (0.007)	0.952 (0.014)
	GBM	0.963 (0.012)	0.997 (0.002)	0.963 (0.012)
	GLM	0.945 (0.03)	0.981 (0.019)	0.944 (0.03)
	MARS	0.916 (0.055)	0.96 (0.028)	0.921 (0.055)
	RF	0.977 (0.009)	0.999 (0.001)	0.977 (0.009)
Asperula cynanchica subsp. *rupicola*	CTA	0.818 (0.032)	0.925 (0.019)	0.819 (0.032)
	GBM	0.851 (0.03)	0.968 (0.011)	0.852 (0.03)
	GLM	0.84 (0.03)	0.958 (0.017)	0.801 (0.034)
	MARS	0.801 (0.069)	0.917 (0.043)	0.823 (0.058)
	RF	0.859 (0.035)	0.972 (0.01)	0.859 (0.034)
Asperula hexaphylla	CTA	0.779 (0.067)	0.911 (0.035)	0.78 (0.067)
	GBM	0.897 (0.043)	0.982 (0.011)	0.897 (0.043)

	GLM	0.913 (0.025)	0.984 (0.012)	0.87 (0.031)
	MARS	0.82 (0.07)	0.932 (0.037)	0.831 (0.069)
	RF	0.915 (0.039)	0.988 (0.008)	0.916 (0.039)
Asplenium jahandiezii	CTA	0.85 (0.07)	0.935 (0.038)	0.85 (0.069)
	GBM	0.937 (0.046)	0.99 (0.012)	0.937 (0.045)
	GLM	0.912 (0.073)	0.964 (0.04)	0.862 (0.086)
	MARS	0.872 (0.069)	0.942 (0.038)	0.876 (0.067)
	RF	0.949 (0.038)	0.994 (0.007)	0.949 (0.038)
Ballota frutescens	CTA	0.801 (0.06)	0.912 (0.033)	0.801 (0.06)
	GBM	0.89 (0.041)	0.973 (0.015)	0.889 (0.041)
	GLM	0.891 (0.061)	0.959 (0.034)	0.817 (0.075)
	MARS	0.828 (0.069)	0.939 (0.039)	0.832 (0.065)
	RF	0.91 (0.038)	0.979 (0.012)	0.91 (0.038)
Berardia subacaulis	CTA	0.905 (0.017)	0.968 (0.01)	0.905 (0.017)
	GBM	0.926 (0.017)	0.991 (0.004)	0.926 (0.017)
	GLM	0.923 (0.015)	0.991 (0.003)	0.924 (0.015)
	MARS	0.892 (0.056)	0.963 (0.032)	0.875 (0.056)
	RF	0.931 (0.015)	0.992 (0.003)	0.931 (0.015)
Brassica repanda subsp. *repanda*	CTA	0.734 (0.035)	0.896 (0.025)	0.733 (0.035)
	GBM	0.771 (0.027)	0.947 (0.01)	0.771 (0.027)
	GLM	0.667 (0.03)	0.894 (0.014)	0.673 (0.028)
	MARS	0.694 (0.076)	0.885 (0.042)	0.594 (0.068)*
	RF	0.811 (0.024)	0.961 (0.008)	0.81 (0.024)
Campanula alpestris	CTA	0.905 (0.01)	0.972 (0.007)	0.905 (0.01)
	GBM	0.909 (0.011)	0.988 (0.002)	0.909 (0.011)
	GLM	0.896 (0.027)	0.981 (0.019)	0.892 (0.027)
	MARS	0.859 (0.06)	0.952 (0.036)	0.783 (0.055)
	RF	0.931 (0.009)	0.993 (0.002)	0.931 (0.009)
Campanula elatines	CTA	0.733 (0.08)	0.877 (0.044)	0.734 (0.08)
	GBM	0.824 (0.06)	0.95 (0.027)	0.826 (0.058)
	GLM	0.862 (0.032)	0.965 (0.012)	0.772 (0.041)
	MARS	0.801 (0.073)	0.923 (0.041)	0.802 (0.07)
	RF	0.853 (0.06)	0.961 (0.023)	0.852 (0.06)
Campanula fritschii	CTA	0.513 (0.12)*	0.767 (0.068)*	0.519 (0.119)*
	GBM	0.643 (0.097)	0.86 (0.052)	0.649 (0.097)
	GLM	0.715 (0.083)	0.88 (0.041)	0.456 (0.083)*
	MARS	0.623 (0.095)	0.846 (0.05)	0.622 (0.095)
	RF	0.701 (0.081)	0.893 (0.043)	0.706 (0.08)
Campanula rotundifolia subsp. *macrorhiza*	CTA	0.848 (0.017)	0.951 (0.009)	0.848 (0.017)
	GBM	0.837 (0.015)	0.973 (0.004)	0.837 (0.015)
	GLM	0.747 (0.025)	0.944 (0.008)	0.744 (0.027)
	MARS	0.723 (0.07)	0.909 (0.041)	0.619 (0.083)
	RF	0.909 (0.012)	0.99 (0.002)	0.909 (0.012)
Campanula sabatia	CTA	0.913 (0.036)	0.965 (0.019)	0.913 (0.036)
	GBM	0.959 (0.023)	0.996 (0.004)	0.958 (0.023)
	GLM	0.959 (0.022)	0.989 (0.011)	0.949 (0.024)
	MARS	0.908 (0.056)	0.96 (0.031)	0.914 (0.044)

	RF	0.964 (0.018)	0.997 (0.003)	0.963 (0.018)
Campanula stenocodon	CTA	0.779 (0.037)	0.919 (0.018)	0.779 (0.038)
	GBM	0.824 (0.03)	0.96 (0.01)	0.825 (0.03)
	GLM	0.818 (0.027)	0.956 (0.009)	0.795 (0.029)
	MARS	0.766 (0.061)	0.922 (0.034)	0.761 (0.061)
	RF	0.84 (0.036)	0.966 (0.012)	0.84 (0.036)
Carex ferruginea subsp. *tenax*	CTA	0.889 (0.009)	0.972 (0.004)	0.889 (0.009)
	GBM	0.869 (0.009)	0.982 (0.002)	0.869 (0.009)
	GLM	0.847 (0.017)	0.972 (0.005)	0.842 (0.018)
	MARS	0.808 (0.067)	0.939 (0.041)	0.682 (0.074)
	RF	0.938 (0.007)	0.995 (0.001)	0.938 (0.007)
Centaurea jordaniana	CTA	0.78 (0.051)	0.912 (0.029)	0.782 (0.051)
	GBM	0.862 (0.038)	0.967 (0.013)	0.864 (0.038)
	GLM	0.791 (0.07)	0.922 (0.042)	0.696 (0.074)
	MARS	0.709 (0.075)	0.877 (0.05)	0.741 (0.076)
	RF	0.901 (0.034)	0.984 (0.009)	0.901 (0.034)
Centaurea paniculata subsp. *polycephala*	CTA	0.692 (0.081)	0.861 (0.046)	0.692 (0.081)
	GBM	0.789 (0.049)	0.944 (0.02)	0.787 (0.049)
	GLM	0.775 (0.053)	0.94 (0.03)	0.706 (0.057)
	MARS	0.757 (0.068)	0.915 (0.031)	0.755 (0.066)
	RF	0.795 (0.059)	0.944 (0.024)	0.792 (0.059)
Centaurea uniflora subsp. *uniflora*	CTA	0.883 (0.013)	0.959 (0.007)	0.883 (0.013)
	GBM	0.891 (0.011)	0.977 (0.004)	0.891 (0.011)
	GLM	0.877 (0.015)	0.97 (0.007)	0.877 (0.015)
	MARS	0.846 (0.052)	0.945 (0.034)	0.75 (0.05)
	RF	0.914 (0.011)	0.989 (0.003)	0.914 (0.011)
Coincya richeri	CTA	0.827 (0.024)	0.942 (0.015)	0.827 (0.024)
	GBM	0.841 (0.022)	0.97 (0.006)	0.841 (0.022)
	GLM	0.806 (0.033)	0.956 (0.01)	0.807 (0.032)
	MARS	0.801 (0.059)	0.916 (0.042)	0.803 (0.058)
	RF	0.878 (0.017)	0.982 (0.004)	0.878 (0.017)
Crocus ligusticus	CTA	0.802 (0.048)	0.913 (0.029)	0.802 (0.049)
	GBM	0.872 (0.039)	0.974 (0.011)	0.872 (0.039)
	GLM	0.89 (0.02)	0.974 (0.008)	0.855 (0.025)
	MARS	0.833 (0.066)	0.944 (0.033)	0.843 (0.058)
	RF	0.891 (0.033)	0.981 (0.01)	0.891 (0.034)
Crocus versicolor	CTA	0.742 (0.026)	0.907 (0.015)	0.743 (0.026)
	GBM	0.753 (0.025)	0.943 (0.008)	0.754 (0.025)
	GLM	0.741 (0.024)	0.926 (0.011)	0.745 (0.024)
	MARS	0.704 (0.07)	0.891 (0.037)	0.632 (0.071)
	RF	0.801 (0.019)	0.965 (0.005)	0.801 (0.019)
Cytisus ardoinii	CTA	0.895 (0.037)	0.957 (0.019)	0.896 (0.037)
	GBM	0.945 (0.026)	0.992 (0.006)	0.945 (0.026)
	GLM	0.938 (0.033)	0.984 (0.019)	0.905 (0.035)
	MARS	0.89 (0.062)	0.956 (0.033)	0.903 (0.058)
	RF	0.951 (0.026)	0.993 (0.006)	0.952 (0.026)
Cytisus sauzeanus	CTA	0.765 (0.066)	0.898 (0.039)	0.766 (0.066)

	GBM	0.826 (0.046)	0.964 (0.013)	0.826 (0.046)
	GLM	0.805 (0.027)	0.96 (0.009)	0.774 (0.03)
	MARS	0.745 (0.08)	0.911 (0.043)	0.739 (0.075)
	RF	0.843 (0.04)	0.971 (0.01)	0.844 (0.04)
Dianthus furcatus subsp. *furcatus*	CTA	0.762 (0.057)	0.9 (0.032)	0.762 (0.057)
	GBM	0.806 (0.043)	0.956 (0.014)	0.806 (0.043)
	GLM	0.815 (0.028)	0.956 (0.009)	0.759 (0.031)
	MARS	0.791 (0.057)	0.932 (0.032)	0.797 (0.057)
	RF	0.821 (0.04)	0.962 (0.012)	0.821 (0.04)
Dianthus pavonius	CTA	0.901 (0.011)	0.964 (0.006)	0.901 (0.011)
	GBM	0.896 (0.011)	0.981 (0.004)	0.896 (0.011)
	GLM	0.894 (0.015)	0.978 (0.006)	0.893 (0.015)
	MARS	0.876 (0.046)	0.961 (0.027)	0.796 (0.055)
	RF	0.929 (0.01)	0.991 (0.002)	0.929 (0.01)
Dianthus subacaulis	CTA	0.857 (0.033)	0.943 (0.019)	0.858 (0.032)
	GBM	0.89 (0.03)	0.98 (0.009)	0.89 (0.03)
	GLM	0.871 (0.025)	0.974 (0.007)	0.842 (0.028)
	MARS	0.845 (0.056)	0.954 (0.028)	0.832 (0.051)
	RF	0.897 (0.028)	0.984 (0.007)	0.896 (0.028)
Epipactis leptochila subsp. *provincialis*	CTA	0.632 (0.099)	0.829 (0.052)	0.633 (0.099)
	GBM	0.785 (0.066)	0.927 (0.031)	0.776 (0.067)
	GLM	0.703 (0.09)	0.889 (0.057)	0.625 (0.098)
	MARS	0.709 (0.084)	0.879 (0.049)	0.707 (0.084)
	RF	0.801 (0.069)	0.941 (0.024)	0.794 (0.069)
Eryngium spinalba	CTA	0.857 (0.019)	0.946 (0.013)	0.858 (0.019)
	GBM	0.866 (0.017)	0.97 (0.006)	0.866 (0.017)
	GLM	0.857 (0.021)	0.962 (0.011)	0.86 (0.021)
	MARS	0.832 (0.057)	0.936 (0.035)	0.798 (0.061)
	RF	0.909 (0.014)	0.988 (0.003)	0.909 (0.014)
Erysimum burnati	CTA	0.556 (0.109)*	0.791 (0.064)*	0.553 (0.11)*
	GBM	0.68 (0.081)	0.878 (0.043)	0.673 (0.083)
	GLM	0.69 (0.055)	0.891 (0.03)	0.564 (0.061)*
	MARS	0.638 (0.076)	0.856 (0.044)	0.638 (0.077)
	RF	0.721 (0.081)	0.907 (0.038)	0.718 (0.083)
Euphorbia canutii	CTA	0.726 (0.059)	0.892 (0.031)	0.726 (0.059)
	GBM	0.82 (0.043)	0.96 (0.014)	0.82 (0.042)
	GLM	0.798 (0.036)	0.953 (0.012)	0.75 (0.038)
	MARS	0.766 (0.074)	0.922 (0.039)	0.764 (0.064)
	RF	0.846 (0.041)	0.968 (0.012)	0.846 (0.041)
Euphorbia graminifolia	CTA	0.699 (0.09)	0.875 (0.05)	0.701 (0.09)
	GBM	0.863 (0.063)	0.959 (0.024)	0.86 (0.062)
	GLM	0.73 (0.046)	0.889 (0.022)	0.499 (0.045)*
	MARS	0.78 (0.072)	0.912 (0.036)	0.783 (0.071)
	RF	0.896 (0.051)	0.974 (0.015)	0.892 (0.051)
Euphorbia variabilis subsp. *valliniana*	CTA	0.553 (0.131)*	0.787 (0.074)*	0.554 (0.131)*
	GBM	0.735 (0.09)	0.908 (0.04)	0.735 (0.089)
	GLM	0.834 (0.055)	0.943 (0.029)	0.683 (0.054)

	MARS	0.731 (0.09)	0.889 (0.059)	0.73 (0.091)
	RF	0.748 (0.085)	0.925 (0.038)	0.746 (0.086)
Festuca scabriculmis	CTA	0.908 (0.028)	0.966 (0.015)	0.908 (0.028)
	GBM	0.935 (0.02)	0.989 (0.006)	0.935 (0.02)
	GLM	0.934 (0.016)	0.987 (0.005)	0.924 (0.019)
	MARS	0.881 (0.064)	0.958 (0.036)	0.877 (0.056)
	RF	0.935 (0.022)	0.988 (0.006)	0.935 (0.022)
Fritillaria involucrata	CTA	0.82 (0.025)	0.94 (0.013)	0.82 (0.025)
	GBM	0.83 (0.018)	0.965 (0.006)	0.83 (0.018)
	GLM	0.74 (0.026)	0.935 (0.009)	0.741 (0.026)
	MARS	0.728 (0.074)	0.904 (0.041)	0.671 (0.075)
	RF	0.893 (0.018)	0.983 (0.004)	0.894 (0.018)
Fritillaria tubiformis subsp. *moggridgei*	CTA	0.795 (0.086)	0.905 (0.045)	0.796 (0.086)
	GBM	0.866 (0.052)	0.959 (0.02)	0.867 (0.052)
	GLM	0.85 (0.036)	0.952 (0.017)	0.71 (0.052)
	MARS	0.834 (0.072)	0.939 (0.039)	0.839 (0.07)
	RF	0.87 (0.056)	0.968 (0.017)	0.871 (0.056)
Fritillaria tubiformis subsp. *tubiformis*	CTA	0.786 (0.046)	0.906 (0.024)	0.787 (0.045)
	GBM	0.84 (0.038)	0.959 (0.014)	0.84 (0.037)
	GLM	0.828 (0.029)	0.959 (0.01)	0.784 (0.032)
	MARS	0.78 (0.075)	0.925 (0.04)	0.788 (0.067)
	RF	0.846 (0.035)	0.963 (0.011)	0.847 (0.035)
Galeopsis reuteri	CTA	0.579 (0.081)*	0.808 (0.048)	0.583 (0.08)*
	GBM	0.69 (0.066)	0.896 (0.032)	0.692 (0.065)
	GLM	0.603 (0.047)	0.838 (0.021)	0.415 (0.046)*
	MARS	0.616 (0.087)	0.824 (0.057)	0.636 (0.083)
	RF	0.741 (0.058)	0.922 (0.024)	0.741 (0.058)
Galium pseudohelveticum	CTA	0.878 (0.02)	0.956 (0.011)	0.879 (0.02)
	GBM	0.897 (0.014)	0.984 (0.004)	0.897 (0.014)
	GLM	0.895 (0.016)	0.982 (0.004)	0.895 (0.015)
	MARS	0.859 (0.06)	0.953 (0.031)	0.821 (0.06)
	RF	0.92 (0.012)	0.99 (0.003)	0.92 (0.012)
Galium saxosum	CTA	0.825 (0.041)	0.918 (0.023)	0.826 (0.041)
	GBM	0.867 (0.034)	0.971 (0.011)	0.867 (0.034)
	GLM	0.873 (0.024)	0.973 (0.01)	0.835 (0.028)
	MARS	0.855 (0.058)	0.953 (0.029)	0.86 (0.055)
	RF	0.884 (0.031)	0.98 (0.008)	0.883 (0.031)
Genista lobelii	CTA	0.951 (0.025)	0.977 (0.013)	0.951 (0.025)
	GBM	0.967 (0.017)	0.994 (0.005)	0.967 (0.017)
	GLM	0.976 (0.014)	0.994 (0.008)	0.969 (0.016)
	MARS	0.914 (0.056)	0.96 (0.028)	0.924 (0.047)
	RF	0.975 (0.012)	0.997 (0.003)	0.975 (0.012)
Gentiana burseri subsp. *actinocalyx*	CTA	0.785 (0.084)	0.895 (0.044)	0.783 (0.084)
	GBM	0.889 (0.068)	0.968 (0.033)	0.888 (0.071)
	GLM	0.878 (0.081)	0.941 (0.042)	0.808 (0.081)
	MARS	0.865 (0.089)	0.937 (0.044)	0.86 (0.087)
	RF	0.91 (0.066)	0.979 (0.027)	0.908 (0.068)

