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The contribution of cold air pooling to the distribution of a rare and endemic plant of the Alps

Patsiou, Theofania S ; Conti, Elena ; Theodoridis, Spyros ; Randin, Christophe F

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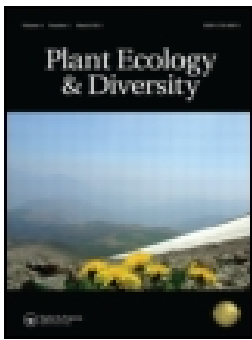
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The contribution of cold air pooling to the distribution of a rare and endemic plant of the Alps

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Background: The topographic complexity typical of alpine landscapes creates a variety of (micro)climatic conditions that may mitigate the effects of a warming climate on alpine plants via such mechanisms as cold air pooling (*CAP*).

Aims: Our primary objectives were to (1) assess whether landscape potential for *CAP* as a predictor improved species distribution models (SDMs) projections and (2) quantify the impact of *CAP* on the microclimate experienced by alpine plants compared to the macroclimate.

Methods: We selected the Maritime Alps as our study area, located on the French–Italian border, and its rare endemic plant, *Saxifraga florulenta*, as model taxon. We generated a spatial layer in GIS (Geographic Information System) that reflected the potential of the landscape for *CAP* and ran five SDM algorithms with and without *CAP* layer as a predictor. Second, we recorded the microclimate plants experience with temperature loggers.

Results: *CAP* as a predictor decreased the omission error of SDMs, mostly at low and mid elevations, where topography may buffer extreme temperatures, resulting in a more stable microclimate compared to macroclimate.

Conclusions: We have shown that plants in an alpine landscape may be less exposed to climate warming than predicted by macroclimate. Topo-climatic GIS layers for SDM projections in mountain environments should integrate such physical mechanisms as *CAP*.

Keywords: climate change; climate projections; macroclimate; microclimate; mountain terrain; persistence; temperature inversions; topography

Introduction

Air temperature is likely to be the main climate factor driving the distribution of species and their physiological processes (Woodward 1987; Walther et al. 2002; Körner 2003; Körner and Paulsen 2004). Many studies predicting plant species distributions in space and time have mostly relied on correlative relationships between long-term averaged temperature at coarse spatial resolutions and observations of organisms (e.g. Thomas et al. 2004; Booth et al. 2014). The spatial and temporal resolution of geographic climate layers (i.e. gridded climate data) used as predictor variables in empirical models can largely determine the prediction of the future distribution of species under a changing climate. In particular, coarse spatial and temporal resolutions cannot adequately represent temperature extremes and variation in the landscape (Randin et al. 2009; Gastón and García-Viñas 2010; Reside et al. 2010; Franklin et al. 2013; Kollas et al. 2014). The latter is evident in a mountainous alpine landscape, because its topographic complexity generates a mosaic of wide temperature conditions over very short distances (Scherrer and Körner 2010, 2011). There exists a variety of microsites hosting a microclimate decoupled to different degrees from the mean local/regional climate characterised by weather stations data, which function as microrefugia. As alpine

plant species are more strongly coupled to air temperature compared to forests (Körner 2003), the topographically driven temperature mosaic is a mechanism that allows alpine plants to avoid climatically unfavourable conditions.

In this context, temperature inversion, such as cold air pooling (hereafter defined as *CAP*), has been proposed as an additional topo-climatic mechanism that has allowed cold-adapted/cold-requiring plants to survive high temperature during interglacials (Dobrowski 2011). Valleys that experience temperature inversions can have temperature patterns at fine geographic scales that deviate markedly from those predicted by elevation. Accordingly, plants growing in such areas display a response to climate change that differs sharply from that observed in adjacent areas, because temperature inversion decouples them from the free atmosphere (Hart et al. 2004; Daly et al. 2009). Although *CAP* has been intensively studied (e.g. Whiteman 1990, 2000; Daly et al. 2007; Lundquist and Cayan 2007; Lundquist et al. 2008), it has rarely been incorporated into the generation of geographical climate grids (but see Curtis et al. 2014). Such gridded spatial climate layers are routinely used for species distribution modelling, which is a rapid, efficient and widespread tool for assessing the potential vulnerability of species under climate change.

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Species distribution models (hereafter referred as SDMs; Guisan and Thuiller 2005) typically relate climate data (obtained by meteorological stations, commonly using a Stevenson screen, at 2 m above the soil surface) from the continental to the regional scales (sensu Walker et al. 1993) with species occurrences. However, SDM predictions based on such climate data can be inaccurate in alpine environments due to topographic complexity and the fact that they do not integrate microrefugia as thermally suitable habitats (Trivedi et al. 2008; Randin et al. 2009). The role of microrefugia in facilitating species persistence, faster range expansions and/or shifts as a response to climatic cycles has been recently tested by Patsiou et al. (2014) for *Saxifraga florulenta*, a rare, arcto-tertiary and relict species endemic to the southwestern Alps (Conti et al. 1999; Szövényi et al. 2009). While projections of SDMs alone failed to explain the persistence of *S. florulenta* during the climate oscillation between the last glacial maximum and the current climate, a mechanistic reconstruction combining SDMs, dispersal and microrefugia locations provided a plausible explanation of its past and present distributions (Patsiou et al. 2014). Microrefugia are likely to continue to play a role in the current climate warming by allowing alpine species to escape from unsuitably high mean and extreme temperatures (Ashcroft et al. 2012). Nevertheless, to our knowledge, specific physical and abiotic mechanisms related to the climate and topography that enable a given species to persist within such patches of favourable climate have not yet been sufficiently characterised.

Climate can be mapped at different geographic scales, ranging from global (>10,000 km) to microscales (<10 m; sensu Peterson Anderson et al. 2011). Spatial representations of climate are usually derived from the interpolation of temperature and precipitation data from standard weather stations (e.g. WorldClim; Hijmans et al. 2005) and refer to the local scale (sensu Peterson Anderson et al. 2011; i.e. 1–10 km). However, such interpolated data do not typically consider climate features related to topography beyond elevation (PRISM Gridded Climate Data, <http://prism.oregonstate.edu>). Topographic parameters can significantly affect inferences on species distribution and their habitat preferences, especially for herbaceous or cushion plant species in complex terrain (Ashton et al. 2009; Illán et al. 2010; Gillingham et al. 2012; Suggitt et al. 2012; Slavich et al. 2014). In particular, topographic shading that influences solar radiation and temperature at fine geographic and temporal scales and *CAP* can be described by topo-climatic factors using landscape metrics at the local scale. As a consequence, plants may experience a microclimate that is quite different from the regional-scale climate data used to quantify climate-occurrence and climate-abundance relationships. While the distribution and abundance of plant species are correlated with topographic factors at the local scale, the microclimatic conditions experienced by habitat specialist plants

living in rock fissures and crevasses need to be examined at an even finer spatial resolution (Scherrer et al. 2011; Pradervand et al. 2014). Following up on our previous study (Patsiou et al. 2014), we selected the Maritime Alps as our study area and a rare endemic plant of this region, *S. florulenta*, as a model taxon for the present study (see Appendix S1 in Supporting Information). We tested whether *CAP* could be a putative mechanism that explained the long-term persistence of *S. florulenta* in the Maritime Alps. We first assessed the observed frequency of occurrence as well as the modelled probability of *S. florulenta* occurrence as a function of *CAP* along elevation. We then tested whether geo-referenced information about *CAP* potential could improve the predictive accuracy of SDM predictions when included as a predicting variable. Here, we hypothesised that occurrence sites prone to *CAP* and the improvement of SDMs would be mostly located at the trailing edge (i.e. the lower elevational end) of the distribution of *S. florulenta* along its elevation distribution. *CAP* therein could counteract the effect of warming temperature (and where macroclimate is not sufficient to depict decoupling of daily mean and extreme microclimate conditions from the regional climate). Lastly, we compared temperature conditions in the microhabitat of *S. florulenta* prone to *CAP* to macroclimatic projections of temperature, hypothesising that daily mean and extreme microclimate is decoupled from the regional climate, thus providing a functional basis to explain how this currently rare alpine plant could have persisted under past climate oscillations.

