



Assessing alpine plant vulnerability to climate change: a modeling perspective

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The potential ecological impact of ongoing climate change has been much discussed. High mountain ecosystems were identified early on as potentially very sensitive areas. Scenarios of upward species movement and vegetation shift are commonly discussed in the literature. Mountains being characteristically conic in shape, impact scenarios usually assume that a smaller surface area will be available as species move up. However, as the frequency distribution of additional physiographic factors (e.g., slope angle) changes with increasing elevation (e.g., with few gentle slopes available at higher elevation), species migrating upslope may encounter increasingly unsuitable conditions. As a result, many species could suffer severe reduction of their habitat surface, which could in turn affect patterns of biodiversity. In this paper, results from static plant distribution modeling are used to derive climate change impact scenarios in a high mountain environment. Models are adjusted with presence/absence of species. Environmental predictors used are: annual mean air temperature, slope, indices of topographic position, geology, rock cover, modeled permafrost and several indices of solar radiation and snow cover duration. Potential Habitat Distribution maps were drawn for 62 higher plant species, from which three separate climate change impact scenarios were derived. These scenarios show a great range of response, depending on the species and the degree of warming. Alpine species would be at greatest risk of local extinction, whereas species with a large elevation range would run the lowest risk. Limitations of the models and scenarios are further discussed.

Keywords: climate change, ecological impact assessment, alpine and subalpine belts, plant distribution, statistical modeling, local scale, GIS, GLM, Swiss Alps

1. Introduction

State of the art

The potential ecological impact of ongoing climate change has been much discussed in recent years. High mountain ecosystems were identified early on as potentially very sensitive areas (see, e.g. [1–4]). Scenarios of upward species – plant or animal – migration and vegetation shifts are commonly discussed in the literature (e.g. [5]; see [6] for a review). Expansion of species range upward was recently evidenced by Grabherr and co-workers [7] for many species (mainly low-stature vegetation) in the Eastern Alps. Mountains being characteristically conic in shape, impact scenarios usually assume that smaller surface area will be available as species move up [5,8]. However, as the frequency distribution of additional physiographic factors (e.g., slope angle) changes with increasing elevation (with, e.g., fewer gentle slopes available at higher elevation), upslope migrating species will encounter increasingly unsuitable conditions [6]. As a result, many species could suffer a severe surface reduction of their preferred habitats, which might in turn affect patterns of biodiversity. One approach for quantifying these changes is to model the distribution of species from environmental predictors in a GIS, and assess the changes in suitable habitats by modifying the climatic parameters in the model (e.g. [8,9]). This approach is sta-

tic (in the sense of [10,11]), i.e., it avoids the temporal dimension, and is the opposite of more dynamic, mechanistic models of plant succession (see, e.g. [8] for a comparison), as applied for instance, in the context of climate change, to tree species in the Alps [8,12]. Dynamic models allow one to cope with problems of succession and other biotic interactions. Static models intrinsically incorporate the influence of competition, through fitting realized (ecological) species response to environmental predictors, although such interactions can hardly be modified in these models, e.g., if competition relationships are expected to change in a climatically changed future. But they can provide quick spatially-explicit evaluations of climate change impact on the distribution of species and on diversity over very large spatial scales [8,11].

1.1. Aims of the study

The objectives of this study were:

- (1) to fit a series of models for predicting the spatial occurrence of a great number of herbaceous plant species in the alpine and upper subalpine belts;
- (2) to derive climate change impact scenarios by changing the climatic parameters in the models;
- (3) to discuss the scenarios on the basis of (i) the selected predictors, (ii) certain features of alpine environment

and (iii) other ecological insights not taken into accounts by the models (i.e., limitations).

The presence/absence models presented in this paper have been improved in several respects over previous work (see [13] for ordinal abundance models, [8] for binomial presence/absence models; see also [14]): (i) they include new predictors (color infrared aerial photographs, snow index 1997, topographic position); (ii) the method for adjusting the models was simplified; (iii) presence/absence models were fitted for 62 species (see appendix) occurring in more than 15 calibration plots; this study thus covers a much greater number of species; (iv) climate change impact scenarios were derived from each of these models, thus providing a broader overview of possible responses.

2. Methods

2.1. Study area

The study area of Belalp is a wide, open, north-south oriented side valley of the Rhone valley, located in the Aletschregion (Valais, Switzerland; figure 1). Elevation ranges from 1867 to 3554 m. Geology is mainly made of siliceous rocks (gneiss, granite). The climate is of a sub-continental type. Soils are mainly of a podzolic type at the subalpine and low alpine belts. The upper subalpine vegetation is mainly dominated by mesophilous heaths, swards, and fens. The alpine vegetation belt, ranging from 2300 to 3000 m, is dominated by low heaths, swards, and snowbed communities. The landscape has been modified by human activity for centuries through intensive grazing by cattle, sheep, and goats, the main effect being the lowering of the timberline by several hundred meters. At present, grazing is extensive.