Gentiana burseri subsp. *villarsii*	CTA	0.845 (0.036)	0.932 (0.02)	0.845 (0.036)
	GBM	0.88 (0.026)	0.97 (0.01)	0.88 (0.026)
	GLM	0.871 (0.02)	0.966 (0.013)	0.854 (0.022)
	MARS	0.843 (0.06)	0.938 (0.043)	0.836 (0.057)
	RF	0.884 (0.025)	0.974 (0.008)	0.884 (0.025)
Gentiana rostani	CTA	0.873 (0.023)	0.951 (0.012)	0.873 (0.023)
	GBM	0.903 (0.02)	0.982 (0.006)	0.903 (0.02)
	GLM	0.91 (0.017)	0.982 (0.007)	0.905 (0.018)
	MARS	0.891 (0.044)	0.96 (0.026)	0.879 (0.04)
	RF	0.905 (0.02)	0.986 (0.005)	0.905 (0.02)
Gymnadenia nigra subsp. *corneliana*	CTA	0.875 (0.021)	0.947 (0.012)	0.875 (0.021)
	GBM	0.892 (0.017)	0.978 (0.006)	0.892 (0.017)
	GLM	0.88 (0.02)	0.975 (0.006)	0.88 (0.02)
	MARS	0.841 (0.064)	0.944 (0.034)	0.816 (0.062)
	RF	0.9 (0.017)	0.98 (0.005)	0.9 (0.017)
Hedysarum hedysaroides subsp. *boutignyanum*	CTA	0.817 (0.029)	0.931 (0.016)	0.817 (0.029)
	GBM	0.84 (0.023)	0.962 (0.009)	0.84 (0.023)
	GLM	0.825 (0.024)	0.961 (0.008)	0.82 (0.024)
	MARS	0.784 (0.066)	0.917 (0.043)	0.789 (0.06)
	RF	0.874 (0.021)	0.978 (0.005)	0.874 (0.021)
Helianthemum lunulatum	CTA	0.851 (0.063)	0.933 (0.036)	0.854 (0.062)
	GBM	0.926 (0.045)	0.981 (0.018)	0.927 (0.044)
	GLM	0.905 (0.073)	0.962 (0.041)	0.833 (0.085)
	MARS	0.88 (0.061)	0.944 (0.034)	0.888 (0.058)
	RF	0.935 (0.041)	0.987 (0.013)	0.934 (0.041)
Helictotrichon sempervirens	CTA	0.901 (0.013)	0.965 (0.007)	0.901 (0.013)
	GBM	0.91 (0.012)	0.985 (0.003)	0.91 (0.012)
	GLM	0.918 (0.012)	0.988 (0.004)	0.917 (0.014)
	MARS	0.845 (0.062)	0.945 (0.034)	0.803 (0.068)
	RF	0.924 (0.011)	0.991 (0.002)	0.924 (0.011)
Helictotrichon setaceum	CTA	0.861 (0.022)	0.945 (0.014)	0.862 (0.022)
	GBM	0.878 (0.022)	0.975 (0.006)	0.879 (0.022)
	GLM	0.888 (0.016)	0.977 (0.006)	0.887 (0.017)
	MARS	0.834 (0.067)	0.936 (0.034)	0.82 (0.054)
	RF	0.901 (0.02)	0.985 (0.005)	0.901 (0.02)
Heracleum pumilum	CTA	0.838 (0.048)	0.926 (0.03)	0.841 (0.047)
	GBM	0.886 (0.032)	0.968 (0.015)	0.886 (0.032)
	GLM	0.882 (0.045)	0.966 (0.024)	0.81 (0.045)
	MARS	0.845 (0.061)	0.945 (0.032)	0.856 (0.059)
	RF	0.877 (0.043)	0.972 (0.015)	0.878 (0.042)
Hesperis inodora	CTA	0.606 (0.17)	0.801 (0.089)	0.612 (0.17)
	GBM	0.759 (0.1)	0.898 (0.054)	0.75 (0.103)
	GLM	0.718 (0.124)	0.87 (0.066)	0.536 (0.099)*
	MARS	0.634 (0.134)	0.827 (0.08)	0.63 (0.129)
	RF	0.724 (0.111)	0.894 (0.063)	0.715 (0.116)
Hormathophylla halimifolia	CTA	0.733 (0.047)	0.894 (0.025)	0.734 (0.047)
	GBM	0.781 (0.038)	0.943 (0.013)	0.782 (0.038)

	GLM	0.698 (0.037)	0.905 (0.016)	0.65 (0.038)
	MARS	0.685 (0.071)	0.875 (0.047)	0.692 (0.068)
	RF	0.833 (0.03)	0.967 (0.01)	0.833 (0.03)
Hyacinthoides italica	CTA	0.815 (0.032)	0.925 (0.02)	0.815 (0.032)
	GBM	0.848 (0.021)	0.973 (0.007)	0.848 (0.02)
	GLM	0.819 (0.023)	0.955 (0.01)	0.819 (0.024)
	MARS	0.787 (0.065)	0.926 (0.032)	0.742 (0.059)
	RF	0.891 (0.022)	0.985 (0.006)	0.891 (0.023)
Iberis aurosica	CTA	0.639 (0.079)	0.845 (0.04)	0.643 (0.079)
	GBM	0.744 (0.063)	0.918 (0.032)	0.747 (0.061)
	GLM	0.724 (0.037)	0.891 (0.017)	0.523 (0.044)*
	MARS	0.69 (0.093)	0.87 (0.058)	0.707 (0.09)
	RF	0.778 (0.053)	0.936 (0.025)	0.779 (0.053)
Iberis nana	CTA	0.756 (0.076)	0.883 (0.042)	0.758 (0.074)
	GBM	0.838 (0.046)	0.963 (0.016)	0.838 (0.046)
	GLM	0.838 (0.035)	0.959 (0.014)	0.743 (0.042)
	MARS	0.807 (0.065)	0.93 (0.038)	0.812 (0.061)
	RF	0.842 (0.049)	0.966 (0.015)	0.843 (0.049)
Jovibarba allionii	CTA	0.849 (0.037)	0.94 (0.022)	0.849 (0.037)
	GBM	0.889 (0.023)	0.981 (0.007)	0.889 (0.023)
	GLM	0.887 (0.019)	0.976 (0.007)	0.875 (0.021)
	MARS	0.862 (0.054)	0.957 (0.026)	0.842 (0.051)
	RF	0.905 (0.018)	0.984 (0.006)	0.905 (0.018)
Leucanthemum burnatii	CTA	0.886 (0.049)	0.951 (0.027)	0.887 (0.048)
	GBM	0.934 (0.034)	0.986 (0.01)	0.934 (0.034)
	GLM	0.9 (0.048)	0.966 (0.029)	0.83 (0.072)
	MARS	0.87 (0.061)	0.948 (0.034)	0.874 (0.059)
	RF	0.934 (0.029)	0.988 (0.008)	0.934 (0.029)
Leucanthemum virgatum	CTA	0.833 (0.034)	0.943 (0.019)	0.833 (0.034)
	GBM	0.88 (0.027)	0.983 (0.006)	0.88 (0.027)
	GLM	0.848 (0.024)	0.967 (0.008)	0.819 (0.027)
	MARS	0.825 (0.062)	0.944 (0.031)	0.831 (0.055)
	RF	0.922 (0.021)	0.992 (0.004)	0.922 (0.021)
Lilium pomponium	CTA	0.855 (0.023)	0.947 (0.013)	0.855 (0.022)
	GBM	0.882 (0.018)	0.981 (0.005)	0.883 (0.018)
	GLM	0.849 (0.019)	0.972 (0.006)	0.842 (0.02)
	MARS	0.835 (0.062)	0.952 (0.03)	0.814 (0.065)
	RF	0.914 (0.022)	0.989 (0.004)	0.914 (0.022)
Limonium cordatum	CTA	0.93 (0.034)	0.969 (0.019)	0.929 (0.034)
	GBM	0.955 (0.023)	0.994 (0.005)	0.955 (0.023)
	GLM	0.887 (0.029)	0.975 (0.017)	0.846 (0.033)
	MARS	0.884 (0.053)	0.947 (0.029)	0.902 (0.048)
	RF	0.966 (0.019)	0.996 (0.004)	0.966 (0.019)
Limonium pseudominutum	CTA	0.924 (0.023)	0.971 (0.011)	0.924 (0.023)
	GBM	0.951 (0.017)	0.996 (0.002)	0.951 (0.017)
	GLM	0.943 (0.014)	0.993 (0.003)	0.937 (0.016)
	MARS	0.893 (0.057)	0.959 (0.033)	0.9 (0.047)

	RF	0.975 (0.011)	0.998 (0.002)	0.975 (0.011)
Micromeria marginata	CTA	0.778 (0.059)	0.914 (0.032)	0.777 (0.059)
	GBM	0.864 (0.033)	0.973 (0.01)	0.864 (0.034)
	GLM	0.813 (0.03)	0.953 (0.012)	0.798 (0.037)
	MARS	0.79 (0.07)	0.93 (0.036)	0.778 (0.072)
	RF	0.884 (0.039)	0.979 (0.012)	0.884 (0.039)
Minuartia glomerata subsp. *burnatii*	CTA	0.813 (0.064)	0.913 (0.035)	0.811 (0.064)
	GBM	0.893 (0.048)	0.978 (0.014)	0.892 (0.048)
	GLM	0.877 (0.047)	0.964 (0.031)	0.806 (0.082)
	MARS	0.853 (0.068)	0.956 (0.034)	0.854 (0.069)
	RF	0.89 (0.054)	0.978 (0.014)	0.89 (0.053)
Minuartia rupestris subsp. *clementei*	CTA	0.641 (0.074)	0.841 (0.042)	0.642 (0.074)
	GBM	0.759 (0.058)	0.931 (0.025)	0.758 (0.058)
	GLM	0.787 (0.038)	0.941 (0.017)	0.687 (0.041)
	MARS	0.745 (0.07)	0.905 (0.037)	0.75 (0.068)
	RF	0.777 (0.058)	0.941 (0.021)	0.777 (0.058)
Moehringia intermedia	CTA	0.722 (0.076)	0.886 (0.044)	0.721 (0.075)
	GBM	0.863 (0.051)	0.972 (0.017)	0.861 (0.051)
	GLM	0.858 (0.073)	0.952 (0.047)	0.753 (0.12)
	MARS	0.818 (0.073)	0.945 (0.037)	0.822 (0.07)
	RF	0.876 (0.055)	0.975 (0.019)	0.873 (0.056)
Moehringia sedoides	CTA	0.724 (0.079)	0.9 (0.037)	0.723 (0.08)
	GBM	0.835 (0.05)	0.963 (0.018)	0.833 (0.051)
	GLM	0.7 (0.038)	0.88 (0.017)	0.496 (0.039)*
	MARS	0.759 (0.086)	0.914 (0.052)	0.762 (0.081)
	RF	0.857 (0.053)	0.972 (0.015)	0.854 (0.054)
Narcissus pseudonarcissus subsp. *provincialis*	CTA	0.815 (0.063)	0.915 (0.035)	0.814 (0.063)
	GBM	0.884 (0.045)	0.974 (0.013)	0.883 (0.045)
	GLM	0.889 (0.04)	0.97 (0.021)	0.838 (0.053)
	MARS	0.846 (0.066)	0.943 (0.039)	0.849 (0.064)
	RF	0.896 (0.038)	0.977 (0.011)	0.894 (0.038)
Ophrys bertolonii subsp. *saratoi*	CTA	0.763 (0.041)	0.905 (0.025)	0.763 (0.041)
	GBM	0.802 (0.034)	0.959 (0.011)	0.802 (0.034)
	GLM	0.69 (0.061)	0.908 (0.042)	0.66 (0.06)
	MARS	0.735 (0.066)	0.908 (0.037)	0.706 (0.064)
	RF	0.854 (0.027)	0.971 (0.008)	0.853 (0.027)
Ophrys exaltata subsp. *splendida*	CTA	0.822 (0.047)	0.92 (0.026)	0.822 (0.047)
	GBM	0.886 (0.034)	0.973 (0.013)	0.885 (0.034)
	GLM	0.847 (0.027)	0.958 (0.011)	0.782 (0.033)
	MARS	0.859 (0.054)	0.95 (0.032)	0.854 (0.05)
	RF	0.905 (0.031)	0.98 (0.01)	0.905 (0.031)
Ophrys provincialis	CTA	0.861 (0.021)	0.95 (0.012)	0.861 (0.021)
	GBM	0.879 (0.018)	0.978 (0.006)	0.879 (0.018)
	GLM	0.824 (0.084)	0.935 (0.052)	0.823 (0.084)
	MARS	0.834 (0.056)	0.94 (0.031)	0.809 (0.058)
	RF	0.912 (0.016)	0.987 (0.004)	0.912 (0.016)
Oreochloa seslerioides	CTA	0.873 (0.035)	0.948 (0.021)	0.873 (0.035)

	GBM	0.914 (0.027)	0.985 (0.008)	0.914 (0.027)
	GLM	0.921 (0.017)	0.987 (0.005)	0.918 (0.017)
	MARS	0.892 (0.051)	0.968 (0.028)	0.878 (0.047)
	RF	0.921 (0.025)	0.987 (0.006)	0.921 (0.025)
Potentilla delphinensis	CTA	0.797 (0.044)	0.916 (0.025)	0.798 (0.044)
	GBM	0.853 (0.039)	0.966 (0.014)	0.853 (0.038)
	GLM	0.833 (0.029)	0.951 (0.01)	0.768 (0.037)
	MARS	0.801 (0.066)	0.93 (0.032)	0.803 (0.061)
	RF	0.869 (0.035)	0.972 (0.011)	0.868 (0.036)
Potentilla saxifraga	CTA	0.776 (0.063)	0.901 (0.036)	0.776 (0.063)
	GBM	0.846 (0.043)	0.967 (0.015)	0.844 (0.043)
	GLM	0.785 (0.05)	0.926 (0.028)	0.678 (0.066)
	MARS	0.766 (0.073)	0.916 (0.039)	0.761 (0.068)
	RF	0.884 (0.039)	0.976 (0.015)	0.882 (0.04)
Potentilla valderia	CTA	0.863 (0.037)	0.948 (0.021)	0.863 (0.037)
	GBM	0.9 (0.029)	0.983 (0.007)	0.9 (0.029)
	GLM	0.899 (0.019)	0.984 (0.005)	0.895 (0.021)
	MARS	0.863 (0.068)	0.957 (0.038)	0.858 (0.061)
	RF	0.916 (0.024)	0.989 (0.005)	0.916 (0.024)
Primula allionii	CTA	0.824 (0.061)	0.922 (0.031)	0.821 (0.061)
	GBM	0.91 (0.047)	0.98 (0.015)	0.906 (0.048)
	GLM	0.877 (0.056)	0.964 (0.034)	0.799 (0.079)
	MARS	0.84 (0.066)	0.934 (0.041)	0.846 (0.058)
	RF	0.922 (0.041)	0.983 (0.013)	0.919 (0.042)
Primula marginata	CTA	0.894 (0.011)	0.971 (0.005)	0.894 (0.011)
	GBM	0.881 (0.012)	0.983 (0.002)	0.881 (0.012)
	GLM	0.879 (0.016)	0.98 (0.004)	0.851 (0.016)
	MARS	0.848 (0.046)	0.952 (0.026)	0.683 (0.061)
	RF	0.94 (0.009)	0.995 (0.001)	0.94 (0.009)
Prunus brigantina	CTA	0.825 (0.025)	0.942 (0.014)	0.825 (0.025)
	GBM	0.836 (0.023)	0.969 (0.007)	0.836 (0.023)
	GLM	0.783 (0.023)	0.948 (0.008)	0.784 (0.023)
	MARS	0.767 (0.063)	0.92 (0.033)	0.714 (0.058)
	RF	0.882 (0.017)	0.984 (0.003)	0.883 (0.017)
Rhaponticum heleniifolium	CTA	0.744 (0.054)	0.887 (0.032)	0.745 (0.053)
	GBM	0.779 (0.046)	0.933 (0.019)	0.78 (0.046)
	GLM	0.776 (0.028)	0.935 (0.01)	0.674 (0.034)
	MARS	0.767 (0.071)	0.905 (0.039)	0.778 (0.067)
	RF	0.804 (0.046)	0.946 (0.017)	0.804 (0.045)
Santolina decumbens	CTA	0.863 (0.024)	0.956 (0.013)	0.863 (0.024)
	GBM	0.89 (0.024)	0.981 (0.006)	0.89 (0.024)
	GLM	0.859 (0.02)	0.971 (0.006)	0.858 (0.02)
	MARS	0.81 (0.064)	0.937 (0.035)	0.755 (0.062)
	RF	0.919 (0.016)	0.988 (0.005)	0.919 (0.016)
Saxifraga cochlearis	CTA	0.823 (0.039)	0.929 (0.025)	0.824 (0.039)
	GBM	0.878 (0.031)	0.981 (0.008)	0.878 (0.031)
	GLM	0.86 (0.022)	0.956 (0.011)	0.819 (0.031)

	MARS	0.844 (0.061)	0.94 (0.038)	0.84 (0.062)
	RF	0.926 (0.026)	0.992 (0.005)	0.925 (0.026)
Saxifraga exarata subsp. *delphinensis*	CTA	0.794 (0.055)	0.907 (0.033)	0.794 (0.055)
	GBM	0.861 (0.042)	0.967 (0.016)	0.861 (0.042)
	GLM	0.86 (0.027)	0.97 (0.008)	0.797 (0.035)
	MARS	0.816 (0.067)	0.942 (0.033)	0.815 (0.062)
	RF	0.872 (0.044)	0.972 (0.014)	0.873 (0.045)
Saxifraga florulenta	CTA	0.913 (0.023)	0.969 (0.014)	0.913 (0.023)
	GBM	0.952 (0.019)	0.995 (0.003)	0.952 (0.019)
	GLM	0.954 (0.016)	0.991 (0.009)	0.948 (0.02)
	MARS	0.913 (0.051)	0.968 (0.027)	0.917 (0.045)
	RF	0.955 (0.018)	0.996 (0.002)	0.955 (0.018)
Saxifraga pedemontana subsp. *pedemontana*	CTA	0.833 (0.053)	0.93 (0.028)	0.832 (0.053)
	GBM	0.891 (0.045)	0.981 (0.012)	0.891 (0.045)
	GLM	0.926 (0.024)	0.989 (0.007)	0.896 (0.028)
	MARS	0.874 (0.064)	0.96 (0.034)	0.877 (0.06)
	RF	0.911 (0.039)	0.987 (0.01)	0.911 (0.039)
Saxifraga valdensis	CTA	0.629 (0.107)	0.825 (0.062)	0.633 (0.105)
	GBM	0.758 (0.085)	0.919 (0.043)	0.758 (0.088)
	GLM	0.821 (0.055)	0.944 (0.03)	0.656 (0.059)
	MARS	0.735 (0.102)	0.891 (0.059)	0.732 (0.101)
	RF	0.799 (0.086)	0.943 (0.037)	0.793 (0.088)
Scrophularia provincialis	CTA	0.751 (0.028)	0.912 (0.015)	0.751 (0.028)
	GBM	0.766 (0.024)	0.946 (0.009)	0.766 (0.024)
	GLM	0.735 (0.024)	0.928 (0.01)	0.735 (0.024)
	MARS	0.707 (0.059)	0.891 (0.035)	0.622 (0.058)
	RF	0.835 (0.024)	0.969 (0.007)	0.835 (0.024)
Sempervivum calcareum	CTA	0.859 (0.019)	0.951 (0.011)	0.859 (0.019)
	GBM	0.868 (0.015)	0.974 (0.004)	0.868 (0.015)
	GLM	0.857 (0.018)	0.973 (0.006)	0.857 (0.016)
	MARS	0.804 (0.064)	0.937 (0.038)	0.723 (0.062)
	RF	0.897 (0.014)	0.985 (0.004)	0.897 (0.014)
Senecio leucanthemifolius subsp. *crassifolius*	CTA	0.912 (0.035)	0.962 (0.018)	0.912 (0.035)
	GBM	0.949 (0.025)	0.994 (0.004)	0.949 (0.025)
	GLM	0.942 (0.019)	0.987 (0.009)	0.921 (0.021)
	MARS	0.898 (0.058)	0.952 (0.032)	0.91 (0.049)
	RF	0.966 (0.017)	0.997 (0.002)	0.966 (0.017)
Seseli annuum carvifolium	CTA	0.677 (0.046)	0.857 (0.027)	0.678 (0.046)
	GBM	0.739 (0.047)	0.922 (0.021)	0.739 (0.047)
	GLM	0.681 (0.029)	0.901 (0.012)	0.643 (0.031)
	MARS	0.683 (0.069)	0.875 (0.04)	0.66 (0.062)
	RF	0.765 (0.04)	0.933 (0.016)	0.765 (0.04)
Sideritis provincialis	CTA	0.856 (0.02)	0.949 (0.01)	0.856 (0.02)
	GBM	0.88 (0.019)	0.976 (0.006)	0.88 (0.019)
	GLM	0.813 (0.038)	0.957 (0.025)	0.815 (0.038)
	MARS	0.842 (0.049)	0.956 (0.027)	0.746 (0.06)
	RF	0.907 (0.016)	0.986 (0.004)	0.907 (0.016)