Materials and methods

CAP mechanism in the terrain

Under a clear night sky, the air in contact with the upper slopes of a valley undergoes radiative cooling, and this dense cold air following the line of the steepest slope subsides into the centre of the valley, generating a temperature inversion. The temperature at the bottom of the valley and located in the *CAP* layer is thus decoupled from the free atmosphere, and measured temperature values in the *CAP* layers are very different from those predicted with a typical adiabatic lapse rate. A warm zone (thermal belt) is formed during the transition time of the evening and above the *CAP* layer in which the temperature increases with increasing elevation and is coupled to the atmosphere. The highest temperatures are found at the sides of the thermal belt in contact with the slopes (Whiteman 2000). This process is called nocturnal drainage (Barr and Orgill 1989; see a detailed description of the phenomenon in Figure S1). As a consequence, valleys that have the tendency to pool cold air due to their topography and radiative cooling are exposed to narrower temperature ranges during night time compared to valleys not prone to *CAP* (Whiteman 2000). Hence, we identified particular topographic features in the landscape of the

study area to characterise their potential for *CAP*. The topographic features used to identify potential for *CAP* were

- (1) the tendency of valleys for pooling or draining cold air based on their shape (estimated by the topographic amplification factor, Figure S2; Liston and Elder 2006; Lundquist et al. 2008);
- (2) local concavities and convexities of the terrain described by the elevation percentile (i.e. the elevation percentile of a pixel compared to the elevation of the surrounding terrain) and curvature (hereafter designated as Ω_c);
- (3) slope (Lundquist et al. 2008 and Appendix S2 in Supplemental Material).

We finally classified all the pixels of the study area 25-m resolution digital elevation model (DEM; IGN and SITAD, details in Appendix S2) as

- (1) prone to *CAP*
- (2) ‘ambivalent’ for rare/unclear tendency to weak *CAP*
- (3) not prone to *CAP* (*no-CAP*)

hence, creating the geo-referenced layer (hereafter designated as *CAP* layer; see Appendix S2 in Supplemental Material).

The distribution of S. florulenta occurrences in relation with CAP

To test whether the pattern of *S. florulenta* distribution related to the *CAP* potential of the landscape, we intersected a point layer of the 410 occurrences of *S. florulenta* with the *CAP* layer. The dataset of occurrences had a horizontal precision and accuracy corresponding to an error of ≤ 10 m (see also Patsiou et al. 2014) and represented all known populations of the species.

Here, we expected the frequency of sites with species occurrences located in the *CAP*-prone areas to increase with decreasing elevation and the frequency of sites with *no-CAP* occurrences to decrease simultaneously due to the effect of warmer air temperatures. We tested this hypothesis as in Vitasse et al. (2012). Generalised linear models (GLMs; Martini McCullagh and Nelder 1989) with a binomial probability distribution and a logit link function were fitted using the presence of each *CAP* category (within the occurrence dataset of *S. florulenta*) against elevation and using the two other remaining *CAP* categories as absences. Second-order polynomials (linear and quadratic terms) were allowed for elevation as the response variable using the polynomial function of the Design library (Azola and Harrell 2006) in R software (R Core Team 2015). This type of response curve was appropriate to allow easy visualisation and comparisons between elevational limits and optima of the three *CAP* layer categories. The model fit was estimated with the adjusted geometric mean

squared improvement R^2 (Cox and Snell 1989; Nagelkerke 1991). This R^2 is rescaled for a maximum of 1 and adjusted for the amount of both observations and predictors in the model. The significance of elevation in logistic regression was tested by an analysis of variance (ANOVA).

SDMs and the cap layer as a predictor

We assessed the improvement of the predictive accuracy of SDMs when the *CAP* layer was included as a predicting variable. Five SDM techniques were used: two regression-based techniques (GLMs; Martini McCullagh and Nelder 1989 and generalised additive models: GAMs; Hastie and Tibshirani 1990), a machine-learning algorithm (maximum entropy; Phillips et al. 2006) and two classification and regression tree techniques (random forest; Breiman 2001 and generalised boosted regression models: GBM; Friedman 2001). For the final ensemble projections, we combined the five techniques to produce binomial maps of presence and absence (Araújo and New 2007; Marmion et al. 2009; see also Appendix S3 in Supplemental Material) considering two possible combinations:

- (1) Four out of five techniques predicting suitable areas, hereafter defined as ‘majority’;
- (2) Five out of five techniques predicting suitable areas, hereafter ‘consensus’.

We assessed whether SDMs including the *CAP* layer better predicted the core, the leading or the trailing edge of the distribution of *S. florulenta*. For this, we compared the variation of the true presences and the omission error predicted by the ensemble of SDMs with and without the *CAP* variable and across elevation classes (i.e. every 200 m; see details in Appendix S3 in Supplemental Material). We also carried out a Pearson’s Chi-squared test for count data (i.e. presence–absence; Agresti 2002, 2007) with *P*-values calculated by Monte Carlo simulation with 2000 repetitions to test whether there was a significant difference in the omission error between the ensembles without and with *CAP* layer. To test whether there was an effect of elevation on those differences, we carried out a Cochran–Mantel–Haenszel Chi-square exact test for count data (Agresti 2002, 2007), stratified by elevation classes of 200 m. With an additional Pearson’s Chi-squared test for count data, we compared whether the omission error differs significantly in all classes of elevation and for ensembles with and without *CAP* layer ensembles.