2.2. Sampling biotic variables

The two species data sets used for calibrating and evaluating the model (figure 1) are the same as described in [13]. Calibration plots ($N = 205$) were sampled following a grid sampling scheme, i.e., all intersection points of a $250 \text{ m} \times 250 \text{ m}$ grid overlaying the whole study area. At this sampling distance, autocorrelation is avoided (see [14]), which ensures that significance tests for selecting predictors remain [15,16]. Evaluation plots ($N = 92$), all distinct from the calibration plots, were later on sampled randomly on a $25 \text{ m} \times 25 \text{ m}$ grid overlaying the study area.

Each point of known coordinates was localized in the field by means of a GPS navigator, a map accurate to a scale of 1 : 10 000 and a Thommen altimeter. At each point, an exhaustive list of observed plant species was made on a 4 m^2 plot. The 4 m^2 size was chosen because: (i) it ensures that, within the micromosaic pattern of alpine vegetation, only one plant community type is sampled in each plot, therefore minimizing environmental heterogeneity, (ii) it is

usually large enough to sample significantly the diversity of most alpine plant communities, i.e., their actual species pool, (iii) it should be large enough to minimize year-to-year species turnover in alpine grasslands, (iv) it allows enough plots to be sampled over the whole study area, and thus (v) it allows the sampling of most plant community types in the study area. Taxonomic nomenclature for plant species names follows the Swiss standards by Aeschmann and Heitz [17].

2.3. Environmental predictors for modeling alpine plant distribution

Important variables for modeling plant distribution in an alpine landscape are (see [18] for a review; see also [13, 14]): (i) temperature (e.g., cold night temperatures limiting growth), (ii) winter precipitation (determining snow cover), (iii) solar radiation (determining the rate of photosynthesis), (iv) slope (influencing radiation, gravitational processes, microclimate, snow cover), (v) topography (i.e., spatial variation of the relief, which determines wind, microclimate, snow cover), (vi) geology (determining plant development), (vii) microclimate (influencing plant development), (viii) snow cover (determining the growth period), (ix) geomorphology (as, e.g., rock outcrops, mobile or stabilised screes, cliffs), (x) hydrography (proximity of mountain streams, fens, springs), (xi) periglacial phenomena (permafrost, gelifluction, cryoturbation), and (xii) natural disturbances (e.g., avalanches) or (xiii) human-induced (e.g., grazing) disturbances.

Making seasonal or day/night variation in temperature spatially-explicit is a difficult task and one can usually only express temperature features through mean annual temperature or, more often, through elevation as a surrogate. Snow cover can be extracted from aerial photographs and solar radiation can be calculated from a digital elevation model (Kienast, unpublished). Both are physiologically important for high altitude plants, through respectively influencing photosynthesis and the duration of the vegetation growth period. Permafrost has a modifying influence on vegetation because frozen ground affects soil stability and the temperature of the soil within the zone of root growth [19]. Soil parameters are difficult to include in a static model because most soil types result from a combination of the underlying substrate, climate and the influence of physiographic factors (e.g., slope angle). Also because vegetation influences soil as much as soil has an effect on vegetation. Moreover, modeling soil distribution in an alpine environment would first require that the typology of alpine soils is sufficiently understood and secondly that enough soil profiles have been sampled throughout the study area, which is rarely the case.

In our study, environmental descriptors – hereafter called the *predictors* – used to model the distribution of species were: (i) obtained from existing vector maps (geology, rocky cover, hydrology), (ii) calculated from the digital elevation model (DEM) covering the study area, or (iii) derived from