Silene campanula	CTA	0.837 (0.048)	0.933 (0.027)	0.837 (0.048)
	GBM	0.909 (0.032)	0.981 (0.01)	0.909 (0.032)
	GLM	0.921 (0.027)	0.982 (0.01)	0.9 (0.028)
	MARS	0.868 (0.068)	0.956 (0.037)	0.864 (0.06)
	RF	0.923 (0.031)	0.984 (0.008)	0.922 (0.031)
Silene cordifolia	CTA	0.861 (0.037)	0.946 (0.025)	0.861 (0.038)
	GBM	0.914 (0.026)	0.988 (0.006)	0.914 (0.026)
	GLM	0.926 (0.017)	0.988 (0.005)	0.919 (0.017)
	MARS	0.882 (0.054)	0.967 (0.031)	0.868 (0.045)
	RF	0.924 (0.023)	0.99 (0.004)	0.924 (0.023)
Teucrium lucidum	CTA	0.846 (0.022)	0.944 (0.012)	0.846 (0.022)
	GBM	0.859 (0.018)	0.971 (0.006)	0.859 (0.018)
	GLM	0.828 (0.021)	0.962 (0.007)	0.832 (0.02)
	MARS	0.811 (0.06)	0.946 (0.026)	0.745 (0.055)
	RF	0.897 (0.016)	0.986 (0.003)	0.897 (0.016)
Veronica allionii	CTA	0.927 (0.009)	0.973 (0.005)	0.927 (0.009)
	GBM	0.929 (0.009)	0.987 (0.003)	0.929 (0.009)
	GLM	0.92 (0.015)	0.984 (0.007)	0.915 (0.015)
	MARS	0.898 (0.048)	0.97 (0.022)	0.806 (0.06)
	RF	0.947 (0.007)	0.993 (0.002)	0.946 (0.007)
Viola valderia	CTA	0.781 (0.058)	0.912 (0.028)	0.781 (0.058)
	GBM	0.871 (0.039)	0.976 (0.011)	0.871 (0.039)
	GLM	0.852 (0.031)	0.967 (0.011)	0.813 (0.033)
	MARS	0.819 (0.064)	0.945 (0.034)	0.81 (0.065)
	RF	0.884 (0.033)	0.977 (0.009)	0.884 (0.033)

Appendix 3 – Persistence, extent of potential range of taxa and types of refugia

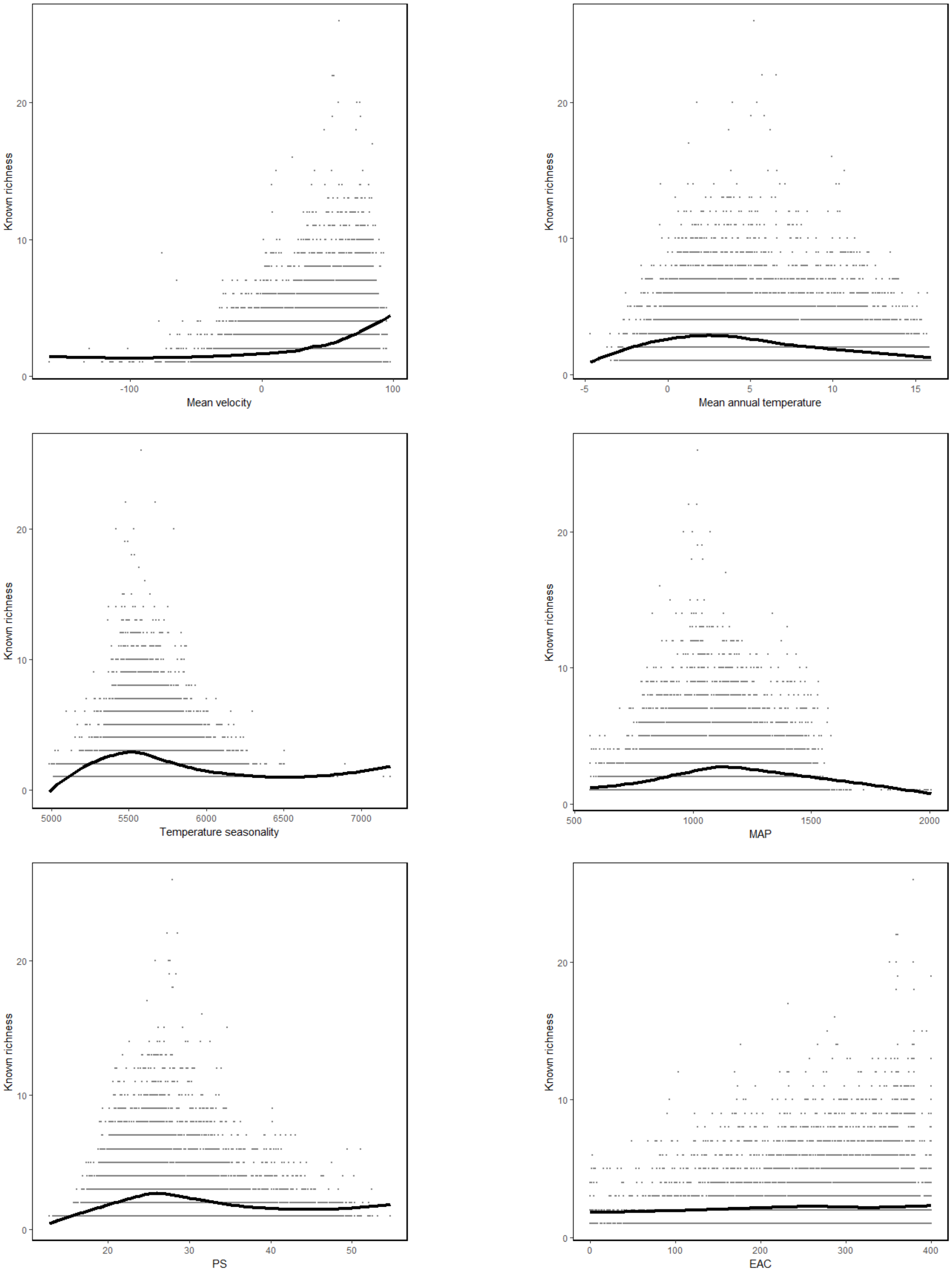
Taxon	persistence (mean value)	persistence (standard deviation)	LIG (N. of suitable pixels)	LGM (N. of suitable pixels)	MID (N. of suitable pixels)	from LIG to LGM range dynamic	from LGM to MID range dynamic	Type of refugium
Acis nicaeensis (Ardoino) Lledo et al.	0.48	0.50	0	158	0	Increase	Decrease	Interglacial
Allium narcissiflorum Vill.	0.11	0.36	0	1156	239	Increase	Decrease	Interglacial
Allium scaberrimum J.Serres	0.34	0.81	250	1314	136	Increase	Decrease	Interglacial
Androsace chaixii Gren.	0.00	0.05	0	454	0	Increase	Decrease	Interglacial
Anthemis cretica L. subsp. *gerardiana* (Jord.) Greuter	0.68	0.50	1219	2805	308	Increase	Decrease	Interglacial
Aquilegia reuteri Boiss.	0.65	0.48	0	6114	0	Increase	Decrease	Interglacial
Arabis allionii DC.	0.90	0.87	1309	0	669	Decrease	Increase	Glacial
Arenaria cinerea DC.	0.00	0.00	0	7	0	Increase	Decrease	Interglacial
Arenaria provincialis Chater & G.Halliday	0.94	0.23	2121	0	0	Decrease	Stable	/
Asperula cynanchica subsp. *rupicola* (Jord.) Berher	0.00	0.05	0	121	0	Increase	Decrease	Interglacial
Asperula hexaphylla All.	0.00	0.00	0	0	0	Stable	Stable	/
Asplenium jahandiezii (Litard.) Rouy	0.00	0.00	0	0	0	Stable	Stable	/
Ballota frutescens (L.) J.Woods	0.95	0.76	1193	0	733	Decrease	Increase	Glacial
Berardia subacaulis Vill.	0.50	0.50	0	6632	0	Increase	Decrease	Interglacial
Brassica repanda (Willd.) DC. subsp. *repanda*	1.57	1.15	1875	6521	1403	Increase	Decrease	Interglacial
Campanula alpestris All.	0.44	0.50	0	4931	0	Increase	Decrease	Interglacial
Campanula elatines L.	0.46	0.68	0	1267	797	Increase	Decrease	Interglacial
Campanula fritschii Witasek	0.00	0.00	0	0	0	Stable	Stable	/
Campanula rotundifolia L. subsp. *macrorhiza* (J.Gay ex A.DC.) Bonnier & Layens	0.55	0.50	0	9153	0	Increase	Decrease	Interglacial
Campanula sabatia De Not.	0.00	0.00	0	0	0	Stable	Stable	/
Campanula stenocodon Boiss. & Reut.	0.04	0.18	0	681	0	Increase	Decrease	Interglacial
Carex ferruginea subsp. *tenax* (H.Christ) K.Richt.	0.30	0.46	0	6740	0	Increase	Decrease	Interglacial
Centaurea jordaniana Godr. & Gren.	0.00	0.00	0	0	0	Stable	Stable	/
Centaurea paniculata L. subsp. *polycephala* (Jord.) Nyman	0.96	0.20	0	9427	0	Increase	Decrease	Interglacial

Centaurea uniflora Turra subsp. *uniflora*	0.12	0.33	0	2584	0	Increase	Decrease	Interglacial
Coincya richeri (Vill.) Greuter & Burdet	0.00	0.00	0	46	0	Increase	Decrease	Interglacial
Crocus ligusticus Mariotti	0.00	0.00	0	0	0	Stable	Stable	/
Crocus versicolor Ker Gawl.	0.37	0.48	0	10240	0	Increase	Decrease	Interglacial
Cytisus ardoinii E.Fourn.	0.00	0.00	0	24	0	Increase	Decrease	Interglacial
Cytisus sauzeanus Burnat & Briq.	0.00	0.00	0	0	0	Stable	Stable	/
Dianthus furcatus Balb. subsp. *furcatus*	0.20	0.40	0	858	0	Increase	Decrease	Interglacial
Dianthus pavonius Tausch	0.08	0.27	0	992	0	Increase	Decrease	Interglacial
Dianthus subacaulis Vill.	0.00	0.00	0	0	0	Stable	Stable	/
Epipactis leptochila (Godfery) Godfery subsp. *provincialis* (Aubenas & Robatsch) J.M.Tison	0.12	0.33	175	0	542	Decrease	Increase	Glacial
Eryngium spinalba Vill.	0.00	0.00	0	0	0	Stable	Stable	/
Erysimum burnatii Vidal	0.26	0.44	22	92	328	Increase	Increase	/
Euphorbia canutii Parl.	0.39	0.51	2510	0	527	Decrease	Increase	Glacial
Euphorbia graminifolia Vill.	0.00	0.00	0	0	0	Stable	Stable	/
Euphorbia variabilis subsp. *valliniana* (Belli) Jauzein	0.03	0.17	0	33	0	Increase	Decrease	Interglacial
Festuca scabriculmis (Hack.) K.Richt.	0.06	0.24	0	445	0	Increase	Decrease	Interglacial
Fritillaria involucrata All.	0.63	0.48	0	10987	0	Increase	Decrease	Interglacial
Fritillaria tubaeformis Gren. & Godr. subsp. *moggridgei* (Baker) Rix	0.00	0.00	0	0	0	Stable	Stable	/
Fritillaria tubaeformis Gren. & Godr. subsp. *tubaeformis*	0.37	0.48	0	5427	0	Increase	Decrease	Interglacial
Galeopsis reuteri Rchb.f.	0.00	0.00	0	0	0	Stable	Stable	/
Galium pseudohelveticum Ehrend.	0.43	0.50	0	1539	0	Increase	Decrease	Interglacial
Galium saxosum (Chaix) Breistr.	0.00	0.00	0	0	0	Stable	Stable	/
Genista lobelii DC.	0.01	0.11	0	0	31	Stable	Increase	/
Gentiana burseri Lapeyr. subsp. *actinocalyx* Polidori	1.27	0.76	138	53	877	Decrease	Increase	Glacial
Gentiana burseri Lapeyr. subsp. *villarsii* (Griseb.) Rouy	0.00	0.00	0	21	0	Increase	Decrease	Interglacial
Gentiana rostanii Reut. ex Verl.	0.09	0.29	0	1356	0	Increase	Decrease	Interglacial
Gymnadenia nigra (L.) Rchb.f. subsp. *corneliana* (Beauverd) J.M.Tison	0.76	0.43	0	7737	0	Increase	Decrease	Interglacial

Hedysarum hedysaroides (L.) Schinz & Thell. subsp. *boutignyanum* (A.Camus) Jauzein	0.02	0.14	0	102	0	Increase	Decrease	Interglacial
Helianthemum lunulatum (All.) DC.	0.00	0.00	0	0	0	Stable	Stable	/
Helictotrichon sempervirens (Vill.) Pilg.	0.39	0.49	0	6925	0	Increase	Decrease	Interglacial
Helictotrichon setaceum (Vill.) Henrard	0.00	0.00	0	16	0	Increase	Decrease	Interglacial
Heracleum pumilum Vill.	0.00	0.00	0	0	0	Stable	Stable	/
Hesperis inodora L.	1.06	0.86	535	263	938	Decrease	Increase	Glacial
Hormathophylla halimifolia (Boiss.) P.Küpfer	0.00	0.00	0	0	0	Stable	Stable	/
Hyacinthoides italica (L.) Rothm.	0.00	0.00	0	40	7	Increase	Decrease	Interglacial
Iberis aurosica Chaix	0.66	0.51	91	2364	453	Increase	Decrease	Interglacial
Iberis nana All.	0.04	0.20	0	0	0	Stable	Stable	/
Jovibarba allionii (Jord. & Fourr.) D.A.Webb	0.02	0.13	0	184	0	Increase	Decrease	Interglacial
Leucanthemum burnatii Briq. & Cavill.	0.01	0.11	0	549	0	Increase	Decrease	Interglacial
Leucanthemum virgatum (Desr.) Clos	0.00	0.00	0	0	0	Stable	Stable	/
Lilium pomponium L.	0.00	0.00	0	0	0	Stable	Stable	/
Limonium cordatum (L.) Mill.	0.85	0.70	1406	0	23	Decrease	Increase	Glacial
Limonium pseudominutum Erben	1.51	0.76	1862	13	842	Decrease	Increase	Glacial
Micromeria marginata (Sm.) Chater	0.00	0.00	0	0	0	Stable	Stable	/
Minuartia glomerata subsp. *burnatii* (Rouy & Foucaud) Favarger & F.Conti	0.00	0.00	0	10	0	Increase	Decrease	Interglacial
Minuartia rupestris subsp. *clementei* (Huter) Greuter & Burdet	0.03	0.16	0	231	0	Increase	Decrease	Interglacial
Moehringia intermedia Loisel. ex Panizzi	0.03	0.16	0	333	0	Increase	Decrease	Interglacial
Moehringia sedoides (Pers.) Cumino ex Loisel.	0.00	0.00	0	0	0	Stable	Stable	/
Narcissus pseudonarcissus L. subsp. *provincialis* (Pugsley) J.M.Tison	0.16	0.37	0	1280	0	Increase	Decrease	Interglacial
Ophrys bertolonii Moretti subsp. *saratoi* (E.G.Camus) R.Soca	0.00	0.07	0	0	113	Stable	Increase	/
Ophrys exaltata subsp. *splendida* (Gölz & Reinhard) R.Soca	0.08	0.27	146	0	0	Decrease	Stable	/
Ophrys provincialis (Baumann & Künkele) Paulus	0.02	0.15	0	502	0	Increase	Decrease	Interglacial
Oreochloa seslerioides (All.) K.Richt.	0.61	0.49	6	2054	0	Increase	Decrease	Interglacial
Potentilla delphinensis Gren. & Godr.	0.00	0.00	0	0	0	Stable	Stable	/

Potentilla saxifraga Ardoino ex De Not.	0.00	0.00	0	0	0	Stable	Stable	/
Potentilla valderia L.	0.00	0.07	0	17	0	Increase	Decrease	Interglacial
Primula allionii Loisel.	0.00	0.00	0	0	0	Stable	Stable	/
Primula marginata Curtis	0.69	0.46	0	9423	0	Increase	Decrease	Interglacial
Prunus brigantina Vill.	0.00	0.00	0	0	0	Stable	Stable	/
Rhaponticum heleniifolium Godr. & Gren.	0.00	0.00	0	0	0	Stable	Stable	/
Santolina decumbens Mill.	0.00	0.00	0	0	0	Stable	Stable	/
Saxifraga cochlearis Rchb.	0.00	0.00	0	0	0	Stable	Stable	/
Saxifraga exarata Vill. subsp. *delphinensis* (Ravaud) Kerguélen	0.03	0.17	0	53	0	Increase	Decrease	Interglacial
Saxifraga florulenta Moretti	0.63	0.48	0	530	0	Increase	Decrease	Interglacial
Saxifraga pedemontana All. subsp. *pedemontana*	0.42	0.49	0	200	0	Increase	Decrease	Interglacial
Saxifraga valdensis DC.	0.13	0.38	57	98	66	Increase	Decrease	Interglacial
Scrophularia provincialis Rouy	0.16	0.37	0	7405	0	Increase	Decrease	Interglacial
Sempervivum calcareum Jord.	0.00	0.06	0	586	0	Increase	Decrease	Interglacial
Senecio leucanthemifolius Poir. subsp. *crassifolius* (Willd.) Ball	1.20	0.74	871	0	583	Decrease	Increase	Glacial
Seseli annuum L. subsp. *carvifolium* (Vill.) P.Fourn.	1.01	0.78	2331	13027	2037	Increase	Decrease	Interglacial
Sideritis provincialis Jord. & Fourr.	0.51	0.50	190	15315	0	Increase	Decrease	Interglacial
Silene campanula Pers.	0.15	0.37	48	19	238	Decrease	Increase	Glacial
Silene cordifolia All.	0.63	0.48	0	818	0	Increase	Decrease	Interglacial
Teucrium lucidum L.	0.01	0.11	0	50	0	Increase	Decrease	Interglacial
Veronica allionii Vill.	0.25	0.44	0	5080	0	Increase	Decrease	Interglacial
Viola valderia All.	0.38	0.49	0	1340	0	Increase	Decrease	Interglacial

Appendix 4 – Bivariate relationships between the endemism richness and six predictor variables, ordered according to their importance (as indicated by hierarchical partitioning). Lines show fitted locally weighted smoothing (LOESS) curves.