We then sought to validate whether a potential mismatch of the microclimate the species experiences in *CAP* and ‘ambivalent’ sites differs from macroclimate projections and whether this could be related to the intensity of *CAP*. To record the temperature conditions *S. florulenta* experiences at sites prone to *CAP*, we installed six temperature loggers (Tid-biT v2 Temp UTBI-001, Onset Computer Corporation) from June 2012 to September

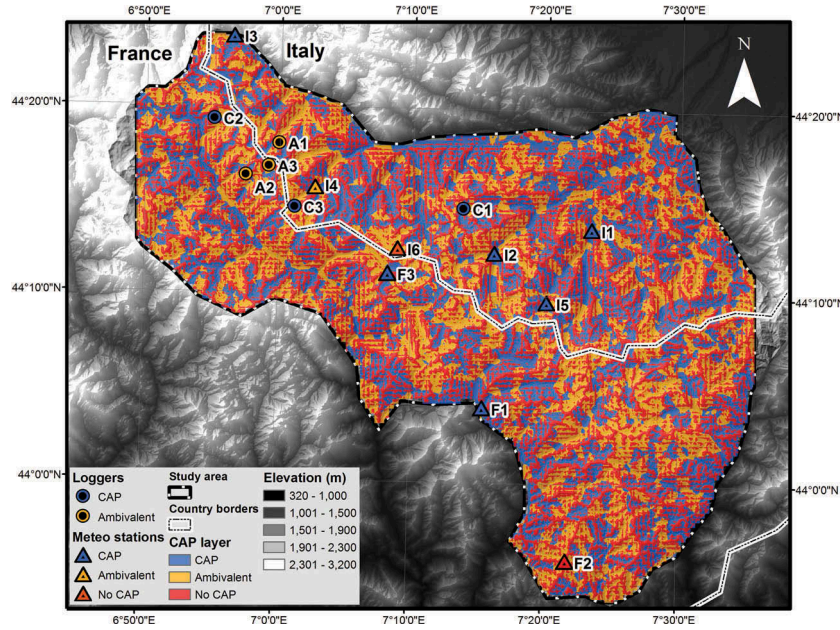


Figure 1. Map of the study area during summers of 2011 and 2012 in the Maritime Alps at the French–Italian border (43°53'16"–44°24'20"N and 7°39'1"–6°47'0"E). Elevational range: 320–3297 m a.s.l. showing the locations of temperature loggers (A1-3, C1-3) and weather stations (Italy: I1-6, France: F1-3) recording daily temperature at the micro- (i.e. within fissures next to plant individuals) and macroscale, respectively (see Tables S1 and S2). Temperature sensors and weather stations at the two scales as well as 25-m cells of the landscape are classified as prone to cold air pooling (CAP), ‘ambivalent’ and not prone to cold air pooling (no-CAP). Logger sites are distributed along the elevation range of *S. florulenta* and on both main slopes of the Maritime Alps.

2013 (Figure 1, and Table S1). Loggers were placed in rock fissures protected from sunlight and temperature was recorded every 30 min. Three selected sites were classified as CAP and three others as ‘ambivalent’. Daily mean, minimum and maximum temperatures at these sites were then derived from measurements, and corresponding daily temperatures from macroclimate projections were extracted for locations where the loggers had been installed (see Appendix S4 in Supplemental Material).

For each of the six sites with temperature loggers and using the *decompose* function from the *stats* library in R (R Core Team 2015), we first decomposed the daily time series of microclimate measurements and macroclimate projections of minimum, mean and maximum temperature to their three basic components:

- (1) the seasonal trend, which represents events that recur within a fixed period,
- (2) the underlying trend of the metrics and
- (3) the random events, which are the residuals of the time series after allocation into seasonal and underlying trends.

We then plotted the decomposed trend and calculated the area under the curve (AUC) at each scale (i.e. micro- and macro-scale) and for the three temperature variables (i.e. minimum, mean and maximum temperatures). We used the difference of AUC for each type of temperature between the two scales as a metric of temperature decoupling between macro- and microclimate. We also

calculated the difference in AUC within each scale (e.g. $dAUC_{\text{within micro}} = AUC_{T_{\text{max micro}}} - AUC_{T_{\text{min micro}}}$) as a proxy for temperature amplitude at the macro- and at the microscale as well as the difference in the AUC between the difference in the AUC within scales (i.e. $dAUC_{\text{between scales}} = dAUC_{\text{within macro}} - dAUC_{\text{within micro}}$). In addition, we compared the extreme random temperature events at the two scales to verify the hypothesis that temperature was more stable at the microscale when compared to the macroscale. We also quantified the relationships between climate projections of temperatures and microclimate measurements by producing Biplots for each site and each temperature variable. We then assessed whether coupling or decoupling of the temperature between micro- and macroscale and temperature stability could be linked to the intensity of CAP.

Results

The distribution of S. florulenta occurrences in CAP classes as a function of elevation

The classification of the study area terrain in CAP, ‘ambivalent’ and no-CAP sites showed, as expected, that CAP sites were more frequent at lower elevations, while the reverse pattern was observed for no-CAP sites, particularly above 2300 m a.s.l. (Figure 2a). The relative frequency of ‘ambivalent’ sites was similar from 1700 to 2500 m a.s.l. and declined above 2500 m a.s.l. We found that the frequencies of CAP and ‘ambivalent’ *S. florulenta* occurrence sites were higher at low elevation (1700–