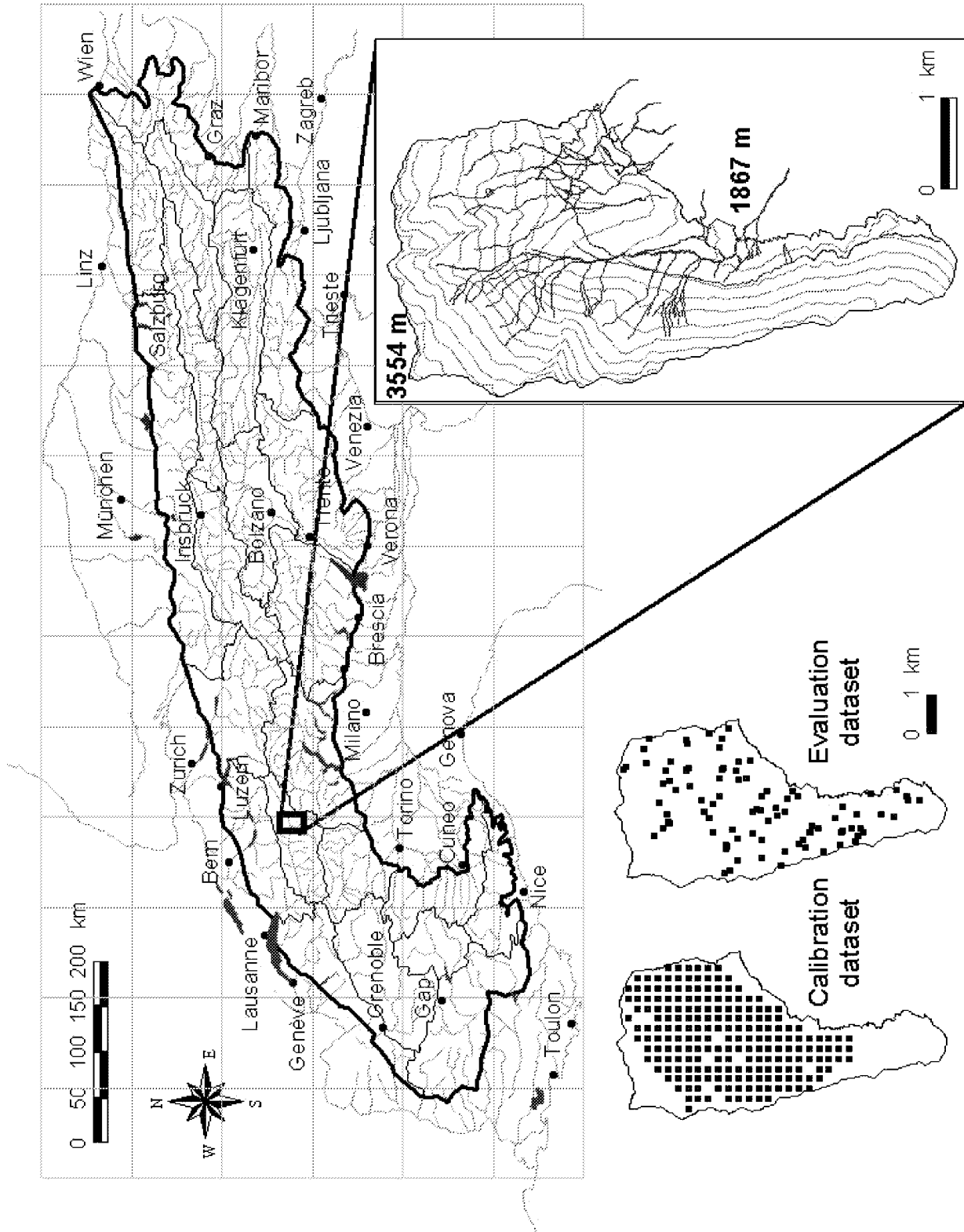


Figure 1. Location of the study area in Switzerland (above Brig, Valais), spatial distribution of sampling points and illustration of a field relevé and measurements.

black and white and color infrared aerial photographs (remote sensing). They are summarized below (see also [13]):

- *amt*: annual mean temperature was used as a better expression of the elevation gradient, as (i) the adiabatic lapse rates do not vary with latitude and distance to the sea, thus allowing a model comparison with other areas at different elevations but similar *amt* values; (ii) it can be modified directly in the models to derive climate change scenarios. It was calculated from elevation using a transition formula calibrated from field measurements during the vegetation period (see [13]);
- *slo*: slope angle was derived from the DEM in the GIS;
- *nness* and *eness*: slope aspect was transformed into two continuous linear gradients, respectively, north–south, called northness (*nness*); and east–west, called eastness (*eness*);
- *tp100*, *tp250*, *tp500*, and *tp1000*: four indices of topographic positions, representing a gradient from ridge top to middle slope to valley were calculated at different scale (moving windows' radii set respectively to 100, 250, 500, and 1000 meters; see [20] for details on their calculation);
- *rad1* and *rad2*: two indices of solar radiation were obtained from running a principal component analysis (PCA) on 19 individual daily solar radiation calculation; the two indices are the first two PCA axes, explaining, respectively, 90 and 9% of the total variance [13]; thus, they are fully independent;
- *cir1*, *cir2*, and *cir3*: the three bands of a color infrared (CIR) aerial photograph taken at the beginning of August 1997 (raw spectral data);
- *snowi96* and *snowi97*: two different indices of snow cover duration were obtained by summing up the standardized spectral values of aerial photographs taken at regular interval in time, two photographs during the year 1996 (*snowi96*) and four during the year 1997 (*snowi97*);
- *perm*: the distribution of potential permafrost was modeled with the PERMAKART model ([21]);
- *rock1*, *rock2*, and *rock3*: rocky cover; respectively, open vegetation with rocks (usually meadows with isolated, but numerous, rocks), rock outcrops and screes;
- *geol0*, *geol1*, *geol2*, and *geol3*: the three geological classes – respectively amphiboles, historical moraines and moraine of Würm – of importance for the vegetation in the study area; pixels without any of these categories correspond to gneiss or granite.

All predictors were standardized prior to fitting the models.

2.4. Plant distribution modeling

Generalized linear models (GLM; [22,23]; see also [13, 20,24] for various applications in ecology) were used to predict the distribution of species. GLMs with a binomial distribution and a logistic link function were fitted from presence–absence data for each species.

A series of exploratory GLMs were first run to assess the importance of the various predictors to reduce the null deviance. A final model was then fitted, which included only those environmental predictors explaining a significant proportion of the deviance (Chi-test with p value <0.05) and which coefficient was simultaneously significantly different from zero (t -test with p value <0.05). Details on the method used to fit all species models can be found in [8,13,14,25]. Overall, 62 presence/absence models were fitted, for the species occurring in at least 15 calibration plots.