4 - INFRA-SPECIFIC VARIATION OF ECOLOGICAL NICHE

4.1 - Introduction

Currently, SDMs represent the best tool for forecasting species response to climate change and the exponential increase of papers in which they are utilized is an indirect demonstration of their importance in biodiversity conservation studies. More in general, they are fundamental to objectively quantify the ecological niche of species and to compare them for taxonomic and systematic purposes.

However, SDMs rely on mathematical calculations that require some biological assumptions and thus, like all mathematical models, they describe a simplified reality. For example, one of these assumptions states that all populations of a given species perform similarly across its distribution range. Conversely, different populations may be locally adapted to different environmental conditions, because of their past biogeographic history or different selective pressures. For this reason, the niche of locally adapted populations may differ to the niche of species as a whole, leading to a complex scenario of infra-specific variation in the ecological niche. The existence, within a species, of populations characterized by different ecological niches led to two considerations: i) there may be an ecological barrier between populations and ii) different populations may respond in different ways to stress (e.g., climate change). The first consideration may have some taxonomical implications, in particular in the identification of taxa boundaries, because the lacking of ecological interchangeability between two populations of the same species may strongly reduce the gene flow between them, and, consequently, trigger a speciation process. The second consideration takes repercussions on the elaboration of conservation strategies, because if different populations of a given species may differently respond to an environmental stress (e.g., climate change), a model that doesn’t take into account such variability may underestimate or overestimate the effects of the environmental stress on the species.

In most cases species occurrences are used altogether in SDMs, preventing to taking into account the possible presence of infra-specific variability in the ecological niche. However, how to partition the occurrences dataset in order to take into account the eventual infra-specific variability in ecological niche is still debated. To our current knowledge, only the partition into subspecies (thus following a taxonomical criterion) has been adequately investigated, showing that SDMs are able to detect fine variations between subspecies or closely related specie. Despite this utilize of SDMs could has important taxonomical implications, this aspect is still less investigated. In order to fill this gap, I explored the ecological differentiation between closely related plant taxa endemic to SW Alps that were recently subdued to taxonomical reviews without explicitly considering ecological evidences.

The results of this study were reported in a manuscript entitled “Divergence is not enough: the use of ecological niche models for the validation of taxa boundaries”, authored by Davide Dagnino, Luigi Minuto and Gabriele Casazza. The integral version of the manuscript, that is proposed in the following section of this chapter, was published on Plant Biology 19(6): 1003-1011 (doi: 10.1111/plb.12600).

The geographic disjunction among populations of the same species might be another appropriate criterion for the partition of the occurrences dataset in order to detect infra-specific variability in the ecological niche. In fact, the disjunction may imply that populations are subdued to different selective pressures potentially affecting their response to climate change. For this reason, I explored the influence of geographic disjunction on both model performance and forecasted effects of climate change on species distribution in six plant taxa endemic to SW Alps. The results of this part of the PhD project were reported in a thesis entitled “Infra-taxon niche structure: implications on the forecasted effects of climate changes” authored by Lucia Varaldo (course of Science of Natural Systems, University of Genoa), of which a brief summary is proposed in the last section of this chapter.

4.2 - Divergence is not enough: the use of Ecological Niche Models for the validation of taxa boundaries.

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KEYWORDS

Ecological niche models - Equivalency test - Integrative taxonomy - Niche differentiation index - Niche overlap - Similarity test - Taxa boundaries.

ABSTRACT

- Delimiting taxa boundaries is a crucial point for any evolutionary research and conservation regulation. In order to avoid mistaken description of species, the approach of integrative taxonomy recommends to consider multidisciplinary lines of evidence, including ecology. Unfortunately, ecological data are often difficult to quantify in an objective way. Here we test and discuss the possible utility of Ecological Niche Models for validating taxa boundaries using three couple of closely related plant taxa endemic to South-western Alps as a case study. We also reflect on the utility of Ecological Niche Models for species delimitation and on the pitfall of different approaches.
- Niche overlap, niche equivalency and niche similarity were assessed both in a multidimensional environmental space and in a geographical space to look for differences in the niche of three couple of closely related plant taxa.
- We detected a high degree of niche differentiation between taxa although this seems not due to difference in habitat selection. Furthermore, the different statistical tests showed contrasting outcomes between environmental and geographical spaces.
- In light of our results, the niche divergence seems not to support taxa boundaries at species level, but it may have had important consequences for local adaptation and in generating phenotypic diversity at the intraspecific level. Furthermore, environmental space should be preferred having less pitfall than geographical spaces. Eventually, even if the different analyses widely disagree on their conclusion about taxa boundaries, our study suggests that Ecological Niche Models may help taxonomists in reach a decision.

INTRODUCTION

Species are conventionally recognized by seemingly discontinuous, non-overlapping patterns of variation in morphological characters of individuals from circumscribed populations (Mayr 1942; Davis & Heywood 1963; Wiens & Servedio 2000; Krell 2004; Libalah *et al.* 2014; Stewart *et al.* 2015). Delimiting species is essential for elucidating evolutionary process and because many conservation laws and regulations use taxonomic categories as operational units. Nevertheless, how to perform this goal is still debated (Sites & Marshall 2004; Wiens 2007; Petit & Excoffier 2009; Hausdorf 2011). The debate ranges from the concept of species (De Queiroz 2007; Lowry 2012; Seifert 2014) to the operational methods necessary for taxa delimitation (Wiens & Servedio 2000; Wiens & Penkrot 2002; Morando *et al.* 2003; Lefébure *et al.* 2006; De Queiroz 2007; O'Meara 2009; Fayer 2010; Reeves & Richards 2010; Puillandre *et al.* 2012). In the same way, because subspecies are also considered useful both in evolutionary and in conservation biology (Phillimore & Owens 2006; Ellison *et al.* 2014), a similar debate, or maybe more heated, exist for their taxonomic definition (Mayr 1942; Wilson & Brown 1953; Mayr 1982; Hamilton & Reichard 1992; Manier 2004; Haig *et al.* 2006; Meiri & Mace 2007; Alström *et al.* 2008; Ennen *et al.* 2014). In addition, subspecies are often mistakenly described in arbitrary way based on morphological extremes along environmental gradients (Mulcahy 2008), a method that does not reflect phylogenetic relationships and which obscures the meaningful variability on which natural selection operates (Ellison *et al.* 2014).

Recently, it was proposed that different lines of evidence should be integrated into taxonomy to assess the delimitation of species, the so-called "integrative taxonomy" (Dayrat 2005; Padial *et al.* 2010; Schlick-Steiner *et al.* 2010; Padial & De La Riva 2010; Yeates *et al.* 2011; Carstens *et al.* 2013; but see also Valdecasas *et al.* 2008 for a contrary opinion). According to this approach, species are to be considered as hypothesis that should be tested with different approaches (Dayrat 2005). However, how much congruence among lines of evidences is necessary to validate species boundaries has still to be determined (De Queiroz 2007; Padial *et al.* 2009; Leaché *et al.* 2009; Padial *et al.* 2010; Padial & De La Riva 2010). The highly stringent approach of "integration by congruence" (Meiri & Mace 2007; Alström *et al.* 2008) identifies species limits with the intersection of evidence from two or more independent lines of evidence and tends to promote taxonomic stability but may underestimate the number of species (Padial *et al.* 2010). Conversely, "integration by cumulation" identifies species limits with divergence in one or more not necessarily overlapping lines of evidence, allowing that observed differences even in a single character may be considered taxonomically relevant (Sites & Marshall 2004; Padial *et al.* 2010; Hong-Wa & Besnard 2014), but this approach may overestimate the number of species (Padial *et al.* 2010).

In recent years, genetic data have been widely used to test taxa boundaries (Fujita *et al.* 2012; Umapathy *et al.* 2014; Shao & Xiang 2015; Schneider *et al.* 2015). Conversely, ecological data are still little considered or arbitrarily used in taxonomy. Although the role of ecology in speciation mechanism is still debate (Sobel *et al.* 2010), a strong ecological differentiation among two supposed taxa suggests that they are likely to remain distinct, because gene flow is often higher among population living in similar environments (Sexton *et al.* 2014; Tocchio *et al.* 2015). For this reason, ecology may be particularly useful to taxa delimitation when limited genetic divergence exist (Wiens & Graham 2005; Rissler & Apodaca 2007; Wiens 2007; Ruiz-Sanchez & Sosa 2010). However, it is clearly necessary that ecological differentiation is supported by rigorous data and statistical analyses, not simply by a kind of "biological intuition" (Wiens 2007).

In this context, ecological niche models (ENMs) might be a useful tool providing a quantifiable measure of niche (Guisan & Thuiller 2005). They are integrated in a broad variety of biological disciplines and they are now playing an increasing role in some systematic applications (Raxworthy *et al.* 2007), even though they are generally underutilized in species delimitation (Carstens et al. 2013). In some studies, ENMs have been used to test the ecological interchangeability among putative taxa (Rissler & Apodaca 2007 - genus *Aneides*; Stockman & Bond 2007 - genus *Promyrmekiaphila*; Martínez-Gordillo *et al.* 2010 - family Muridae; Orr *et al.* 2014 - genus *Anthophora*). In addition, ENMs have been used in taxonomically problematic groups, testing which model among those based on all possible split and lumped taxonomic groupings provides the better fit to the known distribution of investigated taxa (Raxworthy *et al.* 2007; Reeves & Richards 2010). However, previous approaches do not explicitly consider species-specific accessible areas and may lead to incorrect conclusion about relationship between niches. For this reason, Tocchio *et al.* (2015) tested niche similarity taking into account the availability of conditions across accessible areas.

Parapatric putative taxa offers great possibility for the utilize of ENMs for delimitation of taxa boundaries, because there are no clear geographic barriers able to interrupt gene flow. Moreover, infraspecific taxa are often less rigorously described than it does for species rank taxa, and molecular data could be little informative, due to the incomplete separation between taxa. Here we use ENMs to test taxa boundaries in three couples of closely related plant taxa (two couples of subspecies and one couple of species that were previously considered at subspecies rank), endemic to South-western Alps and showing parapatric distribution along an environmental gradient. In particular, we are aimed to use different approaches to test whether ecological niches are significantly different in these three couples of taxa. These analyses allowed us to reflect more generally on the utility of ENM for species delimitation.

Material and Methods

Studied taxa. - We selected three couples of plant taxa endemic to South-western Alps showing contiguous or partially overlapped distributional ranges (Figure 1). The taxonomic affinities between the members of each couple is supported by morphological evidences and only in one couple by molecular evidences too. These taxa are characterized by recent taxonomical revisions, performed without explicitly considering ecological evidences, and now they are evaluated at different taxonomic rank (two taxa at species rank and four taxa at subspecies rank). The study taxa are: *Rhaponticum bicknellii* (Briq.) Banfi, Galasso & Soldano and *Rhaponticum heleniifolium* Godr. & Gren.; *Gentiana burseri* Lapeyr. subsp. *actinocalyx* Polidori and *Gentiana burseri* Lapeyr. subsp. *villarsii* (Griseb.) Rouy.; *Fritillaria tubiformis* Gren. & Godr. subsp. *moggridgei* (Baker) Rix and *Fritillaria tubiformis* Gren. & Godr. subsp. *tubiformis*.

Past taxonomic treatments considered *R. bicknellii* and *R. heleniifolium* (hereafter *Rhaponticum*-group) as two subspecies of *R. heleniifolium,* but now they are considered at species rank according to morphological and chorological evidences (Banfi *et al.*, 2011). Recently, *G. burseri* subsp. *villarsii* and *G. burseri* subsp. *actinocalyx* (hereafter *Gentiana*-group) were distinguished on the basis of morphological features; in particular, *G. burseri* subsp. *villarsii* was split into a couple of taxa, with the description of the new subspecies *actinocalyx* (Polidori 2004, 2008). Similarly, *F. tubiformis* subsp. *moggridgei* and *F. tubiformis* subsp. *tubiformis* (hereafter *Fritillaria*-group) were subdued to different taxonomical treatments (Bartolucci & Peruzzi 2012; Mucciarelli *et al.* 2014); along the history the two entities were considered subspecies (Rix 1978; Noble & Diadema 2011), varieties (Fiori 1929; Pignatti 1982), forma (Bartolucci & Peruzzi 2012) or synonym (Aeschimann *et al.* 2004); recently, despite genetic analysis suggests that *F. tubiformis* subsp. *moggridgei* may be considered as a separate species (Mucciarelli & Fay 2013), a morphometric study of the *F. tubiformis* complex has confirmed the taxonomic status of subspecies for the two entities here considered (Mucciarelli *et al.* 2016).

Study area. - South-western Alps are recognized as a center of biodiversity, characterized by an elevate endemism rate (Médail & Quézel 1997; Médail & Verlaque 1997; Casazza *et al.* 2005). South-western Alps show a climatic gradient, ranging from Oro-submediterranean conditions to Supra-submediterranean and Mesomediterranean conditions (Rivas-Martinez *et al.* 2004).

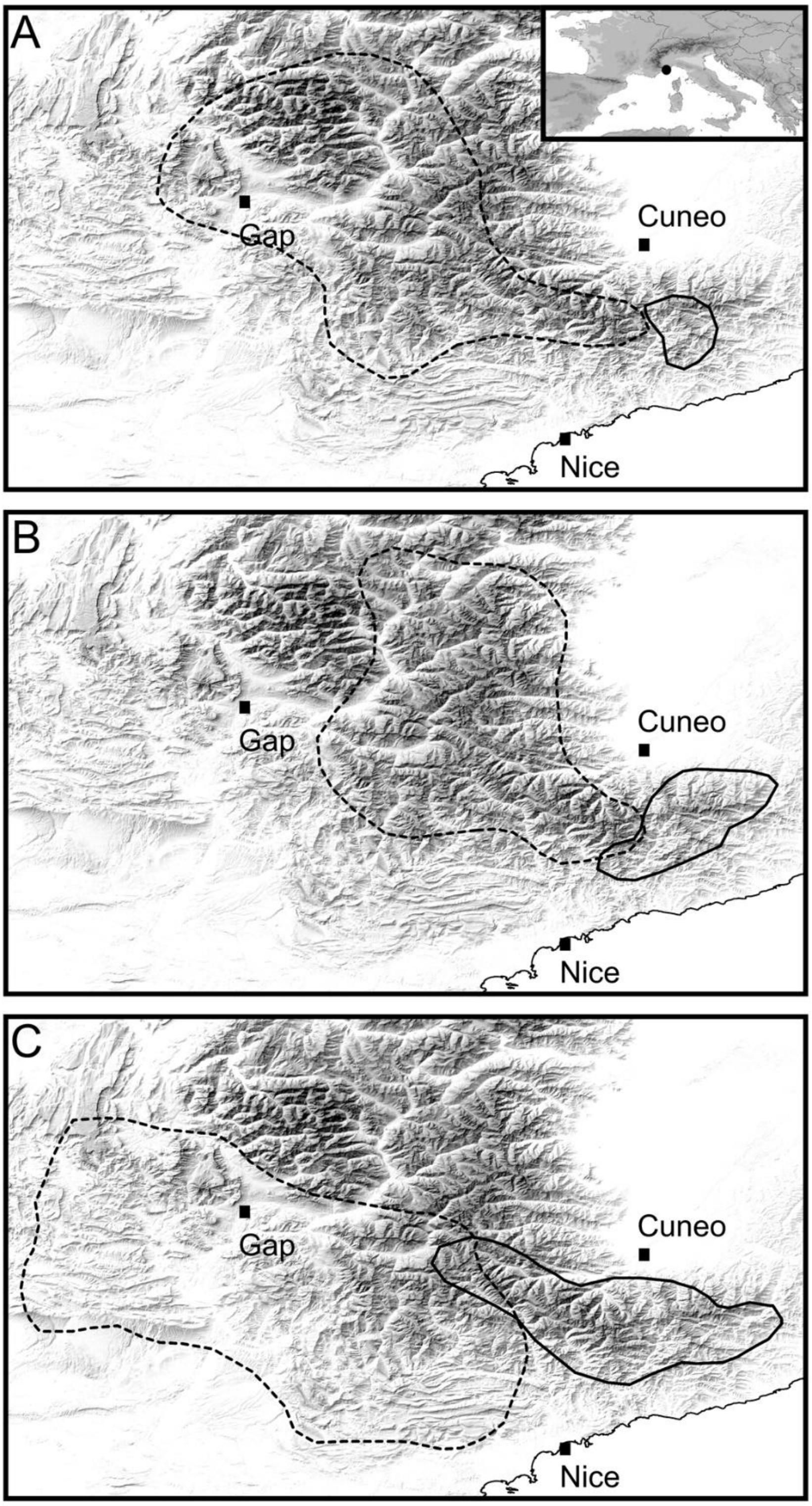

Figure 1. *Distributional ranges of studied taxa.* ***A****, Rhaponticum-group: Rhaponticum bicknellii (continuous line); Rhaponticum heleniifolium (dashed line).* ***B****, Gentiana-group: Gentiana burseri subsp. actinocalyx (continuous line); Gentiana burseri subsp. villarsii (dashed line).* ***C****, Fritillaria-group: Fritillaria tubiformis subsp. moggridgei (continuous line); Fritillaria tubiformis subsp. tubiformis (dashed line).*

Occurrence data. - Occurrence data were obtained from Herbaria (GE, TO and FI), literature (Polidori 2008; Mucciarelli & Fay 2013; Mucciarelli *et al.* 2014) and local databases: SILENE (Système d'Information et de Localisation des Espèces Natives et Envahissantes; Conservatoire Botanique National de Porquerolles and Conservatoire Botanique National Alpin, France) and LI.BI.OSS. (Osservatorio Ligure della Biodiversità; ARPAL, Regione Liguria, Italy) accessed in December 2014. Overall, a final dataset of 1296 occurrences records was used in the analyses (in detail: 29 occurrence points for *R. bicknellii*, 267 for *R. heleniifolium*, 472 for *G. burseri* subsp. *villarsii*, 51 for *G. burseri* subsp. *actinocalyx*, 341 for *F. tubiformis* subsp. *tubiformis*, and 136 for *F. tubiformis* subsp. *moggridgei*). Although there isn’t a minimum number that is widely accepted and applicable to any model algorithm, our dataset for each species is sufficiently large, according to the more recent indications provided in literature (Hernandez *et al.* 2006; Wisz *et al.* 2008; Jarnevich *et al.* 2015).