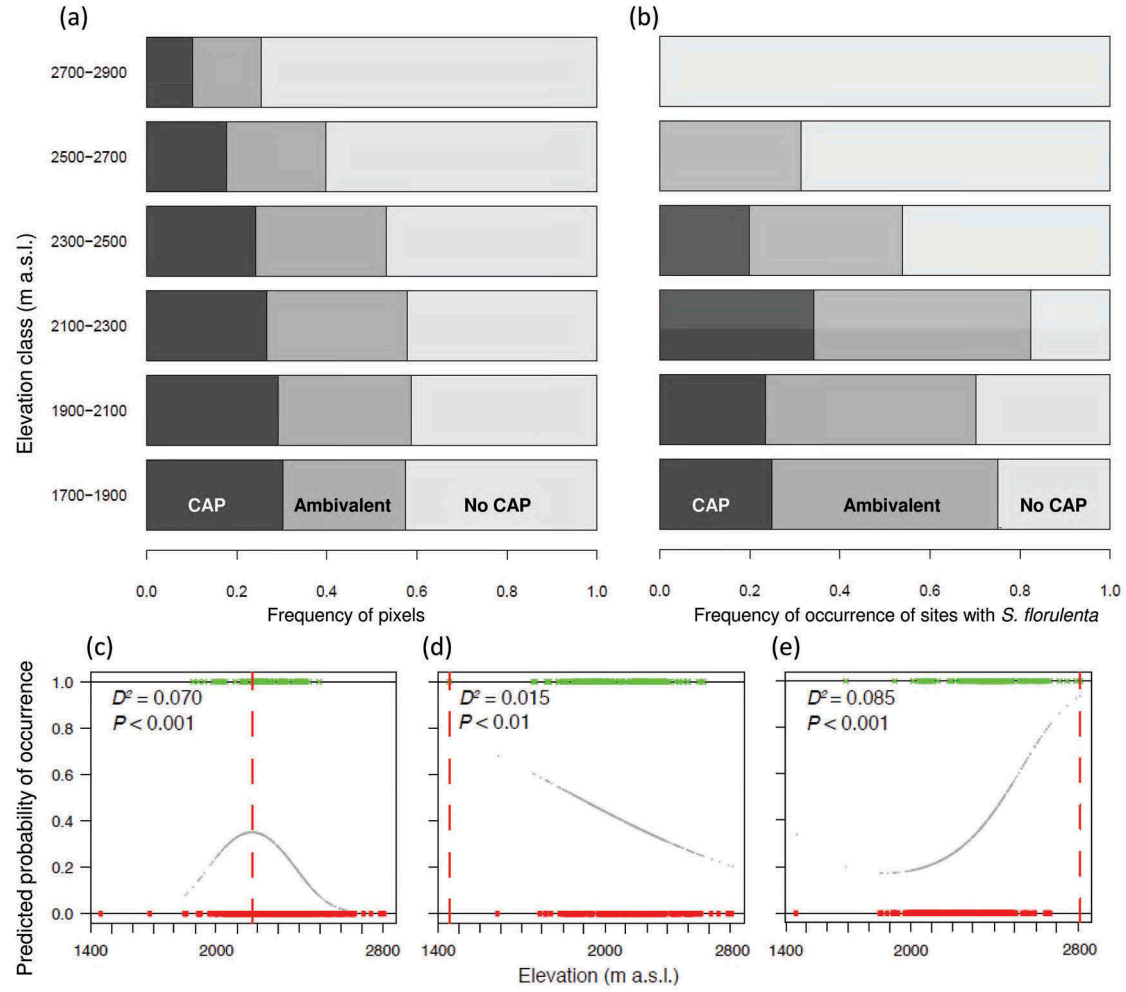


Figure 2. Relative frequency of elevation pixels classified as CAP, ‘ambivalent’ and no-CAP (a), the relative frequency of *S. florulenta* occurrences distributed in 25-m pixels classified as prone to cold air pooling (CAP), ‘ambivalent’ and not prone to cold air pooling no-CAP within elevation classes (b). Predicted probability of finding occurrences within a (CAP) (c), an ‘ambivalent’ (d) and a no-CAP cell (e) calibrated with GLMs; light green dots at the upper part of the graph represent occurrences whereas red dots at the bottom are pseudo-absences. The vertical red dashed line indicates the elevation corresponding to the highest probability of occurrence.

2300 m) compared to high elevations (i.e. above 2300 m; Figure 2b). In contrast, the frequency of no-CAP sites increased from low to high elevation. This was confirmed by GLMs showing that the probability of finding CAP and ‘ambivalent’ sites significantly increased at low elevation (Figure 2c; ANOVA: $P < 0.001$; $D^2 = 0.07$ and Figure 2d; ANOVA: $P < 0.01$; $D^2 = 0.015$), whereas it was the reverse pattern for no-CAP sites (Figure 2e; ANOVA: $P < 0.001$; $D^2 = 0.085$). We found that the distribution of *S. florulenta* occurrences in CAP classes (Figure 2b) was independent of the terrain (DEM pixels) distribution in CAP classes along elevation (Figure 2a).

SDM output with and without the CAP layer as a predictor

The inclusion of the CAP layer predicting variable in SDMs had a marginal but slightly negative effect on the predictive power of most of the modelling algorithms. Overall, the mean True Skills Statistics (TSS) among the

five modelling techniques was marginally reduced by 0.03 units when including the CAP layer except for GBM, which was decreased by 0.13 TSS units (Table 1). In contrast, the omission error (i.e. false-predicted absences) of all modelling techniques was reduced when the CAP layer was included, with the highest improvement observed for GAM, where the omission error was decreased from 67.7% to 53.8%. Most importantly, predictions by the two ensembles of SDMs (majority and consensus of techniques) were also improved when using the CAP layer as a variable: the omission error was reduced by 5.7% for the majority and by 14.6% for the consensus ensemble (Table 1 and Figure 3). The number of pixels predicted as potentially suitable when including the CAP layer comprised only 6% of the observed occurrences for the majority ensemble, but 21% of the occurrences for the consensus of techniques (Figure 3). The Pearson's Chi-squared test confirmed that the omission error differed significantly for the majority and consensus

Table 1. Species distribution models (SDMs) predictive performance with and without the cold air pooling (CAP) spatial layer as a predictor; omission error for each of the SDM techniques, the majority and consensus of the SDM ensembles.

SDM	Max TSS (i.e. true skill statistics)		Omission error rate (i.e. false-predicted absences)	
	Without CAP layer	With CAP layer	Without CAP layer	With CAP layer
GLM Modav	0.5	0.49	0.1	0.09
GLM StepW	0.52	0.48	0.11	0.09
GAM	0.48	0.45	0.68	0.54
GBM	0.5	0.37	0.83	0.1
ME	0.48	0.5	0.14	0.12
RF	0.38	0.41	0	0
Mean TSS	0.57	0.54	Majority	0.19
			Consensus	0.71
Pearson's Chi-squared test for count data			Majority	$\chi^2 = 216.2$, P -value < 0.01
(P -values by Monte Carlo simulation: 2000 replicates)			Consensus	$\chi^2 = 90.93$, P -value < 0.01
Cochran–Mantel–Haenszel Chi-squared exact test for			Majority	CMH-S = 50, P -value < 0.01
count data, stratified by elevation classes				Max L estimate = 459.08
			Consensus	CMH-S = 171, P -value < 0.01
				Max L estimate = 11.56

ensembles with and without CAP (P -values < 0.01; Table 1) but also between elevational classes (Cochran–Mantel–Haenszel Chi-squared test; P -values < 0.01; Table 1). Finally, and in line with the increasing probability of finding occurrences in CAP at low elevation, the predictions of occurrences were improved (i.e. a reduction of the omission error rate). For the two ensembles of SDM techniques, the improvement was observed from the middle to the low elevational range (2500–1900 m a.s.l., respectively) of *S. florulenta* (Figure 4). This improvement at middle-to-lower elevation was higher in the ensemble based on the consensus of techniques than the one based on the majority modelling techniques (Figure 4). The Pearson's Chi-squared test showed that the omission differences were significant for elevations above 1900 m and below 2700 m a.s.l. for the majority ensemble (P -values < 0.01) with/without the CAP layer, but not below 1900 and above 2700 m a.s.l. (P -values = 0.2 and 1, respectively). For the consensus ensemble, the omission error differed significantly for all elevation classes above 1900 m a.s.l. (all P -values < 0.01), but not below 1900 m a.s.l. (P -value = 0.19).

Comparison of micro- vs. macroclimate temperature time series

Trends of the decomposed time series of temperature showed that four out of six sites had lower mean temperature measurements than macroclimate projections for the entire growing season (Figure 5a–c and e) or most of its duration (Figure 5d). Overall, the mean AUC of mean temperature at the macroscale and for all sites was 57.7 AUC units higher (hence, warmer) than the microscale and for four out of six sites. Those included all three CAP sites (Figure 5a, c and e) and two of the ‘ambivalent’ sites (Figure 5b and d). In contrast, minimum temperature measurements were overall higher than the macroclimate

projections by 25 AUC units and in particular for half of the sites (Figure 5d–f). The minimum temperatures of two CAP sites and one ‘ambivalent’ site were marginally lower or lower at the microscale (Figure 5c, e and b, respectively). Maximum temperature measurements were lower than macroclimate projections by 112.7 AUC units and for four out of six sites (Figure 5a, b, d and e). In addition, the dAUC showed a trend for linear regressions against elevation for first- (P -value < 0.01) and second-order polynomial (P -value < 0.01), but only for mean temperatures; for the minimum and maximum temperature variables, no trend was found (all P -values > 0.5; Table S3). Therefore, the amount of energy accumulated by the plant over the growing season at the microscale tends to be similar to the macroscale around 2500 m a.s.l. Above these elevations, the microclimate is warmer compared to the macroclimate. We observed that the sites with lower maximum temperature measurements compared to projections were also the sites with higher minimum temperatures and vice versa (Figure 5a–f). Overall, microclimate presented smaller oscillations during the growing season for all temperature variables compared to those of the macroclimate. The values of dAUC (i.e. the difference “AUC macro – AUC micro”) oscillated but, in general, decline with increasing elevation for all types of temperatures, with the maximum having the most variation compared to the mean and minimum (Figure 5g). Above an elevation of 2500 m a.s.l., the microclimate indicates a higher amount of energy accumulated by the plant compared to the macroclimate.