Models were evaluated using the independent data set, by comparing observed to predicted values with an appropriate measure of agreement. Cohen's Kappa [26] (see also [27]) was used to evaluate binary predictions, cut into binary 0/1 values using a calibrated species-specific threshold (as used by [20]). For each species, the threshold providing the best Kappa at the calibration was then used to evaluate the quality of model prediction made on the evaluation data set. This measure provides agreement on a scale from 0 to 1, with 1 being a perfect agreement and 0 no agreement at all. Kappa, although sometimes criticized for some of its undesirable properties (as, e.g., attributing the same weight to omission and commission errors or being sensitive to prevalence) proved useful in our case for comparing the 62 presence–absence models (see [25]). However, as often discussed in the literature, it should preferably not be used alone to evaluate model prediction when a single species is in focus in a conservation management context. In the latter case, it should preferably be used as a complement to other measures of prediction errors such as the omission/commission error rates and, more ideally, the AUC measure (ROC Plot methodology [28]).

2.5. Climate change scenarios

The climate change scenarios which we used in this study are based on a rise in annual mean temperature of, respectively, 1.5, 3, and 4.5 K. We used these simple hypothetical values because:

- (1) using these three scenarios of temperature warming – low, moderate and high – provides a large range of possible responses in terms of species' habitat suitability and shows how these might differ, for any given species, depending on the intensity of the climatic change;
- (2) improved impact scenarios can easily be derived in the future from the present models, once more accurate local climate change scenarios are available for our study area (possibly including differential predictions of change for, e.g., north- versus south-oriented slopes).

Hence, the present assessment aims mainly at providing a range of possible changes which could be expected in the distribution of plant species, following a significant change in climatic parameters. It is thus to be considered as a sensitive study providing a provisional view. Our exploratory results should nevertheless prove useful for environmental managers and decision makers, who need to make up their

minds about the potential ecological changes which can be expected from ongoing atmospheric changes.

3. Results

3.1. Model results

The percentage of variance explained by the various GLMs range from less than 10 to more than 65% for the 62 most frequent species in the study area (see [25] for more details). In the following, we provide only an overview of the environmental predictors most frequently selected in the models. As a reminder, the selection of a predictor in a model does not necessarily imply an ecologically meaningful cause–effect relationship, and thus, the models should be interpreted with caution.

Over the 62 presence/absence species' models, the predictor most often selected and usually explaining the greatest amount of deviance was annual mean temperature (*amt*, in 59 models out of 62, hereafter written 59/62; in most cases, linear + quadratic terms). The second predictor retained was topographic position calculated with a moving window radii of 100 m (*tp100*, 24/62), followed very closely by the second index of radiation (*rad2*; 21/62), slope angle (*slo*; 19/62), the snow cover index of 1997 (*snowi97*; 19/62), the first index of radiation (*rad1*; 18/62), the snow cover index of 1996 (*snowi96*; 18/62) and the topographic position with radius 1000 m (*tp1000*; 17/62). The second and third bands of the color infrared aerial photograph came next (*cir2* and *cir3*; both selected in 9/62 models). All remaining predictors were selected in less than 8 out of 62 models.

Evaluating the models revealed a diversity of model quality, with values of Kappa ranging from 0.16 to 0.84 when calculated on the calibration data set, and from 0 to 0.62 when calculated on the evaluation data set.

3.2. Change in plant species distribution

The result of running the models, assuming a rise in temperature of, respectively, 1.5, 3, and 4.5 K together with associated changes in the distribution of permafrost, are summarized in tables 1 and 2, and in the appendix.

Table 1 provides an overview of changes in predicted occurrence of the 62 modeled species, once the predictions have been cut into binary 0/1 values using the calibrated species-specific threshold (figures 2(a) and 3(a)). According to the three warming scenarios of 1.5, 3.0, and 4.5 K increases in annual mean temperature, 1.6, 1.6, and 4.8%, respectively, of the modeled species would become extinct in the study area, 61.3, 67.7, and 67.7% would undergo a reduction of their present potential habitats relatively to their present potential distribution, whereas 29, 22.6, and 19.4% would be favored. Only 8.1% would keep similar surfaces (no change) over all scenarios. The trend here is that the number of favored species decreases with increasing change in temperature and, inversely, that the number of species

Table 1

Overall change in predicted occurrence, relatively to the present potential distribution, resulting from the three warming scenarios. The first four categories represent the possible situations that a species might face (total by column is always 62). The last row provides the number of species in each scenario which potential habitat would decrease of more than ninety percent. Thus, it is a complementary view to the categories of decreasing occurrence and extinct in the study area. Unit for the values in the table is in number of species (100% = 62 species).