Climatic variables. – The process of variable selection plays a key role in model building (Porfirio *et al.* 2014 and references therein), but there is no universally accepted criteria for this purpose (Harris *et al.* 2013). Although climatic parameters alone depict only a simplified picture of the niche of a species, climatic variables related to temperature and precipitation play a significant role, directly and indirectly, in plant physiology (Körner 2004). Nineteen bioclimatic variables were downloaded from WorldClim dataset website (http://www.worldclim.org) at 30-s (c. 1 km^2) spatial resolution (Hijmans *et al.* 2005). The selected spatial resolution is widely accepted and used in environmentally heterogeneous areas (e.g. Franklin *et al.* 2013 – California Floristic Province; Casazza *et al.* 2014 – Western Mediterranean coast; Guerrina *et al.* 2015 – South-western Alps). To reduce the multicollinearity between predictors, in order to minimize model overfitting, we performed a pairwise Pearson correlation between bioclimatic predictors, and we retained predictors that were not highly correlated ($r \leq |0.80|$). Six variables were selected for the analysis: BIO2 (mean diurnal range), BIO7 (temperature annual range), BIO8 (mean temperature of the wettest quarter), BIO9 (mean temperature of the driest quarter), BIO13 (precipitation of the wettest month), BIO15 (precipitation seasonality).

Environmental vs geographical space. – Because niche differentiation in environmental space (E-space) may or may not translate into occupation of different geographical space (G-space), it is preferable to quantify and compare niches in either E-space using multivariate statistics (Thuiller *et al.* 2005; Hof *et al.* 2010; Broennimann *et al.* 2012) or in G-space using ENMs (Guisan & Thuiller 2005; Warren *et al.* 2008).

Ecological Niche Models settings and background delimitation – Several studies have shown that there is no a best overall algorithm for building ecological niche models (Elith *et al.* 2006; Tsoar *et al.* 2007; Jarnevich *et al.* 2015) but the simultaneous use of several algorithms is certainly recommended (Araújo & New 2007). For this reason, we selected six algorithms for model building: Generalized Linear Models (GLM - McCullagh & Nelder 1989); Generalized Boosted Models (GBM - Ridgeway 1999); Classification Tree Analysis (CTA - Breiman *et al.* 1984); Flexible Discriminant Analysis (FDA - Hastie *et al.* 1994); Multivariate Adaptive Regression Splines (MARS - Friedman 1991); Random Forest (RF - Breiman 2001). These algorithms are included in the BIOMOD2 package (Thuiller *et al.* 2009) implemented in R (R Development Core Team 2008). For pseudo-absence selection we followed the indication of Barbet-Massin *et al*. (2012); in particular, given the high environmental heterogeneity of our study area, we used the spatial exclusion method to generate pseudo-absence, setting minimum and maximum distances at 5 and 50 km, respectively.

Our dataset was split, keeping 30% of occurrence points for model evaluation, performed by using three measures included in BIOMOD2 package: area under the relative operating characteristic curve (AUC - Hanley & McNeil 1982); Cohen’s K (KAPPA - Monserud & Leemans 1992); true skill statistic (TSS - Allouche *et al.* 2006). Only the models exceeding the thresholds proposed by Araújo *et al.* (2005) to identify a “good” model (AUC>0.8; K>0.6; TSS>0.6) were retained for the final ensemble projection.

To calculate niche differentiation in G-space (see below), continuous probability values given by ENMs output were converted into a binary distribution of presence (i.e. cells with suitable habitat) and absence (i.e. cells with unsuitable habitat). Because the choice of threshold is critical by increasing or decreasing prediction bias, we selected three different thresholds implemented in the PresenceAbsence package (Freeman & Moisen): sens=spec, threshold where sensitivity equals specificity; MaxSens+Spec, threshold maximizing the sum of sensitivity and specificity; MinROCdist, threshold minimizing the distance between ROC plot and the upper left corner of the unit square. These thresholds are out-performing or performing equally as well as other commonly used thresholds (Liu *et al*. 2005; Cao *et al.* 2013).

Because some tests (see below) require the definition of a background area that might influence the analysis (Warren et al. 2010), we created five background areas for each taxon following two different approaches: the first used a 5 and 10 km buffer zone around the occurrence points of each couple of taxa; the second was attempted using the suitable habitat distribution in the binary ENMs outputs, generating one background for each threshold previously selected.

Statistical analysis

We followed different approaches to evaluate relationship between niches. A niche overlap metric and a niche differentiation index were used to evaluated how much the niches are overlapped. We used niche equivalency test to determine whether ecological niches of taxa are significantly interchangeable. Finally, we used niche similarity test to investigate whether ecological niches of the taxa are more similar than expected by chance taking into account their geographical ranges. Niche overlap, niche equivalency test and niche similarity test were assessed both in E- and G-space, while niche differentiation index was computable in G-space only.

The niche overlap was calculated using Schoener's D which ranges from 0 (no overlap) to 1 (full overlap; Schoener 1970), and it is considered one of the best niche overlap metrics (Rödder & Engler 2011). Niche overlap in E-space was calculated on the basis of density of occurrence of environmental factors along the environmental axes of a multivariate analysis (Broennimann *et al.* 2012), while in G-space this metric is calculated with a cell by cell comparison of the normalized probability values of habitat suitability provided by ENMs using the cells belonging to at least one background (Warren *et al.* 2008). Schoener's D values were then used to test for niche equivalency and niche similarity (see below).

Niche differentiation index (NDI; Peterson & Holt 2003) evaluate how much an ENM from one species predicts the range of another species relative to the capability to predict its own distribution. It is calculated as the ratio between alloprediction accuracy and autoprediction accuracy. Autoprediction accuracy indicates how well a taxon model predicts the distribution of the same taxon, while alloprediction accuracy indicates how well a taxon model predicts the distribution of another taxon. Autoprediction and alloprediction accuracy averaged values were calculated as the mean of the two taxa of each group. Because the ratio of alloprediction accuracy to autoprediction accuracy is considered an inverse measure of niche differentiation (Peterson & Holt 2003), we subtracted the result of the previous operation from 1 to ensure that the highest values correspond to high niche differentiation. The index was given a lower bound of zero because negative indices (greater alloprediction than allopredicition ability) are not informative in the current context; with this arrangement NDI ranges from 0 (no differentiation) to 1 (totally different).

The niche equivalency test determines whether niches of two entities are interchangeable testing whether the niche overlap is constant when the occurrences of both entities are randomly reallocated to the two species. All occurrences were then pooled and randomly split into two datasets 100 times, maintaining the number of occurrences as in the original datasets to compare the D values with a random distribution (Warren *et al.* 2008; Broennimann *et al.* 2012). If the observed value of D is statistically significantly different from the 100 simulated D values, the null hypothesis of niche equivalency can be rejected and the two niches cannot be considered interchangeable; to evaluate this hypothesis the observed D values were compared to the percentiles of the null distribution in a one-tailed test.

Niche similarity test evaluate whether the overlap between observed niches in two ranges is different from the overlap between the observed niche in one range and niches selected at random from the other range (Warren *et al.* 2008; Broennimann *et al.* 2012). Briefly, the observed niche overlap between two species was compared to the overlap measured between the niche of one species and the randomized niche of the other one. We repeated this randomization procedure 100 times. Actual D values were compared to the percentiles of the null distribution in a two-tailed test; significant results indicate that the ecological niches of taxa are either more or less similar than expected by chance, suggesting that the observed niche differentiation is a function of habitat selection and/or suitability rather than simply an artifact due to habitat availability in the background areas (Warren *et al.* 2008). In E-space, simulated D values were obtained randomly shifting the entire observed density of occurrence in one range and calculating the overlap of the simulated niche with the observed one in the other range (Broennimann *et al.* 2012); in G-space they are obtained comparing the ENMs output of the first taxon with a ENMs output for the second taxon based on simulated occurrences randomly chosen in its geographical range maintaining the number of occurrences (Warren *et al.* 2008). All previous analyses were performed in R (R Development Core Team 2008) using ‘ecospat’ package (Broennimann *et al.* 2016) for E-space and ‘raster’ package (Hijmans *et al.* 2016) for G-space.

Results

Under current climate conditions AUC, TSS and Kappa indicated a good model performance for all modelling algorithms (Supporting Information, Table S1). Therefore, all model outputs were used for ensemble projections.

The three couples of taxa varied in their degree of niche overlap between partners based on both D (Table 1) and NDI (Table 2). In E-space the lowest value of niche overlap was detected in *Rhaponticum*-group (D mean = 0.04; ranging from 0.03 to 0.05); an intermediate value was detected in *Gentiana*-group (D mean = 0.22; ranging from 0.18 to 0.27); finally, the highest value was detected in *Fritillaria*-group (D mean = 0.37; ranging from 0.34 to 0.42). In G-space D values were higher and showed an opposite trend than those obtained in E-space; therefore, the lowest value of niche overlap was detected in *Fritillaria*-group (D mean = 0.50; ranging from 0.48 to 0.52) and in *Gentiana*-group (D mean = 0.50; ranging from 0.44 to 0.56), while the highest value was detected in *Rhaponticum*-group (D mean = 0.59; ranging from 0.50 to 0.66).

The same trend detected by D in E-space was detected in G-space by NDI (Table 2). *Rhaponticum*-group showed the most differentiated niches with NDI = 1 (completely differentiated niches) as a result of the null alloprediction ability of both taxa. An intermediate value was detected in *Gentiana*-group (NDI = 0.6) in which subsp. *actinocalyx* is a very poor predictor for subsp. *villarsii*, that conversely is a good predictor for him. Higher value was recorded in *Fritillaria*-group (NDI = 0.7) in which both taxa are mildly able to predict the distribution of their partner. The autoprediction ability is always high (more than 95%), indicating that the ENMs of each taxon correctly predict its own distribution (i.e. good quality model).

	Niche overlap D	**BACKGROUND**				
		5 km buffer	**10 km buffer**	**sens=spec**	**Max Sens+Spec**	**Min ROCdist**
E-space						
Rhaponticum-group						
hel vs bic	0.04	ns; ns	ns; ns	ns; M	M ; M	ns; M
Gentiana-group						
vil vs act	0.22	M ; M	M ; M	M ; M	M ; L	M ; ns
Fritillaria-group						
tub vs mog	0.37	ns; M	ns; M	ns; M	M ; M	ns; M
G-space						
Rhaponticum-group						
hel vs bic	0.59	ns; L	ns; L	L ; L	L ; L	L ; L
Gentiana-group						
vil vs act l	0.50	ns; L	ns; L	L ; L	L ; L	L ; L
Fritillaria-group						
tub vs mog	0.50	ns; M	ns; M	L ; L	L; ns	L ; L

Table 1*. Results of niche overlap and niche similarity test in environmental (E-) and geographical (G-) spaces between the three couple of closely related taxa. Backgrounds are defined by applying 5 and 10 km buffer zones around the occurrence points of each species and by each taxon's ecological niche model set to three baseline thresholds: (i) threshold where sensitivity equals specificity (sens=spec); (ii) threshold maximizing the sum of sensitivity and specificity (MaxSens+Spec) and (iii) threshold minimizing the distance between ROC plot and the upper left corner of the unit square (MinROCdist). hel = Rhaponticum heleniifolium; bic = Rhaponticum bicknellii; vil = Gentiana burseri subsp. villarsii; act = Gentiana burseri subsp. actinocalyx; tub = Fritillaria tubiformis subsp. tubiformis; mog = Fritillaria tubiformis subsp. moggridgei. ns =* $P \geq 0.05$*; less / more =* $P < 0.05$*.*

The niche equivalency test showed that niche overlap in all three couples of taxa is significantly smaller than the null distribution (Supporting Information, Table S2). This means that partners of each couple of taxa occupy not equivalent niches (i.e. not interchangeable), both in E- and G-space for all backgrounds.

The niche similarity test in E-space suggested that the ecological niches are generally more similar than expected given their environmental backgrounds (Table 1). Conversely, results of similarity test in G-space showed that niches are generally less similar to each other than expected by chance (Table 1). Nevertheless, results in E-space showed that *R. bicknellii* and *F. tubiformis* subsp. *moggridgei* select habitat that are significantly more similar to that of their respective taxa, but not the contrary.

	Prediction accuracy		**Autoprediction average**	**Allopredicion average**	**Niche differentiation index (NDI)**
Predictor taxa	*Predicted taxa*				
***Rhaponticum*-group**					
	bic	hel			
bic	100	0	97.2	0	1
hel	0	94.3			
***Gentiana*-group**					
	act	vil			
act	99.3	2.8	99.1	41.0	0.6
vil	79.1	98.8			
***Fritillaria*-group**					
	mog	tub			
mog	96.8	20.9	95.1	32.9	0.7
tub	44.9	93.4			

Table 2*. Summary of predictive tests and niche differentiation index between taxa; bic = Rhaponticum bicknellii; hel = Rhaponticum heleniifolium; act = Gentiana burseri subsp. actinocalyx; vil = Gentiana burseri subsp. villarsii; mog = Fritillaria tubiformis subsp. moggridgei; tub = Fritillaria tubiformis subsp. tubiformis.*

DISCUSSION

Our results in G-space show that D values support a moderate degree of divergence between taxa while NDI values indicate a high degree of differentiation, as also suggested by D values in E-space. The moderately high degree of niche differentiation seems to support taxa differentiation, in line with the morphological (and genetic, in *Fritillaria*-group) difference detected between taxa. This result suggests that in our study species genetic isolation by environment or ecology, that has been found to be more common than isolation by distance (Sexton *et al.* 2014), may be occurred. Furthermore, the niche differentiation together with substantial range asymmetry between taxa is also consistent with a ‘budding’ speciation, in which a larger ranged progenitor gives rise to a smaller ranged derivative species (Anacker & Strauss 2014), probably as a result of ecological differentiation of taxa (Rundle & Nosil 2005).

The difference in G-space between D and NDI indices may result from difference in how the indices are calculated. In fact, D is affected by the asymmetry in potential range size predicted by ENMs, even if less affected than other metric indices (Rödder & Engler 2011). This occurs because D is based on normalized suitability scores for species in grid cells (so that the sum of all suitability scores is 1). In this way, similar suitability scores might be divided by different relative weight, that in turn is affected by the predicted potential range size, resulting in different values (if there are many highly suitable cells its weight will be low). On the contrary, NDI does not suffer this problem because does not compare suitability scores but it measures the ability of the binarized ENM of one species to correctly predict the range of the other species relative to its own distribution (Peterson & Holt 2003). Similarly, D in E-space directly measures differences in occurrence densities in each environmental combinations taking into account their frequency in the study area (Broennimann *et al.* 2012).

Congruently with the moderately high degree of niche divergence, our results of niche equivalency test both in E- and G-space clearly indicate that the niches of investigated taxa are not interchangeable, suggesting a certain degree of niche divergence. This result is in line with the other lines of evidence (Polidori 2004, 2008; Banfi *et al.* 2011; Bartolucci & Peruzzi 2012; Mucciarelli *et al.* 2014), particularly in *Fritillaria* group in which both morphological and genetic evidences support taxa split (Mucciarelli & Fay 2013). Nevertheless, niche equivalency test evaluates niche conservatism in the strictest sense (Warren *et al.* 2008) and it is considered very conservative (Aguirre-Gutiérrez *et al.* 2015). In fact, if a group of individuals occupied a wider climatic niches than another group of individuals, but they do not differ in optimal position of the climatic niches, the niche equivalency test would indicate that these two groups have distinct niches. However, the second group might occupy a subset of climatic niche of first one, as a result of other factors like competition (Glennon *et al.* 2014). This is likely to occur in our study cases where one taxon in each pair occupies a narrower range than the other one (Figure 1), suggesting difference in niche variance. Furthermore, the equivalency test will accurately reflect the probabilities under the null hypothesis only if sampling is unbiased with respect to the species environmental tolerances (Warren *et al.* 2008). However, biases can be introduced by many factors, including differences in the habitat available to populations in geographic regions where they do not overlap (Warren *et al.* 2010). For this reason, the niche of populations of the same taxon occurring at the extremes of an environmental gradient or in new geographical areas (as in the case of invasive species) may result not identical (Warren *et al.* 2008; Lowry 2012; Strubbe *et al.* 2015). This likely occurs in our study species growing along a gradient showing Mediterranean nuance in the South and Alpine climate in the North. For these reasons, the rejection of niche equivalency should be interpreted with caution (Warren *et al.* 2008; Peterson 2011)and seems not to be sufficient for delineate taxa boundaries in our study case.

As in the niche overlapping measures, similarity test is characterized by contrasting outcomes between E- and G-space. In the first case the niches are usually more similar to each other than expected by chance, while in the second case we detected an opposite trend.