Biplots of mean daily microclimate temperatures as a function of the macroclimate showed that CAP and ‘ambivalent’ sites had similar mean R^2 values (i.e. 0.76 and 0.72, respectively; Figure 6 and Table S4). Mean R^2 for minimum temperature values for the CAP sites were also similar to the R^2 for minimum temperature for the ‘ambivalent’ sites (i.e. 0.73 and 0.71, respectively;

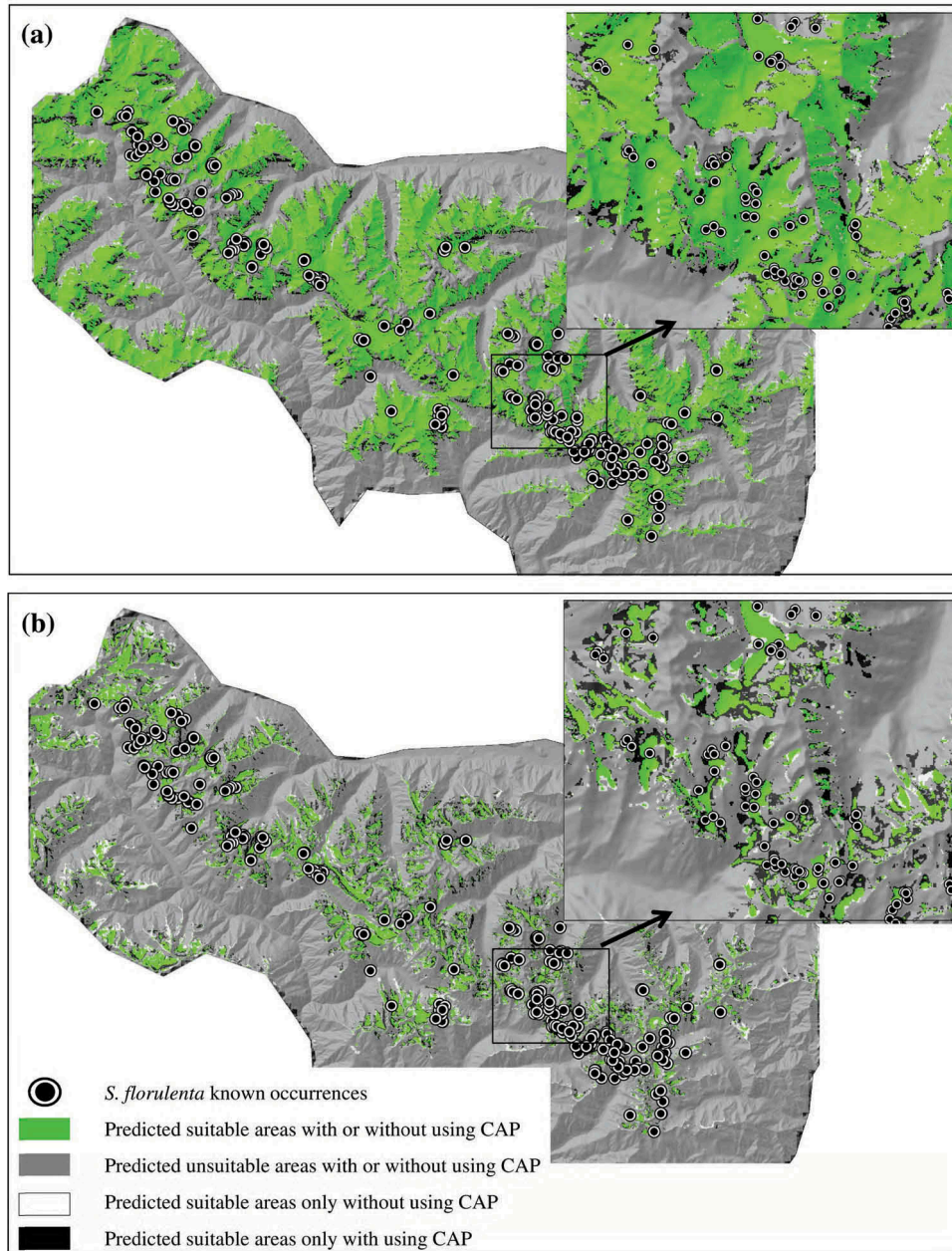


Figure 3. Spatial projections of the two ensembles of five species distribution modelling (SDM) techniques: (a) with the majority of SDM techniques (i.e. 4 out of 5) predicting 25-m cells as potentially suitable with and without the cold air pooling layer (*CAP* layer), (b) with the consensus of SDM techniques (i.e. 5 out of 5) predicting cells as suitable with and without the *CAP* layer. Potentially suitable cells of the majority ensembles both with and without the *CAP* layer (green; a) enclose 80% of the occurrences. Potentially suitable cells of the two full-consensus ensembles both with and without the *CAP* layer (green; b) include 23.2% of the occurrences. Areas predicted as suitable only when using the *CAP* layer (black) include 21% of the occurrences for the consensus and 6% for the majority ensemble. Areas predicted as suitable only when not using the *CAP* layer (white) include 6% of the occurrences for the consensus and only one occurrence only for the majority ensemble.

Figure 6 and Table S4). Maximum temperatures also showed almost no difference for mean R^2 , with ‘ambivalent’ sites mean $R^2 = 0.64$ and *CAP* sites mean $R^2 = 0.65$ (Figure 6 and Table S4). However, the highest elevation *CAP* site (Figure 6e) showed very low R^2 compared to any of the ‘ambivalent’ sites for mean, minimum and maximum temperatures (i.e. $R^2 = 0.38$, 0.37 and 0.24, respectively; but see Figure 6d). Overall, we observed no relationships between R^2 and elevation

for both linear first- and second-order regressions between micro- and macroclimate (Figure 6g and Table S3; all P -values > 0.5). A possible explanation could be that the low and mid-elevation *CAP* sites showed high R^2 , while the mid-elevation ‘ambivalent’ site showed a low R^2 compared to the low and high ‘ambivalent’ sites. Therefore, for *CAP* sites, R^2 declined along elevation, while for ‘ambivalent’ sites, it showed a decline for mid elevations.