	1.5 K	3 K	4.5 K
Occurrence increases	18 (29.0%)	14 (22.6%)	12 (19.4%)
No change	5 (8.1%)	5 (8.1%)	5 (8.1%)
Occurrence decreases	38 (61.9%)	42 (67.7%)	42 (67.7%)
Extinct in the study area	1 (1.6%)	1 (1.6%)	3 (4.8%)
Percent decrease >90%	2 (3.2%)	11 (17.7%)	24 (38.7%)

Table 2

Predicted trends in the distribution of species habitat between the lowest and the highest climate change scenarios.^a

CC1 1.5 K	CC2 3 K	CC3 4.5 K	Total # species	A	S-A	M-S	M-A
↑	↑	↑	12	2	3	4	3
↑	↑	↓	2	0	0	1	1
↑	↓	↓	3	1	2	0	0
↑	≡	↓	1	0	0	0	1
≡	≡	≡	3	0	2	0	1
↓	≡	↓	1	0	1	0	0
↓	↓	≡	1	0	1	0	0
≡	↓	↓	2	0	0	2	0
↓	↓	↓	34	7	24	2	1
↓	↓	†	2	1	1	0	0
†	†	†	1	1	0	0	0
Total			62	12	34	9	7

^a Explanation of signs: ↑ = increase, ↓ = decrease, ≡ = no change, † = extinct in the study area, # = number. Elevation categories: A = alpine species, S-A = subalpine to alpine, M-S = montane to subalpine, M-A = montane to alpine. See appendix to see the attribution of an elevation category to each species.

negatively affected increases. In particular, the percentage of plants showing a decrease of more than 90% of their extent increases continuously with temperature (respectively, of 3.2, 17.7, and 38.7%; see last row in table 1).

Table 2 provides a more detailed overview of such trends in the predicted distribution of potential habitats of the 62 modeled species when they are divided in altitudinal categories. Detailed trends for each species are additionally documented in the appendix table, as well as in figures 4 and 6. Figure 4 shows, for each species, the proportion of change to be expected, from the present proportion of occurrence of the species in the study area, under each of the three climate change scenarios. Figure 5 provides a complementary view to figure 4, by documenting, for each species, the amount of pixels (i.e., the modeling unit) which will be classified as (1) loss of suitable habitat, (2) habitat remaining