Results in E-space suggests that the observed divergence could not be the result of an actual difference in habitat selection between taxa. Nevertheless, the moderate niche overlap values may suggest that taxa differ in their optimal niche position. Congruently with this result in some background analyses the niche of one taxon is more similar to the other one, while the vice-versa is not significant (see *Rhaponticum*- and *Fritillaria*-groups; Table 1). This suggest that despite the two taxa share the climatic niche, one taxon might occupy a marginal portion of the niche of its partner, the so-called “niche included” pattern (Peterson & Holt 2003; Hutchinson 1957; Miller 1967; Schoener 1974; Giller 2012). Contrary to previous results, this outcome seems not corroborate the taxonomic separation despite of the morphological (and genetic) differences detected between taxa. In fact, ecologically marginal populations can show some degree of morphological differentiation (Schuldt *et al.* 2012; Bessega *et al.* 2015), especially when distributed along an environmental gradient such as in our cases (Byars *et al.* 2007; DeWoody *et al.* 2015; Volynchik 2012), a potentially misleading scenario for the delimitation of taxa boundaries.

The discrepancy between similarity test in E-space and G-space was expected because they use contrasting approaches to reduce the dimensions of an environmental dataset (Broennimann *et al.* 2012). Simulated niche overlap values in E-space are obtained randomly shifting the entire observed density of occurrences in one range. On the contrary, simulated models in G-space are obtained randomly selecting occurrences in the background area that may lead to significant variation in potential range size, with the consequence of a biased overlap estimation (Rödder & Engler 2011). For these reason, results of similarity test in G-space should be interpreted with caution.

In conclusion, we detected a high degree of niche difference between taxa even if this seems not to be the result of difference in habitat selection. For this reason, the niche divergence detected seems not to support taxa boundaries at species level. Nevertheless, this divergence may have had important consequences for local adaptation and in generating phenotypic diversity at the intraspecific level (Peterson & Vargas-Barajas 1993; McCormack & Smith 2008), corroborating a subspecies rank separation at most.

Furthermore, our study suggests that the different analyses widely disagree on their conclusion about taxa boundaries, probably as a result of the variety of niche patterns that may occur between taxa. Moreover, several limits in analysis methods and in rigor in the approach still persist when ENMs are used for taxonomic purposes (Schlick-Steiner *et al.* 2010). In fact, despite a large increase in inferential power and statistical robustness of niche analysis was recently achieved (Warren *et al.* 2008; Broennimann *et al.* 2012) detailed conceptual frameworks and analytical guides still lack, leading to analytical missteps (Tocchio *et al.* 2015). Nevertheless, tests performing directly in E-space may reduce bias associated with geographical space (Broennimann *et al.* 2012) and so should be more extensively used in species delimitation. Similarly, similarity test should be preferred to equivalency test, because the latest is too sensitive for testing niche conservatism appropriately (Peterson 2011). Furthermore, evidence of strong ecological differentiation may be useful to delimit separate species (Raxworthy *et al.* 2007; Rissler & Apodaca 2007; Hawlitschek *et al.* 2011), but in its absence, taxa may still be separated by other mechanisms such as phenology, behavior, or genetic incompatibility (Coyne & Orr 2004) or niche divergence may occur along an ecological dimension not included in the analysis (Graham *et al.* 2004; Evans *et al.* 2009; Nakazato *et al.* 2010). Despite these problems, because integrative taxonomy deals with the different modes of speciation taking into account the different lines of evidence (Dayrat 2005; Padial *et al.* 2010; Schlick-Steiner *et al.* 2010; Padial & De La Riva 2010; Yeates *et al.* 2011; Carstens *et al.* 2013), a tool aimed to explore the role of ecological differentiation in speciation mechanisms may help taxonomists in reach a decision - which may be always falsified – about species boundaries.

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SUPPLEMENTARY INFORMATION

Table S1 – Evaluation of individual modelling techniques. Statistics given are the mean values for area under the curve (AUC), the true skill statistic (TSS) and Kappa statistic (KAPPA). Values given in brackets are the associated standard deviations. Accuracy classification for AUC: 1>excellent>0.9>good>0.8>fair>0.7>poor>0.6>fail; accuracy classification for TSS/KAPPA: 1>excellent>0.8>good>0.6>fair>0.4>poor>0.2>fail (Araújo et al., 2005). CTA, Classification Tree Analysis; FDA, Flexible Discriminant Analysis; GLM, Generalized Linear Models; GBM, Generalized Boosting Models; RF, Random Forest; MARS Multiple Additive Regression Spline.

		CTA	**FDA**	**GLM**	**GBM**	**RF**	**MARS**
bic	**TSS**	0.77(0.04)	0.75(0.03)	0.78(0.03)	0.8(0.03)	0.82(0.03)	0.77(0.03)
	AUC	0.89(0.02)	0.93(0.01)	0.94(0.01)	0.95(0.01)	0.96(0.01)	0.94(0.01)
	KAPPA	0.7(0.04)	0.71(0.04)	0.72(0.03)	0.74(0.03)	0.78(0.03)	0.72(0.04)
hel	**TSS**	0.83(0.05)	0.82(0.04)	0.87(0.02)	0.87(0.04)	0.87(0.04)	0.84(0.04)
	AUC	0.92(0.03)	0.96(0.01)	0.97(0.01)	0.97(0.01)	0.97(0.01)	0.96(0.01)
	KAPPA	0.69(0.06)	0.72(0.05)	0.71(0.04)	0.77(0.04)	0.81(0.05)	0.73(0.04)
act	**TSS**	0.85(0.02)	0.84(0.03)	0.87(0.02)	0.87(0.02)	0.89(0.02)	0.87(0.02)
	AUC	0.93(0.01)	0.96(0.01)	0.96(0.01)	0.97(0.01)	0.98(0.01)	0.97(0.01)
	KAPPA	0.83(0.02)	0.82(0.03)	0.85(0.02)	0.85(0.02)	0.87(0.02)	0.84(0.03)
vil	**TSS**	0.86(0.09)	0.91(0.06)	0.93(0.07)	0.92(0.07)	0.95(0.06)	0.91(0.06)
	AUC	0.93(0.04)	0.96(0.04)	0.98(0.04)	0.98(0.04)	0.99(0.02)	0.97(0.03)
	KAPPA	0.73(0.11)	0.87(0.07)	0.79(0.08)	0.83(0.06)	0.87(0.07)	0.87(0.07)
mog	**TSS**	0.78(0.04)	0.77(0.04)	0.77(0.03)	0.81(0.03)	0.81(0.03)	0.79(0.03)
	AUC	0.9(0.02)	0.92(0.02)	0.93(0.01)	0.95(0.01)	0.96(0.01)	0.93(0.01)
	KAPPA	0.68(0.05)	0.68(0.04)	0.7(0.04)	0.73(0.03)	0.77(0.04)	0.71(0.04)
tub	**TSS**	0.9(0.12)	0.93(0.05)	0.9(0.1)	0.95(0.09)	0.96(0.05)	0.94(0.05)
	AUC	0.95(0.06)	0.98(0.02)	0.95(0.05)	0.98(0.05)	0.99(0.02)	0.97(0.04)
	KAPPA	0.69(0.16)	0.64(0.11)	0.71(0.15)	0.81(0.1)	0.84(0.09)	0.75(0.1)

bic = Rhaponticum bicknellii; hel = Rhaponticum heleniifolium; act = Gentiana burseri subsp. actinocalyx; vil = Gentiana burseri subsp. villarsii; mog = Fritillaria tubiformis subsp. moggridgei; tub = Fritillaria tubiformis subsp. tubiformis.

Table S2 – Results of equivalency test in environmental (E-) and geographical (G-) spaces between the three couple of closely related taxa.

		BACKGROUND				
	Niche overlap D	**5 km buffer**	**10 km buffer**	**MTP**	**ETSS**	**MTSS**
E-SPACE						
***Rhaponticum*-group**	0.04	0.02*	0.02*	0.02*	0.02*	0.02*
***Gentiana*-group**	0.22	0.02*	0.02*	0.02*	0.02*	0.02*
***Fritillaria*-group**	0.37	0.02*	0.02*	0.02*	0.02*	0.02*
G-SPACE						
***Rhaponticum*-group**	0.59	0.01*	0.01*	0.01*	0.01*	0.01*
***Gentiana*-group**	0.50	0.01*	0.01*	0.01*	0.01*	0.01*
***Fritillaria*-group**	0.50	0.01*	0.01*	0.01*	0.01*	0.01*

hel = *Rhaponticum heleniifolium*; bic = *Rhaponticum bicknellii*; vil = *Gentiana burseri* subsp. *villarsii*; act = *Gentiana burseri* subsp. *actinocalyx*; tub = *Fritillaria tubiformis* subsp. *tubiformis;* mog = *Fritillaria tubiformis* subsp. *moggridgei*.
* significant ($P < 0.05$).

4.3 - Infra-taxon niche structure: implications on the forecasted effects of climate changes

(Summary of the thesis of Lucia Varaldo, Science of Natural Systems, University of Genoa).

INTRODUCTION

The infra-specific variability in the ecological niche may affect the projected potential distribution of a species (Osborne et al., 2002) and, consequently, the forecasted effects of climate change on species distribution (Gonzalez et al., 2002). For this reason, taking into account the infra-specific ecological variability may be an improvement of studies that use species distribution models for assessing the effects of climate change on biodiversity. However, the best operative criteria (taxonomical, ecological, geographical, etc) to split the occurrences dataset of a species are still debated.

It was demonstrated that arbitrary partitions of the occurrences dataset (for example the artificial subdivision of the range of distribution in four quadrants) lead to biased models like those that not attempt to incorporate infra-specific variability (Gonzalez et al., 2011). Major improvements may be obtained applying a biologically meaningful partition of the dataset. Some studies showed that taking into account subspecies may improve the performance of models and probably the accuracy of species distribution projection under future climate change (Pearman et al., 2010; Gonzalet et al., 2011; Oney et al., 2013). However, other possible partitions are still less explored, such a (not arbitrarily) geographic criterion based on the geographic disjunction occurring in some species.

Disjunctions are geographical subdivisions of the distributional range of species into two or more partial ranges. Disjunctions can be originated by the rising of a geographical barrier or by the occasional overcoming of a preexisting barrier (Cox & Moore, 2009). Whatever was its origin, geographic disjunction has a biologically and evolutionary meaning reducing or preventing the gene flow between populations (Lomolino et al., 2010). In addition, in species occurring along an environmental gradient, the ecological niches of disjointed populations may be very different, even when the geographic distance between them is scarce (Austin et al., 1990; Araùjo & Guisan, 2006).

Here we are aimed to test whether the ecological differentiation among population induced by geographical disjunction affects the forecasted distribution of species under climate change using species distribution models.

MATERIAL AND METHODS

Studied taxa, areas and climatic data

We selected six plant taxa endemic or sub-endemic to SW Alps showing a disjointed distribution: the populations of each species are partitioned into two subtaxa at least 30 km away from each other. The six taxa are: *Erysimum collisparsum* Jord., *Crocus ligusticus* Mariotti, *Cytisus ardoinii* E. Fourn., *Allium narcissiflorum* Vill., *Eryngium spinalba* Vill., *Carex ferruginea* subsp. *tendae* W. Dietr. (Table I).

Occurrence data were obtained from regional databases (SILENE - Système d'Information et de Localisation des Espèces Natives et Envahissantes, Conservatoire Botanique National de Porquerolles and Conservatoire Botanique National Alpin, France; LI.BI.OSS - Osservatorio Ligure della Biodiversità, ARPAL, Regione Liguria, Italy; accessed in July 2016), literature (Garbari et al., 2000; Mariotti, 1988), herbarium specimens (GE, TO, FI) and personal communications from local very expert botanists (Barberis G. – *Carex ferruginea* subsp. *tendae*; Mariotti M.G. – *Crocus ligusticus*; Peccenini S. – *Erysimum collisparsum*). A final dataset of 5.697 occurrences were obtained (Table II).

The six studied taxa are characterized by very different geographical ranges (Table I). For this reason, we used a specific study area for each studied taxa. Bioclimatic data were obtained from WorldClim database (Hijmans et al., 2005 – http://www.worldclim.org – accessed in July 2016) at the resolution of 30 arcses (≈1 km^2). For each study areas we performed a pairewise Pearson correlation among bioclimatic variables, retaining only the bioclimatic variables that were not highly correlated (Pearson correlation < |0.7|; Table III).

Taxon	Distribution	Altitudinal range	Life Form
Erysimum collisparsum	Italy, France, Spain	300-500 m	Hemicryptophyte
Crocus ligusticus	Italy, France	600-1300 m	Geophyte
Cytisus ardoinii	France	900-1200 m	Chamaephyte
Allium narcissiflorum	Italy, France	1500-2600 m	Geophyte
Eryngium spinalba	Italy, France	1000-2100 m	Hemicryptophyte
Carex ferruginea subsp. *tendae*	Italy, France	1600-2700 m	Hemicryptophyte

Table I – Studied taxa

Taxon	**Occurrences** **tot**	**subtaxon 1**	**subtaxon 2**	**Subtaxa ratio**
Erysimum collisparsum	425	392	60	0.15
Crocus ligusticus	330	303	27	0.09
Cytisus ardoinii	214	28	186	0.15
Allium narcissiflorum	1190	30	1160	0.03
Eryngium spinalba	1065	961	104	0.11
Carex ferruginea subsp. *tendae*	2473	2450	23	0.01

Table II – Occurrence data for the six studied taxa; the subtaxa ratio values are obtained by the ratio between the occurrence of the smaller substaxon and the occurrences of the bigger subtaxon.

Bioclimatic variable	***Ery_col***	***Cro_lig***	***Cyt_ard***	***All_nar***	***Ery_spi***	***Car_fer***
BIO3 - Isothermality	X	X	X	X	X	X
BIO4 – Temperature seasonality	X	X	X			
BIO6 – Min. temperature of the coldest month	X		X		X	
BIO7 – Annual temperature range				X	X	X
BIO8 – Mean temperature of the wettest quarter		X				X
BIO9 – Mean temperature of the dryest quarter	X	X	X	X	X	X
BIO12 – Total annual precipitations				X		
BIO13 – Total precipitation of the wettest month	X		X			X
BIO15 – Precipitation seasonality	X	X	X	X	X	X
BIO16 – Precipitation of the wettest quarter		X				
BIO19 – Precipitation of the coldest quarter	X		X		X	

Table III – Bioclimatic variables for each studied taxa. Ery_col = Erysimum collisparsum; Cro_lig = Crocus ligusticus; Cyt_ard = Cytisus ardoinii; All_nar = Allium narcissiflorum; Ery_spi = Eryngium spinalba; Car_fer = Carex ferruginea subsp. tendae.

For future climatic scenarios (year 2070) we selected two Representative Concentration Pathways (RCPs) representing moderate (RCP2.6) and extreme (RCP8.5) possible future emission trajectories and four General Circulation Models (GCMs): IPSL-CM5A-LR, Institut Pierre-Simon Laplace; MPI-ESM-LR, Max Planck Institute for Meteorology; HadGEM2-ES, Met Office Unified Model; CCMS4, Community Earth System Model. Combining RCPs and GCMs we obtained eight future scenarios.

Species distribution models

To account for model-based uncertainties in the modelling process (Araújo and New, 2007; Petchey et al., 2015), six SDM techniques included in the R package (R Development Core Team, 2008) BIOMOD2 v 3.3.7 (Thuiller et al., 2009) were used: Generalized Linear Models (GLM - McCullagh and Nelder, 1989); Generalised Boosted Models (GBM – Ridgeway, 1999); Classification Tree Analysis (CTA - Breiman et al., 1984); Multivariate Adaptive Regression Splines (MARS – Friedman, 1991); Random Forest (RF – Breiman, 2001), Flexible Discriminant Analysis (FDA - Hastie *et al.* 1994).

For each models we selected 1000 pseudo-absence with the spatial exclusion criterion in a buffered zone between 5 and 50 km from the occurrences. This process was repeated 10 times. For each models the occurrence dataset was splitted into two parts: 70% of occurrence data were used for the model calibration, while 30% of the occurrence data were used for the model evaluation. The process of model evaluation was repeated 10 times using three different criteria implemented in the BIOMOD2 package: ROC (Relative Operating Characteristic - Hanley and McNeil, 1982); TSS (True skill statistic - Allouche et al., 2006); KAPPA (Cohen's Kappa - Monserud and Leemans, 1992). For the final ensemble projection, only the "good" models (following Araùjo et al., 2005; ROC>0.8; TSS and K > 0.6) were used. Finally, the suitability projections obtained with SDMs were converted into binary distributions using three different thresholds included in the PresenceAbsence package (Freeman & Moisen, 2016) implemented in R: sens=spec (hereafter t1), MaxSens+Spec (hereafter t2), MinROCdist (hereafter t3).

We obtained two types of models for each taxon: i) the "taxon model", in which all occurrences are used without taking into account the geographic disjunction; and ii) two "subtaxa models", in which the occurrences of the two subtaxa are modelled separately (i.e., subtaxa are treated as separated entities). Finally, a third type of models iii) "aggregate model" was obtained by the sum of the output of the subtaxa models.

Niche differentiation

The analysis of niche differentiation was performed in a multidimensional environmental space (hereafter E-space) using the Ecospat package (Broennimann et al., 2016) implemented in R. In particular, we calculated an index of niche overlap and we tested both niche equivalency and similarity between the two subtaxa of each studied taxon.

Niche overlap was assessed using Schoener's D (Schoener, 1970) ranging from 0 (niches are not overlapped) to 1 (niches are fully overlapped). Niche equivalency test is used in order to verify whether the ecological niche of the two taxa are or not interchangeable (Broennimann et al., 2012). Niche similarity test is used to verify whether the ecological niches of two taxa are more or less overlapped than predicted by chance; in particular, this test allow to understand if the observed niche differentiation is due to a different habitat selection made by the tested taxa or simply by a difference in habitat availability in the two background areas (Broennimann et al., 2012; Warren et al., 2008).

The niche differentiation analysis requires the individuation of a background area, whose extension could affect the results. For this reason, we selected five backgrounds using two different approaches: a geographic approach (using two buffered zone around occurrences of each taxon, of 5 and 10 km wide respectively) and an ecological approach (using the binary maps of distribution of each taxon, obtained by the three binarization thresholds – t1, t2 and t3).

Range analysis

In order to assess the climate change effects on species distributional range we perform for each taxon a range analysis using the model projections into the geographical space (hereafter G space). In particular, we calculated for each future scenario the range change index (RC) as follows:

$$RC = 100 \times (RG - RL) / PR$$

Where, for a given species:

- RG (range gain): is the number of pixels that are currently unsuitable but that will be suitable in the future;
- RL (range loss): is the number of pixels that are currently suitable but that will be unsuitable in the future;
- PR (present range): is the number of pixels that are currently suitable.

The values of RC are ranging from -100 to 100: positive values indicate a range expansion in the future, while negative values indicate a range contraction. In order to avoid that the RC calculations is biased by large areas in which the studied taxon is and will be in the future absent (i.e., pixels that are too far from the known occurrences), we restricted the analysis to a buffered zone of 6 km wide around occurrence data.