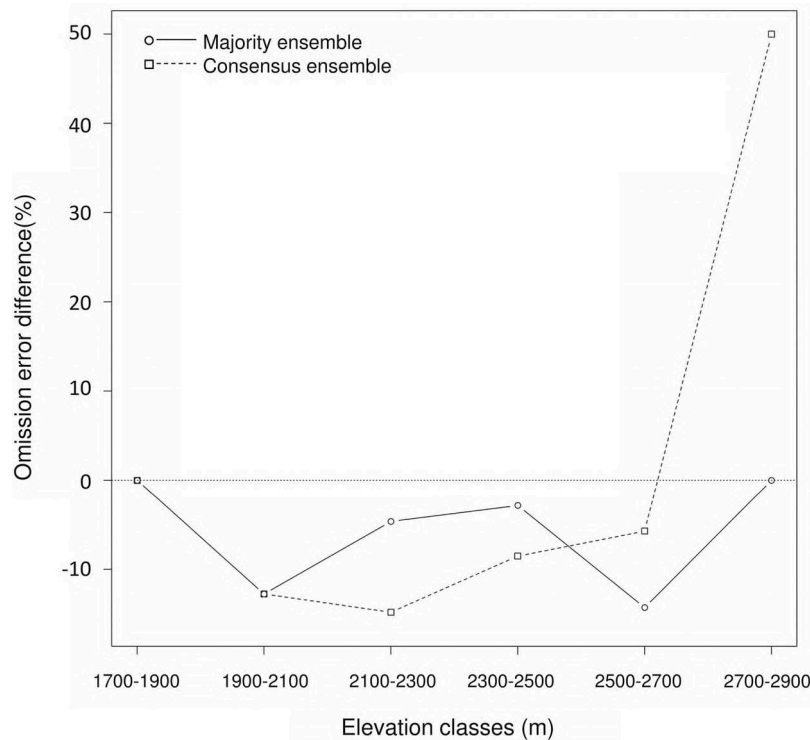


Figure 4. Difference in omission error between the ensembles with and without *CAP* layer as predicting variable for each elevation class. The Δ omission error rate was calculated as the difference between the frequency (%) of falsely predicted absences without the *CAP* layer and the frequency (%) of falsely predicted absences with the *CAP* layer, within an elevation class. A value <0 thus indicates a reduction of the omission error (%) when including the *CAP* layer.

Random events of the microclimate were, overall, less variable than those of the macroclimate projections for mean temperatures (Figure S3). For minimum temperatures, extreme random events were overall less variant compared with those at the macroscale and regardless of *CAP* classification [Figure S4; but see (a)]. For maximum temperatures, extreme random events of the microclimate were less variable for most sites compared to those of macroclimate (Figure S5b–e; but see 5a and f). The microclimate for the night-time periods showed very similar trends among all sites (Figure S6), as well as the random events for all sites (Figure S7) indicating stable conditions at the microscale with lower variances, particularly at the *CAP* sites.

Discussion

Our study demonstrated that *CAP*, a candidate mechanism explaining the persistence of plants within microrefugia (Dobrowski 2011), could have contributed to the distribution of and formation of microhabitats for the rare and endemic alpine plant *S. florulenta*. Such a finding is significant, given that the Maritime Alps, where *S. florulenta* is found, is one of the main glacial refugia of European alpine taxa (Bennet et al. 1991; Tzedakis et al. 2013). We first demonstrated that the probability of finding populations of *S. florulenta* in *CAP* sites significantly increased,

mostly at the centre and at the trailing edge of the species distribution. However, we showed that the distribution of species occurrences in *CAP* classes along elevation was not linked to the frequency of the *CAP* classes' distribution of the mountain terrain where *CAP* was more prevalent at lower elevations (e.g. *S. florulenta* was found more frequently in *CAP* sites at mid-elevation, i.e. at 2100–2300 m a.s.l.). We showed that both the observed frequency and the modelled probabilities of identifying *CAP* and 'ambivalent' sites occupied by *S. florulenta* were higher at low elevation (but above 1900 m a.s.l.) compared to high elevation, while the frequency and probability of no-*CAP* sites increased from low to high elevation. The latter could both provide populations from low elevation and close to the tree line with temperatures lower and more stable than the surrounding regional climate, thus lessening competitive interaction with species from lower elevations (Dullinger et al. 2012; Pauli et al. 2012). *CAP* potential of the terrain could have an effect on the distribution of alpine plant species by modulating climate at the microscale. In particular, *CAP* at mid and low elevations could delay snowmelt (Lundquist and Flint 2006) and, combined with topographic shading, may favour snow-dependent species (Curtis et al. 2014) such as *S. florulenta* and other alpine plant species. Additionally, *CAP* can buffer the impacts of climate warming for cold-adapted plants in general despite seasonal