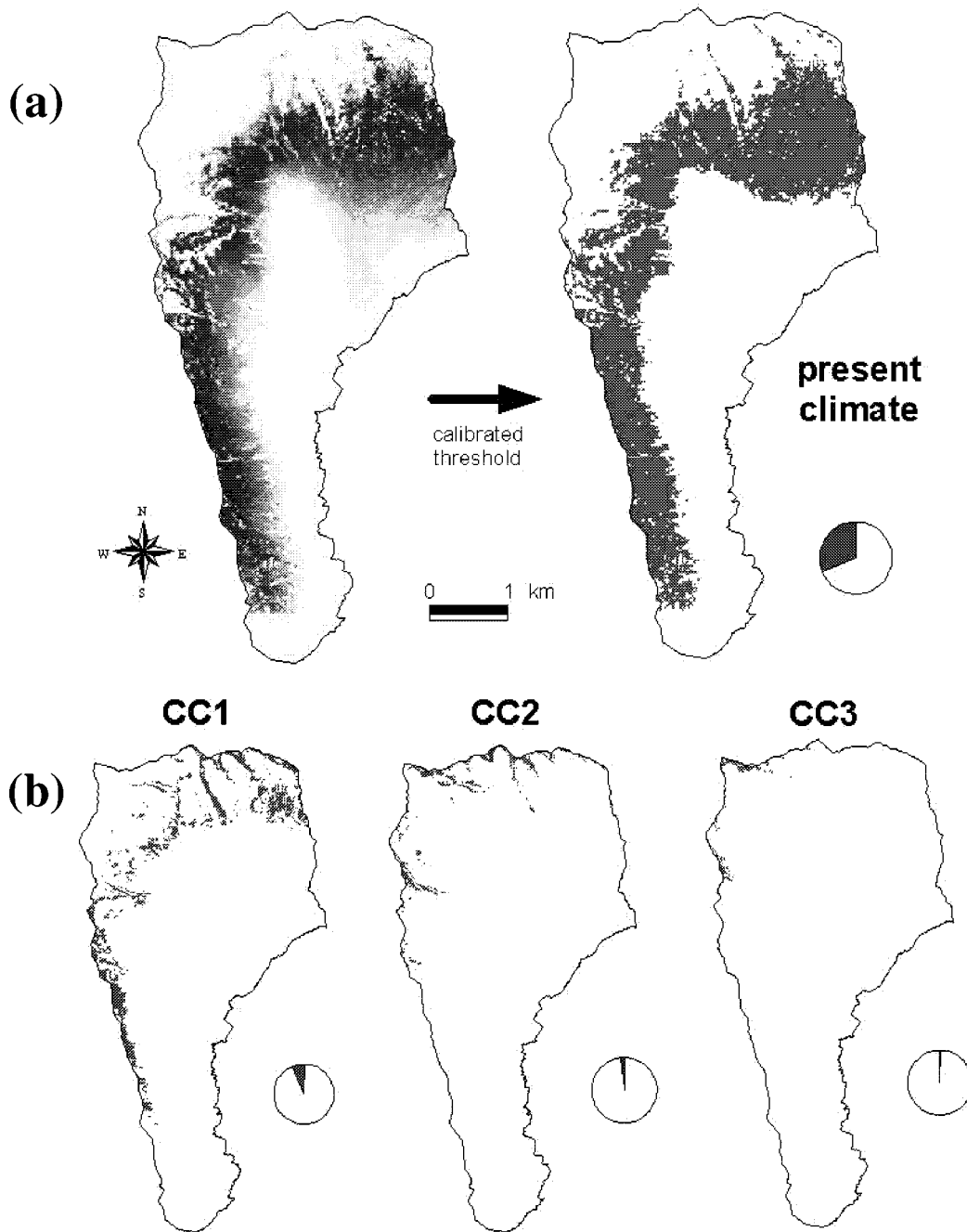
Ligusticum mutellina

Figure 2. Distribution of potentially suitable habitats for the alpine Apiaceae species *Ligusticum mutellina* under (a) present climate and (b) future climates. First map in (a) shows the probabilistic predictions by the model. Using a species-specific calibrated threshold, these probabilities are cut back into a binary yes/no (0/1) map showing suitable versus unsuitable habitats. The same threshold optimized from the calibration data set is then used to evaluate the model predictions on the independent evaluation data set. Overall, this species would lose important areas of suitable habitats under all scenarios of climate change.

unsuitable (negative status-quo), (3) gain of suitable habitat and (4) habitat remaining suitable (positive status-quo), as illustrated in figure 6 for the alpine legume species *Trifolium alpinum* over the study area. Figure 2 illustrates the change in the distribution of a species regressing but not disappearing in the highest scenario (*Ligusticum mutellina*) and

figure 3 illustrates the change in the distribution of a species increasing its potential habitat (*Calluna vulgaris*).

With the lowest scenario already (CC1, table 1), the models show that the distribution of potential habitat of 38 species may decrease in relation to their present situation. In the three scenarios (CC1, CC2, CC3), the poten-

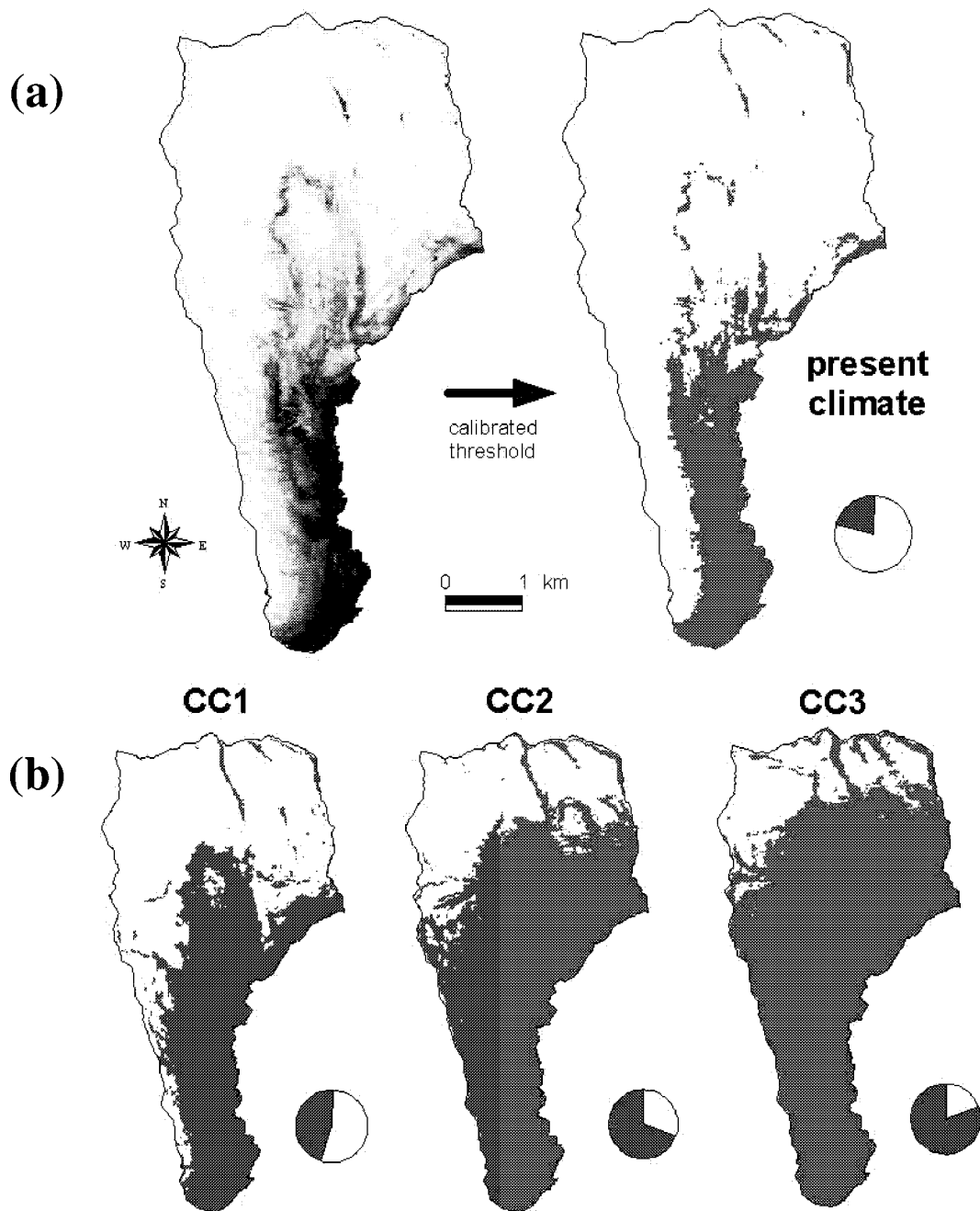
Calluna vulgaris

Figure 3. Distribution of potentially suitable habitats for hosting the heath species *Calluna vulgaris* (Ericaceae) under (a) present climate and (b) future climates. See legend of figure 2 for the explanation of maps. Overall, this species would gain surfaces of suitable habitats under all scenarios of climate change.