RESULTS

Niche differentiation

Under current climatic conditions, ROC, TSS and KAPPA indicate a good model performance for almost all studied taxa (Table IV).

	ROC	**TSS**	**KAPPA**
Erysimum collisparsum			
T	0.9 (0.03)	0.7 (0.07)	0.7 (0.08)
S1	0.9 (0.03)	0.7 (0.07)	0.7 (0.08)
S2	0.9 (0.06)	0.7 (0.11)	0.5* (0.13)
Crocus ligusticus			
T	1 (0.02)	0.8 (0.04)	0.8 (0.05)
S1	1 (0.02)	0.8 (0.05)	0.8 (0.06)
S2	0.9 (0.06)	0.8 (0.12)	0.7 (0.15)
Cytisus ardoinii			
T	1 (0.02)	0.9 (0.04)	0.8 (0.06)
S1	1 (0.04)	0.9 (0.08)	0.9 (0.09)
S2	1 (0.02)	0.9 (0.04)	0.8 (0.07)
Allium narcissiflorum			
T	0.9 (0.01)	0.8 (0.03)	0.8 (0.03)
S1	0.8 (0.08)	0.6 (0.13)	0.3* (0.14)
S2	0.9 (0.01)	0.8 (0.03)	0.8 (0.03)
Eryngium spinalba			
T	0.9 (0.02)	0.8 (0.05)	0.8 (0.05)
S1	0.9 (0.01)	0.8 (0.04)	0.8 (0.04)
S2	1 (0.02)	0.9 (0.05)	0.8 (0.07)
Carex ferruginea* subsp. *tenax			
T	0.9 (0.01)	0.8 (0.03)	0.8 (0.03)
S1	0.9 (0.01)	0.8 (0.03)	0.8 (0.03)
S2	0.9 (0.08)	0.8 (0.16)	0.5* (0.19)

*Table IV – Model evaluation: for each models the mean evaluation value is reported; standard deviation values are in brackets. The symbol * indicates models with no good values of model performance (according to Araùjo et al., 2005).*

The niche overlap between all subtaxa is low in all backgrounds (Table V); in fact, D-overlap values are ranging from 0 (*Carex ferruginea* subsp. *tendae*) to 0.3 (*Crocus ligusticus*).

The result of niche equivalency test is significant in all backgrounds; this means that the niche of all pairs of subtaxa are not interchangeable. Conversely, the result of niche similarity test is not significant in all backgrounds; this means that the niches of all pairs of subtaxa are neither more nor less similar than expected by chance.

Taxon	**Background**					**Mean**
	5 km buffer	*10 km buffer*	*T1*	*T2*	*T3*	
Erysimum collisparsum	0.2	0.1	0.2	0.2	0.2	0.2
Crocus ligusticus	0.1	0.2	0.3	0.3	0.3	0.2
Cytisus ardoinii	0.2	0.2	0.2	0.2	0.2	0.2
Allium narcissiflorum	0.1	0.1	0.1	0.1	0.1	0.1
Eryngium spinalba	0.1	0.1	0.1	0.1	0.1	0.1
Carex ferruginea subsp. *tendae*	0	0	0	0	0	0

Table V – D-overlap values between subtaxa.

Range analysis

Under future climatic conditions, negative values of range change are predicted by all types of models (taxon, subtaxa and aggregate) for all studied taxa in all future scenarios (Figure 1). Less negative values of RC were obtained in more "optimistic" scenarios (RCP2.6), while in more pessimistic scenarios (RCP8.5) the RC values were often near to -100 (i.e., total loss of potential range).

In most cases, more negative values of range change were predicted by aggregate model than by taxon model (Table VI); the only exceptions are *Cytisus ardoinii* and *Crocus ligusticus* (in RCP2.6 scenarios) and *Allium narcissiflorum* and *Carex ferruginea* subsp. *tendae* (in all scenarios). However, the predicted values of RC in taxon and aggregate models are resulted non-significantly differentin all studied taxa.

In four studied taxa, the smaller subtaxon has a RC value that was significantly more negative than those predicted by taxon or aggregate model (*Erysimum collisparsum*, *Allium narcissiflorum* and *Eryngium spinalba* in RCP2.6; *Carex ferruginea* subsp. *tendae* in RCP2.6 and RCP8.5 – Figure 1). In few cases, the values of RC of the two subtaxa models were significantly different from each other (*Erysimum collisparsum* in RCP2.6; *Allium narcissiflorum* and *Carex ferruginea* subsp. *tendae* in RCP2.6 and RCP8.5 – Figure 1).

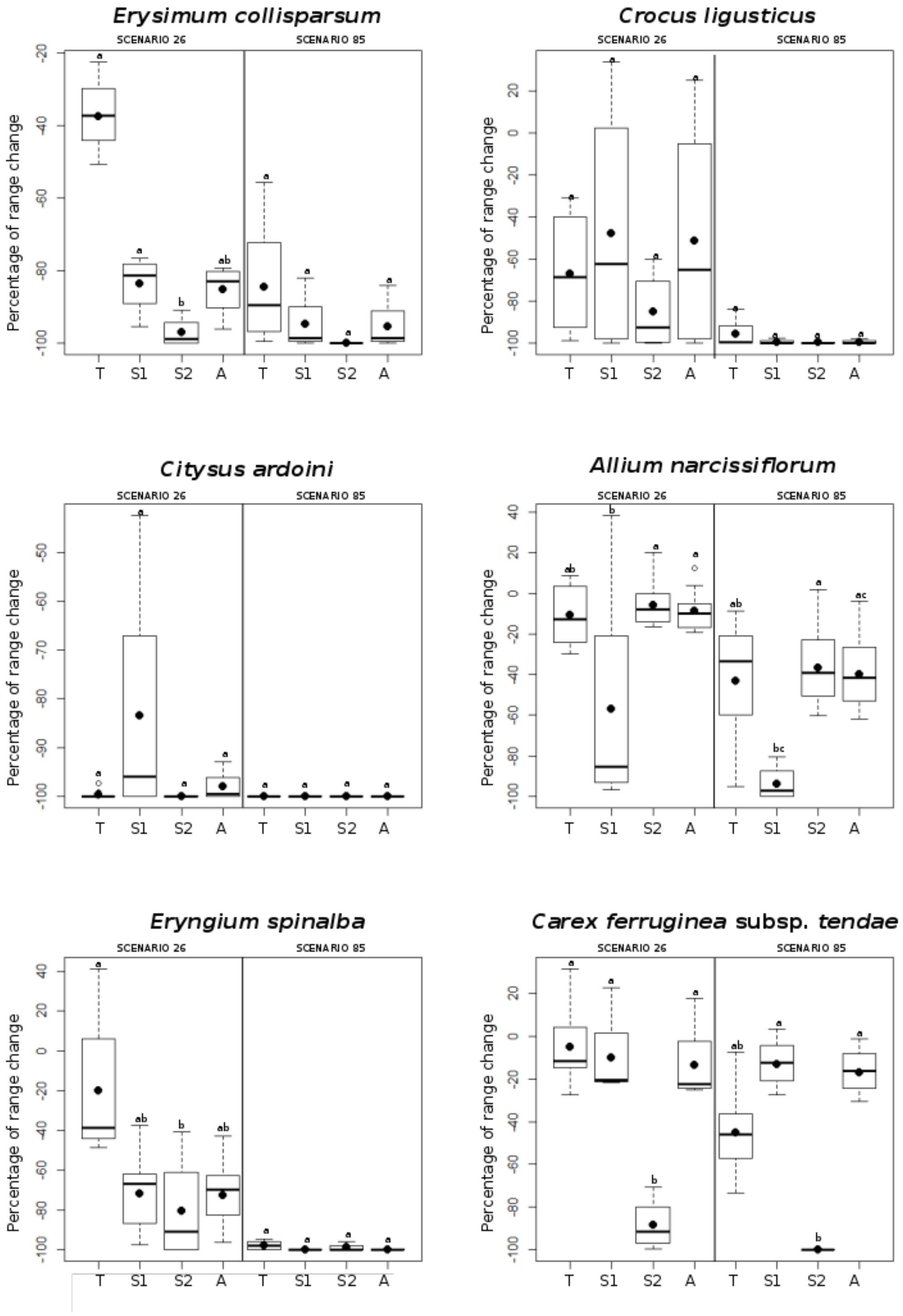

*Figure 1 – Potential range change predicted by different types of model on six studied taxa. The black line represents the median, black circle represents the mean, edge box corresponds to the first and third quartiles (the 25th and 75th percentiles), whiskers are 1.5 * IQR (where IQR is the inter-quartile range). T = taxon model; S1 and S2: models of the subtaxon 1 or 2, respectively; A = aggregate model.*

Taxon	RCP 2.6		RCP 8.5	
	T	**A**	**T**	**A**
Erysimum collisparsum	-38%	-85%	-84%	-95%
Crocus ligusticus	-67%	-52%	-96%	-98%
Cytisus ardoinii	-100%	-98%	-100%	-100%
Allium narcissiflorum	-11%	-9%	-43%	-40%
Eryngium spinalba	-20%	-73%	-98%	-100%
Carex ferruginea subsp. *tendae*	-5%	-13%	-45%	-17%

Table VI – Comparison of the predicted range change values between taxon and aggregate models. T = taxon model; A = aggregate model.

DISCUSSION

The low values of niche overlap between subtaxa (always less than 30%) suggest that the geographic disjunction between populations may be due to the ecological differentiation. This is a remarkable result, because there are no other evidences (morphological or genetic) supporting a differentiation between subtaxa and no one taxonomical separation was never proposed for them. Similar overlapping values were obtained in comparisons of species or subspecies endemic to SW Alps (Dagnino et al., 2017). The results of niche equivalency test, indicating that the niches of the subtaxa are not interchangeable, are in line with the low values of niche overlap. However, niche equivalency test is very conservative (Aguirre-Gutiérrez et al., 2015), and the niches of populations of the same taxon occupying different positions along an environmental gradient are expected to be not interchangeables (Warren et al., 2008; Lowry, 2012). This imply that we must be cautious in the interpretation of the results of this test. Conversely, the not significant results of niche similarity test don't corroborate the ecological separation between subtaxa: the observed niche differentiation (niche overlap, niche equivalency test) may be caused by a different habitat availability in the backgrounds of the subtaxa, rather than by habitat selection or local adaptation (Warren et al., 2008; Broennimann et al., 2012). In conclusion, our results indicate that there isn't a clear ecological separation between subtaxa, but anyway they are currently occupying areas with different climatic conditions, so they might respond differently to future climate change.

Model evaluation indices showed a good model performance in almost all models, with few exceptions in KAPPA index. Differently from ROC and TSS, KAPPA is influenced by prevalence (Allouche et al., 2006), which is the ratio between presence and absence (or pseudo-absence) in the occurrence dataset. In fact, the low values of KAPPA were obtained in models of subtaxa with few occurrences in which a strong predominance of pseudo-absence (very low values of prevalence) may affect KAPPA. In general, it was demonstrated that the geographical and taxonomical partitioning of the occurrences can improve model evaluation increasing AUC values (Gonzalez et al., 2011). Nevertheless, the evaluation values not different between subtaxa and taxon model indicate that there is no an influence of the partitioning of the dataset. However, it should be noted that the evaluation values of the taxon models (in particular AUC) were very close to maximum value of the index, making difficult further improvements.

Under future climatic conditions, a strong contraction of potential range was predicted for all taxa in all scenarios. The mean values of range change (-62%) are in line with previous previsions on plant taxa of Mediterranean mountains (Thuiller et al., 2006). In fact, mountain environments are dangerously exposed to climate change (Dirnböck et al., 2011; Dullinger et al., 2012), in particular where the increase in temperature will be accompanied by a decrease in precipitation, as in Southern Europe (Engler et al., 2011; Pauli et al., 2012). Under optimistic scenarios (RCP2.6) the range change values presented a higher variability rather than in pessimistic scenarios (RCP8.5), where the predicted range contraction is very high (near to 100% in *Cytisus ardoinii*, more than 80% in *Eryngium spinalba*, *Erysimum collisparsum* and *Crocus ligusticus*). This is concordant with the results of previous studies (Thuiller et al., 2006; Engler et al., 2011; Casazza et al., 2014).

The predicted values of range change are not significantly different between taxon and aggregate models, despite subtaxa are living in different climatic conditions. Probably, the high disproportion between occurrences of subtaxa (observed for example in *Allium narcissiflorum* and *Carex ferruginea* subsp. *tendae*) affected the analysis: in fact, the subtaxon with the narrowest geographic range had a negligible influence on the total potential range of the taxon both when its occurrences are merged with the occurrences of the other subtaxon (taxon model) and when its occurrences are used separately and the model projection is summed to the model projection of the other subtaxon (aggregate model). The smallest subtaxon resulted characterized by a significantly higher value of range change with respect of the entire taxon and the other subtaxon. Nevertheless, the low number of grids cells predicted to change in the smallest subtaxon is uninfluential on taxon and aggregate models. Conversely, when the occurrences are less disproportioned (for example in *Eryngium spinalba* and *Erysimum collisparsum*), both subtaxa contribute to taxon and aggregate models; however, if subtaxa occupy climatically different areas, as in our case, the taxon model may not represent the response of one or both subtaxa, while the aggregate models (which include the contributes of each subtaxon separately) provide a more realistic projection (i.e., more similar to the subtaxa models).

CONCLUSIONS

In conclusion, our results showed that the distinct ecological features of few disjointed populations may be not taken into account in species distribution models when all the occurrences of the species are used together. Conversely, isolated populations could be very important for the conservation of biodiversity, as they may show morphological or genetic peculiarities. Therefore, predictions of climate change effect that do not incorporate the contribute of disjointed populations could be two-ways biased: i) the potential range of the species is predicted to be relatively stable despite the area occupied by the disjointed populations will be mostly lost; ii) a strong or total contraction of the potential range of the species is predicted, despite disjointed populations will be relative stables. In both cases the information provided by the disjointed population is lost in the model of species, and consequently the forecasted effects of climate change on the species will be biased. In the first case the effects of climate change will be underestimated: if the species as a whole is not at risk, the local extinction of the disjointed populations represent a severe loss of biodiversity. In the second case, the effects of climate change will be overestimated: a species for which extinction is expected is actually less endangered than what it seems to be due to some disjointed populations on which climate change will be less baleful (maybe thanks to local adaptation). In all cases, the biased predictions prevent to understand which populations of the species are more exposed to climate change, making difficult to elaborate appropriate conservation strategies. Moreover, when disjointed populations are less disproportioned, the contribute of both groups are incorporated in the model of species. However, such model could be biased if the groups of disjointed populations are ecologically different (i.e., the model of species don’t represent the response to climate change of one or both groups of populations); this make the independent incorporation of the contributes of both groups (aggregate model) preferable. In any case, before modeling the response to climate change of a species that show geographic disjunctions among populations (especially when distributed along an environmental gradient or in very heterogeneous areas), a previous step of detection of eventual niche differentiation is recommended.

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5 – CLIMATE CHANGE AND CONSERVATION OF BIODIVERSITY

5.1 – Introduction

Biotic elements and areas of endemism have been proposed as basic units of biogeography. Biotic element is defined as a group of taxa whose ranges are significantly more similar to each other than to those of taxa of other groups (Hausdorf, 2002). An area of endemism is defined as an area that has at least two endemic taxa with a maximally congruent range (Linder, 2001). Because species characteristic of a given area of endemism or biotic element are supposed to show similar distribution as result of similar biogeographic history, these biogeographic units can be used as conservation units. For conservative purposes, such areas could be those on which it is more worthwhile to invest financial resources in the elaboration of conservation strategies. Here we use the approach of both biotic elements and areas of endemism to identify the areas of SW Alps that can play a priority role for conservation of endemic flora. Moreover, using the predicted range change values under future climate conditions of the characteristic taxa of such areas, we discuss explore their relative exposure to climate change effects.

5.2 – Methods

The biotic elements were determined with the methodology proposed by Hausdorf (2002) using the prabclus package (Hennig & Hausdorf, 2015) implemented in R (R Development Core Team, 2008). The areas of endemism were identified with cluster analysis applying the Kulczynski index (Shi, 1993) as a measure of distance, using the vegan package (Oksanen et al., 2017) implemented in R; the number of groups was established using the NbClust package (Charrad et al., 2014) implemented in R, choosing the number indicated as the optimal number of groups by the majority of the evaluation methods implemented in the package. In order to recognize the species associated to each area of endemism, we applied the indicator species analysis (INDVAL, Dufrêne & Legendre, 1997) using the indicspecies package (De Caceres & Legendre, 2009) implemented in R; following Casazza & Minuto (2009), the INDVAL values were used to compare the results of biotic element approach with those obtained by determining areas of endemism. All the analyses were conducted using a resolution of 10x10 km.

5.3 – Biotic elements

In the study area, six biotic elements were identified by our analysis (Figure 1, Table I). Altogether they cover almost all the alpine region of the study area and the Mediterranean coastal regions of Provence, with the highest overlap in the Ligurian and Maritime Alps (Figure 2). About half of the studied taxa (53%) were identified as characteristic of a given biotic element (note that each taxon can be assigned to only one biotic element).