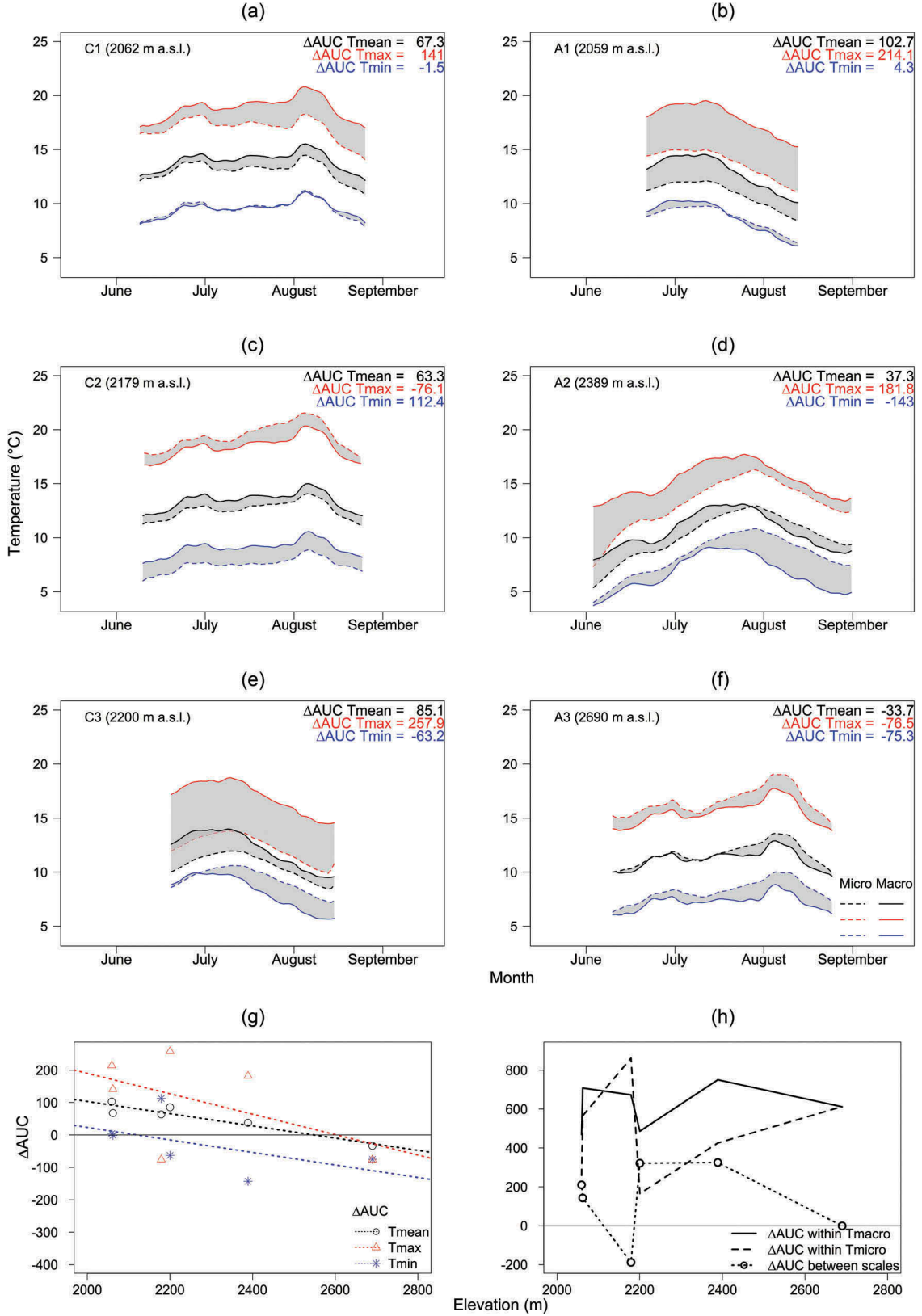


Figure 5. Trends of decomposed time series (i.e. without the seasonal trend and the random events) at the micro- and the macroscale for minimum, mean and maximum daily temperatures for each of the six sites with temperature logger. Area under the curve difference (dAUC) between trends at the two scales (i.e. macro–micro) is indicated for each and all sites in (g) along elevation. dAUC values above 0 indicate higher temperatures overall and more energy accumulated at the sites during the growing season predicted by the macroclimate. The period focuses on the snow-free days (temperature $\neq 0$) of the growing season (i.e. June–September; the tick marks at the x-axis correspond to the first day of each month). In sites, names C stands for *CAP* and A for ambivalent; the elevation of the sites is indicated in meters above sea level next to the site names). In (h) AUC difference between T_{\max} and T_{\min} within scales as a proxy for temperature amplitudes; the comparison of amplitudes between scales was made using the difference of the within scales dAUC (dAUC between scales).*

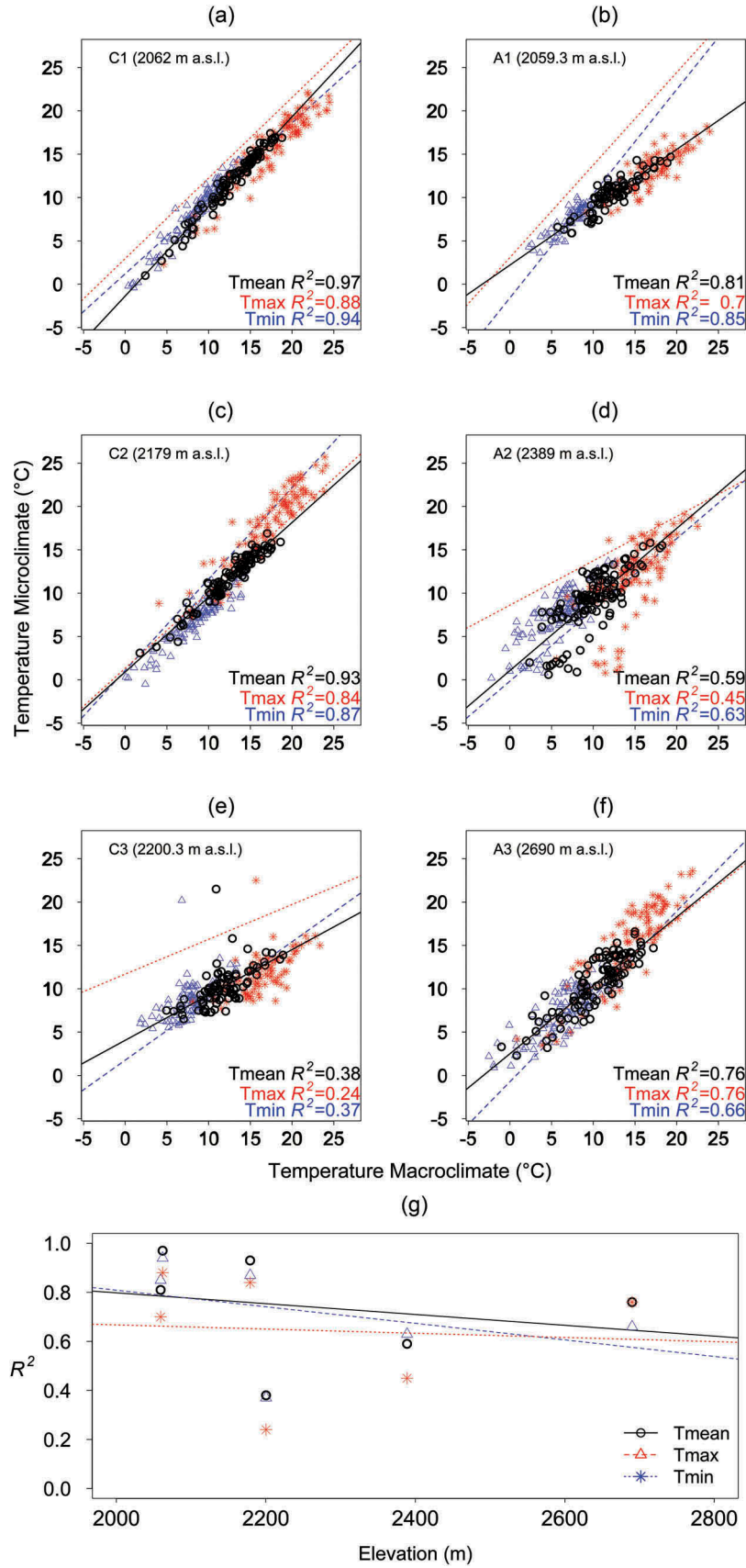


Figure 6. Linear regression of the microclimate as a function of the macroclimate for mean, maximum and minimum temperature (a–f) and R^2 of the linear models as a function of elevation (g). The period focuses on the snow-free days (temperature $\neq 0$) of the growing season (i.e. June–September; in sites, names C stands for *CAP* and A for ambivalent; the elevation of the sites is indicated in meters above sea level next to the site names).

temperature increases, while *CAP*-affected areas may be sources of water for the surrounding areas during periods of drought in summer.

However, we found that *S. florulenta* did not occur in *CAP* sites at high elevations (i.e. above 2500 m) even though such sites are present, although in low frequency. A likely explanation could be that such alpine species as *S. florulenta* are usually more exposed to strong abiotic and biotic factors at the leading and trailing edge of their distribution, respectively (Normand et al. 2009). In particular, at the leading edge of an alpine species distribution, *CAP* may not be needed to compensate for high temperatures, as temperatures above 2500 m in the Alps are already low. On the other hand, the dominant, limiting biotic factor of such alpine plant species distribution at low elevation, may be competition with other species. However, the effect of competition could be alleviated, to a certain extent, by topography and *CAP* given the fact that *CAP* is confounded with nutrients and water abundance. This parameter is of particular importance to take into account when making projections under climate change to avoid spurious correlations of species distribution with, for instance, water-based environmental factors such as water balance and evapotranspiration. Therefore, the effects of both biotic interactions and abiotic factors specific to a given terrain should be integrated into SDMs (Austin and Van Niel 2011a, 2011b; De Frenne et al. 2014; Harwood et al. 2014). As a result, it will be possible to predict more accurately the trailing edge of a species and especially for alpine plants potentially threatened by higher stature species at their lower distribution.