tial habitat of two species (*Veronica alpina*, *Viola calcarata*) may more or less regularly decrease until disappearing in the highest scenario, whereas 34 other species, like *Ligusticum mutellina* (figure 2) and *Trifolium alpinum* (figure 6), might continuously decrease but not disappear (table 2; see also the appendix). One species (*Cerastium pedunculatum*) might become extinct in the study area since the lowest scenario already.

For 10 species, the predictions do not show a regular decrease or increase of their potential habitats (table 2). *Luzula multiflora* and *Potentilla erecta* might extend their present potential habitat in the lowest and moderate scenarios, but then decreased it in the highest scenario. *Campanula barbata*, *Luzula alpino-pilosa*, and *L. spicata* subsp. *mutabilis* may benefit a little increase of their potential habitat with a low warming, and then clearly lose habitats with the medium

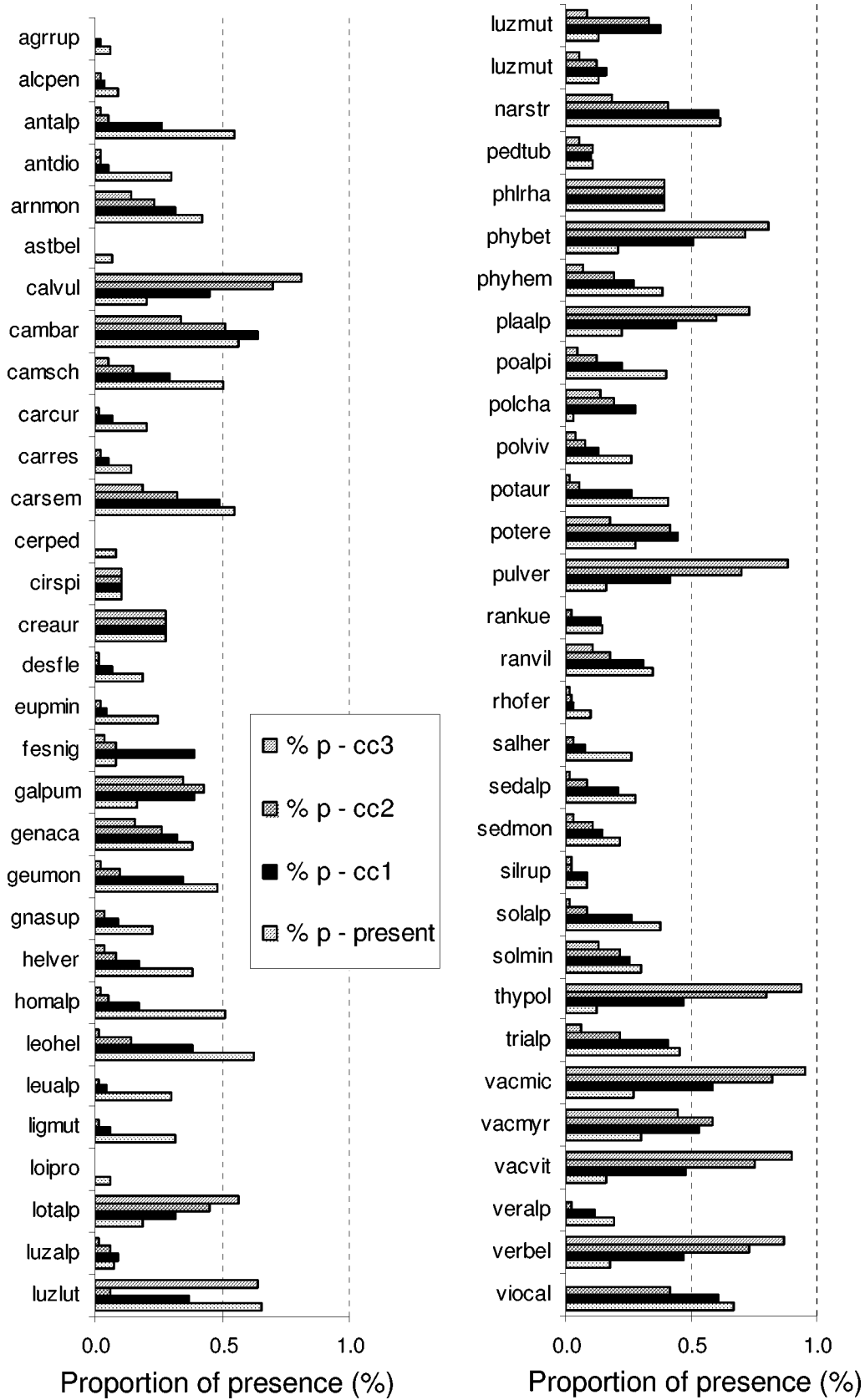


Figure 4. Histograms, for all modeled species, of the percentages of pixels with suitable habitat predicted by the model, under (i) present climatic conditions and after (ii) a 1.5 K (CC1), (iii) a 3 K (CC2) and (iv) a 4.5 K (CC3) warming, respectively. Very low percentage values may not clearly appear on the graph (compare it with the values in the appendix table). Species are listed alphabetically (see also the appendix for the acronyms).