Cod.	**Geographic range**	**Characteristic taxa**
BE_1	Ligurian, Maritime and Cottian Alps	*Arabis allionii, Dianthus furcatus* subsp. *furcatus, Erysimum burnati, Fritillaria tubiformis* subsp. *moggridgei, Jovibarba allionii, Potentilla valderia, Saxifraga florulenta, Saxifraga pedemontana* subsp. *pedemontana, Silene cordifolia, Viola valderia*
BE_2	Ligurian, Maritime, Dauphiné and Cottian Alps	*Campanula stenocodon, Centaurea uniflora* subsp. *uniflora, Dianthus pavonius, Festuca scabriculmis, Gentiana burseri* subsp. *villarsii, Gentiana rostani, Gymnadenia nigra* subsp. *corneliana, Oreochloea seslerioides, Prunus brigantina, Veronica allionii*
BE_3	Ligurian and Maritime Alps	*Asperula hexaphylla, Euphorbia variabilis* subsp. *valliniana, Gentiana burseri* subsp. *actinocalyx, Hesperis inodora, Leucanthemum virgatum, Micromeria marginata, Moehringia sedoides, Primula allionii, Saxifraga cochlearis, Silene campanula*
BE_4	Provence	*Anthemis cretica* subsp. *gerardiana, Arenaria provincialis, Centaurea paniculata* subsp. *polycephala, Genista lobelia, Limonium cordatum, Limonium pseudominutum, Ophrys exaltata* subsp. *splendida, Ophrys provincialis, Santolina decumbens, Senecio leucanthemifolius* subsp. *crassifolius*
BE_5	Ligurian and Maritime Alps, Provence	*Ballota frutescens, Campanula rotundifolia* subsp. *macrorhiza, Cytisus ardoini, Euphorbia canutii, Fritillaria involucrata, Lilium pomponium, Minuartia glomerata* subsp. *burnati, Narcissus pseudonarcissus* subsp. *provincialis*
BE_6	Cottian, Dauphiné, Graian, Maritime and Ligurian Alps	*Berardia subacaulis, Brassica repanda* subsp. *repanda, Campanula alpestris, Hedysarum hedysaroides* subsp. *boutignyanum, Rhaponticum heleniifolium*

Table I *– Biotic elements in SW Alps.*

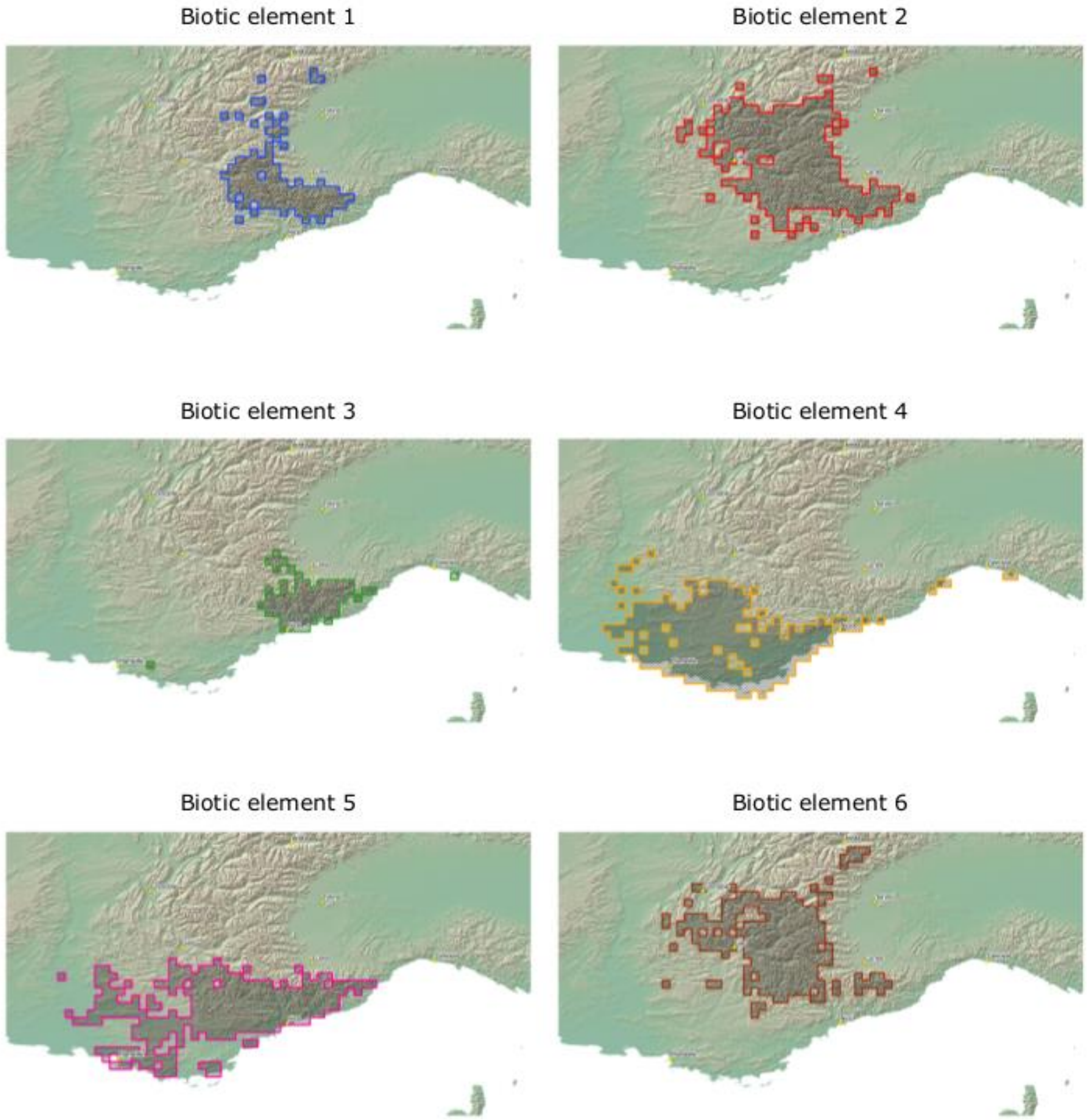

Figure 1 *– Biotic elements identified in SW Alps.*

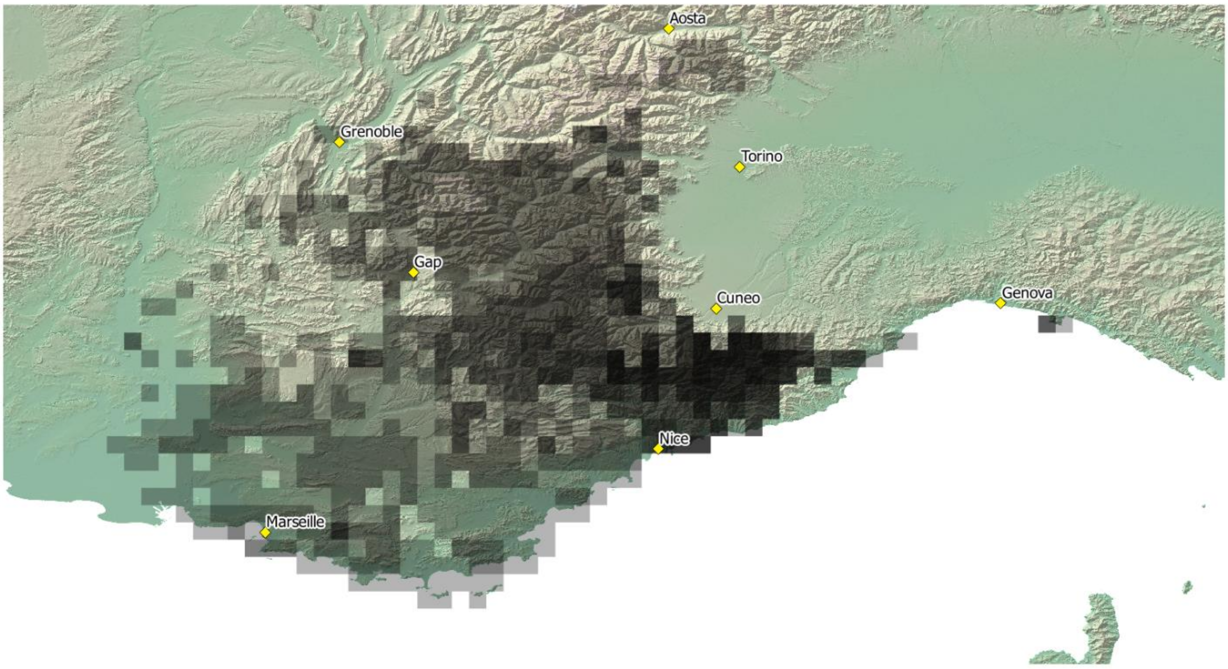

Figure 2 *– Overlapping of the six biotic elements identified for endemic flora of SW Alps. Darker colours indicate the overlap of several biotic elements*

5.4 – Areas of endemism

We identified four areas of endemism in the study area (Figure 3). Altogether, the four areas of endemism cover the Provence and almost all the Alpine and pre-Alpine regions of the study area (note that each pixel of the study area can be assigned to only one area of endemism; i.e., the geographical overlapping between different areas of endemism is not admitted). Almost all studied taxa (98%) are recognized as characteristic of one area of endemism, but the different areas of endemism showed high variability in the number of characteristic taxa (Table II).

Cod.	**Geographic range**	**Characteristic taxa***
AoE_1	Ligurian, Maritime, Cottian, Dauphiné and Graian Alps	*Allium narcissiflorum, Aquilegia reuteri, Asperula cynanchica* subsp*. rupicola, Berardia subacaulis, Brassica repanda* subsp. *repanda, Campanula alpestris, Campanula stenocodon, Carex ferruginea* subsp*. tenax, Centaurea uniflora* subsp*. uniflora, Coincya richeri, Dianthus pavonius, Eryngium spinalba, Festuca scabriculmis, Galium pseudohelveticum, Gentiana burseri* subsp*. villarsii, Gentiana rostani, Gymnadenia nigra* subsp*. corneliana, Hedysarum hedysaroides* subsp*. boutignyanum, Helictotrichon sempervirens,*

		Helictotrichon setaceum, Jovibarba allionii, Oreochloa seslerioides, Potentilla valderia, Primula marginata, Prunus brigantina, Rhaponticum heleniifolium, Sempervivum calcareum, Seseli annuum subsp. *carvifolium, Silene cordifolia, Teucrium lucidum, Veronica allionii, Viola valderia*
AoE _2	Eastern (italian) part of Cottian and Graian Alps	*Campanula elatines*
AoE _3	Southern part of Maritime Alps, Dauphiné pre-alps and Provence	*Androsace chaixii, Anthemis cretica* subsp. *gerardiana, Campanula rotundifolia* subsp. *macrorhiza, Centaurea paniculate* subsp. *polycephala, Crocus versicolor, Fritillaria involucrate, Limonium pseudominutum, Ophrys bertolonii* subsp. *saratoi, Ophrys provincialis, Santolina decumbens, Scrophularia provincialis, Sideritis provincialis*
AoE _4	Ligurian Alps and Apennines	*Campanula sabatia, Crocus ligusticus, Hyacinthoides italica, Leucanthemum virgatum*

***Table II** – Areas of endemism in SW Alps. *only taxa with INDVAL values higher than 0.3 and pValue lower than 0.05 are showed.*

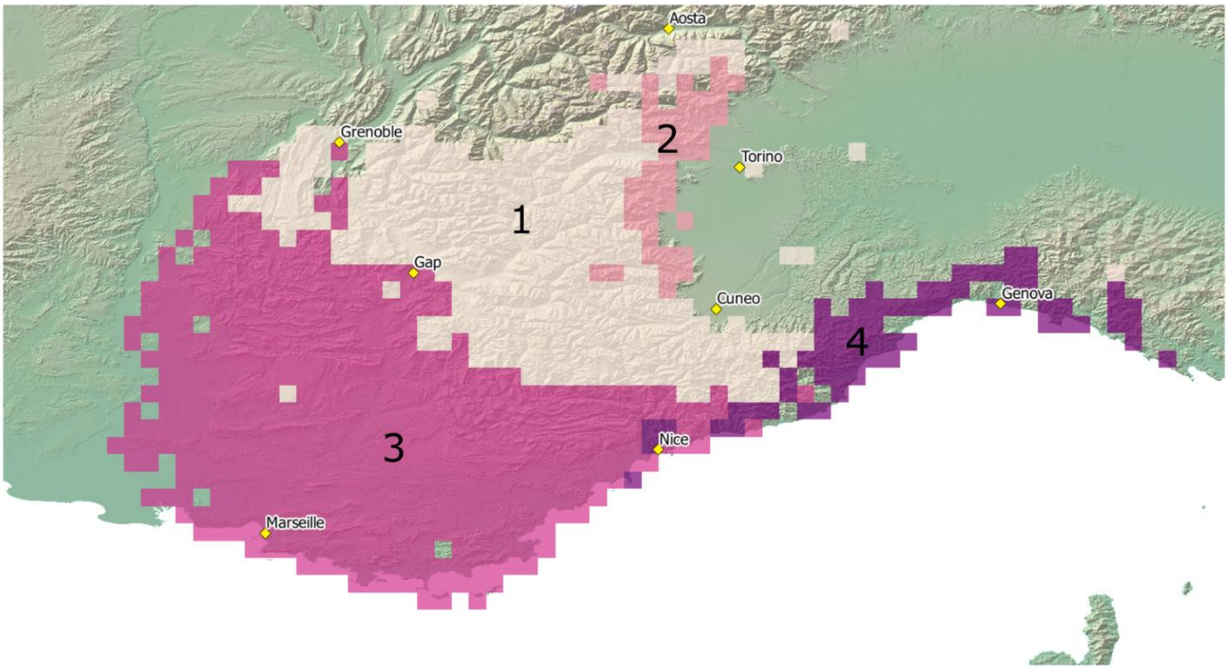

***Figure 3** – Areas of endemism in SW Alps.*

5.5 – Effects of climate change

The characteristic species of all biotic elements and areas of endemism showed highly negative values of range change, which translates into highly negative mean values of range change of both biotic elements and areas of endemism under all future scenarios (Table III). Interestingly, all groups showed similar mean values of range change, without differences between biotic elements and areas of endemism. Slightly less negative values were showed by BE_4, which is characterized by lowland species: these taxa are probably more adapted to hot and arid environments, and thus they are less exposed to climate change; however, a major risk for the taxa of this biotic element is represented by the high levels of anthropization, and, consequently, the changes in land cover. Conversely, slightly more negative values were showed by BE_5, which is characterized by mountain species which are currently living in Mediterranean mountains (i.e., subalpine habitats); in fact, the mountainous habitats of the Mediterranean region will experience stronger decrease in precipitation due to climate change than the alpine region.

Group	RC_26_1	RC_26_1	RC_85_1	RC_85_2
Biotic element				
BE_1	-57,221	-50,309	-80,651	-81,269
BE_2	-61,949	-47,085	-84,434	-79,663
BE_3	-60,985	-63,125	-81,05	-86,293
BE_4	-41,692	-20,554	-46,835	-21,511
BE_5	-75,3538	-76,3863	-89,5863	-91,575
BE_6	-64,702	-61,588	-77,44	-75,56
Area of endemism				
AoE_1	-60,9503	-54,0529	-80,3552	-78,8143
AoE_2	-45,91	-50,41	-63,38	-74,05
AoE_3	-60,2519	-48,3478	-71,7103	-59,5406
AoE_4	-64,4417	-67,3917	-83,21	-87,8333

Table III *– Percentage of range change for each biotic elements and areas of endemism. The showed values are the mean values of range change of taxa characteristic of each group.*

5.5 – Conclusion

Our results showed that the approach of biotic elements and areas of endemism led to the identification of different priority areas in SW Alps. While all the main sub-regions of the study area (Alpine, pre-Alpine, Provence) were more or less covered by the four areas of endemism, the biotic elements showed a marked preference for the Alpine sub-region, with the highest overlap values in the Ligurian and Maritime Alps. However, climate change seems will equally affect all these areas, as showed by the predicted values of range change of the characteristic taxa.

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6 – CONCLUSION

Climate change is currently one of the greatest threat to biodiversity, and forecasting the potential species distribution under future climate represents a fundamental tool for conservation purposes. This is particularly true for endemic plant taxa, which are likely more dispersal-limited and less genetically variable, thus less able to rapidly adapt to climate change than species with broader distribution. Several studies have investigated the effects of climate on single endemic species of SW Alps, but a comprehensive assessment of the climate-induced effects on the endemic flora of this center of endemism was still lacking. With the statistical approach of SDMs, I investigated the climate-induced dynamics of potential range of 100 endemic or sub-endemic plants of SW Alps, in relation to both past and future climates.

In the next half century, climate change will deeply affect the pattern of distribution of endemic plant taxa in SW Alps (Chapter 2). Despite very few species are predicted to be extinct in 2070, for all the studied taxa a strong range reduction is expected. Moreover, since climate change is not the only threat for these taxa (e.g.: changing in land use, habitat fragmentation, alien species invasion, etc.) the list of extinct taxa in 2070 may be longer than here reported. The climate threat will impact on all the major vegetation belts of the study area, but lower vegetation belts (i.e., colline) will be less exposed, probably because these species are already exposed to the warm and dry forecasted conditions. Conversely, mountain and subalpine species will experience stronger environmental changes, caused by a simultaneous increase of temperature and decrease of precipitation. Despite niche properties emerged as useful indictors of species sensitivity to climate change, their influence is variable among vegetation belts, suggesting a complex scenario of species-specific individualistic response to climate change. To recognize useful conservation units, I individuated both areas of endemism and biotic elements in SW Alps (Chapter 5). Four areas of endemism and six biotic elements were detected, and the characteristic taxa of each of them were determined. The predicted impact of future climate change on all these putative conservation units is high, coherently to the individual projected impact on species distribution.

Past climate also affected the current distribution of endemic flora of SW Alps, and, consequently, determined the “starting point” for the assessment of impact of future climate (Chapter 3). SW Alps are defined as a refugial areas in the Mediterranean Basin, where species persistence was favoured from the Tertiary. Thus, past climate stability is expected to have led to the current high levels of both species richness and endemism rate observed in this area. However, since the last 120.000 years (from Last Interglacial to current day) several climatic oscillations occurred in SW Alps (as in all boreal hemisphere), alternating cold and dry periods (e.g., the Last Glacial Maximum) to warmer periods (e.g., the Mid Holocene). Thus, past range dynamics have probably occurred even in species with poor dispersal abilities, such as the taxa here investigated. Indeed, my analyses showed that in situ persistence through time is not enough to explain the current distribution of endemic flora of SW Alps. Particularly, most of the investigated taxa are currently occupying sites that were unsuitable for them in the past. The majority of species showed a range dynamic that suggest the existence of interglacial refugia for them, indicating that these taxa are currently facing an adverse (warm) period because they prefer cold climates. The pattern of species richness is affected by both current and past climate. In particular, endemics richness is affected by temperature-related variables and is positively correlated to past climate change velocity. This suggest that the current areas with highest endemism richness in SW Alps are not determined by long-term persistence nor short-distance migrations, but rather a mixture of both.

I also investigated the influence of infra-specific ecological variability on the projections of ecological niche provided by SDMs (Chapter 4). Such infra-specific variability may have influence on both speciation mechanism and taxonomical status of taxa. My results showed that for taxonomical purposes SDMs can be a useful tool for exploring ecological differentiation between putative taxa in an objective way. However, I also showed several limitations of this innovative use of SDMs, first the need to test if the observed divergence is due to an actual ecological differentiation between putative taxa or is only an artefact caused by differences in the background areas in which putative taxa occur. Moreover, I investigated the influence of infra-specific ecological variability associated to disjointed distribution on forecasted effects of climate change on species distribution. My results showed that it is recommendable to test the existence of such differentiation before to forecast the climate change’s effect and, if such differentiation exists, it is preferable to take it into account with the independent modeling of the ecologically differentiated sub-taxa. In fact, a model that don’t consider the infra-specific variability may led to biased estimation of climate effects on species distribution.

In conclusion, the present study constitutes an original contribution to the knowledge of the endemic flora of SW Alps. In particular, the results of my research can be useful for the elaboration of proactive conservation strategies of this center of endemism and, more in general, of biodiversity.