In line with these results, including *CAP* as a predictor variable in SDMs decreased their omission error rates, mostly at the low- and mid-elevation range of the distribution of *S. florulenta*. Simultaneously, SDMs still predicted absences where occurrences were recorded at low elevations and the trailing edge (between 1700 and 1900 m a.s.l.) of the distribution of *S. florulenta*. Likely explanations for this latter result could be the low number of occurrences (five) at the lowest elevational class or the unaccounted impact of biotic interactions on the distribution of the species. However, this result could also be interpreted as a failure of SDMs to represent topo-climatic features at a 25-m spatial resolution properly. Future studies should investigate the improvement in the accuracy of SDM when working with higher resolution predicting variables or with variables derived from GIS remote sensing (Lassueur et al. 2006; Scherrer and Körner 2010; Scherrer et al. 2011; Pradervand et al. 2014; van Ewijk et al. 2014; but see Leempoel et al. 2011). The model performance based on TSS was marginally lower for GLM and GAM and lower for GBM using *CAP* as a predictor. Taking into account that TSS is a prevalence-independent metric and that the omission error was decreased, the lower performance of the algorithms above in our models could be attributed to lower specificity with *CAP* (i.e. the probability that the model will correctly classify an absence; Allouche

et al. 2006). However, the latter could be mitigated by better projections as a result of the decrease of the omission error. Focusing further on GBM, the regularisation terms of the model could have been set higher. For instance, shrinkage was 0.01 but could have been set to 0.001 for better performance, however, with significantly higher computation time (Friedman 2001).

By comparing microclimatic measurements to commonly used climate projections of temperature, we could show that *CAP* and ‘ambivalent’ sites were consistently decoupled from the regional climate, with a similar mean but less extreme temperatures. We could overall show narrower amplitudes of microclimate measurements compared to projections. Additionally, we found less variable random and extreme low or high-temperature events in the time series of the minimum and maximum temperatures at the microscale compared to the macroclimate. This latter result confirmed *S. florulenta* individuals experience more stable conditions in their microhabitats. Nevertheless, our results also demonstrated that there is not always an obvious linear relationship between micro- and macroclimate, with microclimate being decoupled and hard to predict from macroclimate in most cases, in particular at high elevation. Therefore, the challenge of accurately predicting microclimate from macroclimate should be addressed in future studies, especially for extreme temperatures, which create a source of error in SDMs. Thus, more physiologically meaningful climate data based on extremes and variability (e.g. Zimmermann et al. 2009; Reyer et al. 2013; Kollas et al. 2014) and the use of extreme temperature data as proxies are needed to better explain the range limits of alpine plants.

Conversely, at two of the three *CAP* sites, a linear model showed that the microclimate could be well predicted from the macroclimate ($T_{\text{mean}} R^2 > 0.9$), with the microclimate being on average slightly colder than the macroclimate. A likely explanation is that at each site, predicted macroclimate was affected by the distance from the nearest weather station and whether both were recorded at the same *CAP* class. For example, site C1 is surrounded by three to four meteorological stations in *CAP* sites and only one in no-*CAP* sites, and therefore, its predicted macroclimate was more similar to the *CAP* stations. Conversely, for site C3, there is only one weather station in proximity, in an ‘ambivalent’ site. Hence, although site C3 is located in *CAP*, its predicted macroclimate is more similar to the ‘ambivalent’ pattern of the nearest station. Our study thus suggests that increasing the density of the weather stations above 2000 m should be encouraged in European countries possessing regions in the Alps (see also Kollas et al. 2014) and highlights the need to infer the effects of *CAP* at finer geographic scales to better derive climate-based predicting variables for SDMs. This strategy could potentially overcome the low density of temperature records available.

As discussed above, extremely low temperatures, in addition to high-temperature events, can be buffered for alpine plants at the microscale. On the one hand, this suggests that habitats at the microscale could be a type of microrefugium providing conditions that might help alpine species to

overcome heat stress under current climate change. On the other hand, it additionally suggests that such specialist alpine plants survive in habitats which also allow them to avoid extremely low temperatures and ensure that tissues remain protected from freezing events, particularly during the growing season (Körner 2003). These results have important implications for the validity of future projections of alpine plant distributions in a warming climate and could be an element for a functional explanation of microrefugia. With our study, we confirm that some specialised alpine plants have already shown a preference for sites that buffer extreme temperatures at the low-elevation range. Such habitat selection can potentially alleviate the short-term effects of extremely high temperature. Thus, plants living in such specialised habitats may not need to immediately migrate to new favourable habitats under ongoing climate change, as has also been shown for forest species living below the canopy (De Frenne et al. 2014). Our results also support our previous study showing that *S. florulenta*, as well as other alpine species, may have persisted past climate change in microrefugia with very specific climate conditions (Patsiou et al. 2014).

Our results confirmed our hypothesis that *CAP* could be a candidate-persistence mechanism for our study species, particularly at mid- and low elevations, because of its buffering effects on warming temperature. In addition, *CAP*, when used as a predictor, can improve, to some extent, SDM projections by reducing their omission error. Finally, we also confirmed our hypothesis that daily mean and extreme microclimate is decoupled from the local climate (sensu Peterson Anderson et al. 2011), explaining how *S. florulenta* or other cold-adapted alpine plant species could have persisted under past climate oscillations.

Conclusions

Our study underlines the role of topography and its effect on the distribution of alpine plants, for it controls the microclimate they experience. It further emphasises that strong differences in temperature across geographic scales in mountain regions are not only elevation related but also generated by topography. Most importantly, to our knowledge, we quantified for the first time the temperature differences between proximal measurements and projections at population sites of an alpine plant in a region of topo-climatic microrefugia. We could thus provide a mechanistic explanation of such microrefugia by taking the effect of *CAP* into account. Our results corroborate several recent studies (Pearson 2006; Daly et al. 2009; Mosblech et al. 2011; Scherrer et al. 2011; Ashcroft et al. 2012; Curtis et al. 2014; Patsiou et al. 2014). Hence, we suggest that alpine plants may be less exposed to extremely high temperatures in the future than predicted by studies based on macroclimate only. Therefore, we propose that spatial climatic layers used for SDMs in alpine ecosystems should better represent microclimatic variations by integrating more proximal measurements and mechanisms, including *CAP*.

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Disclosure statement

No potential conflict of interest was reported by the authors.

Supplemental data

Supplemental data for this article can be accessed [here](#).

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Digital elevation models

France: IGN (Institut National de l'Information Géographique et Forestière; <http://www.ign.fr/>).

Italy: Area SITAD (Sistemi Informativi Territoriali Ambientale Diffuso – Negozio cartografico; <http://www.csipiemonte.it>).