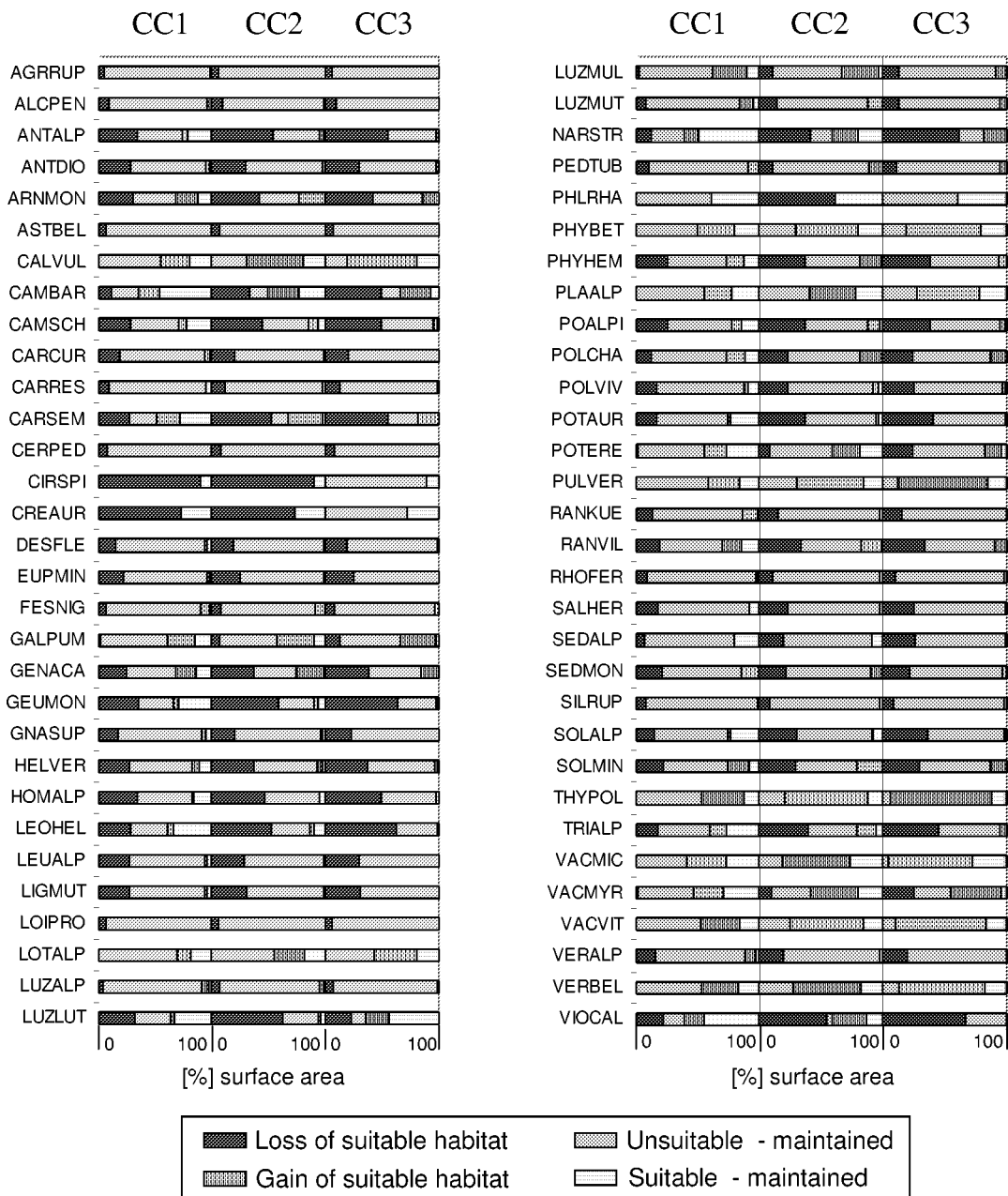


Figure 5. Histograms, for each species, of the percentage of pixels belonging to the following four categories (see legend in the graph) of possible environmental situations, as provoked by, respectively, a 1.5 (CC1), a 3 (CC2), and a 4.5 K (CC3) annual mean temperature warming: (i) loss of suitable habitat, (ii) unsuitable habitat maintained, (iii) gain of suitable habitat and (iv) suitable habitat maintained. Very low percentage values may not clearly appear on the graph (compare it with the appendix). Species are listed alphabetically (see the appendix for the acronyms.)

or highest warming, whereas *Festuca nigrescens* might first benefit a low climate change, but regress to its present extent in the second scenario and finally lose surfaces of potential habitat in the highest scenario. In contrast, *Luzula lutea* would lose considerable surface of suitable habitat according to the low and medium scenarios, but would recover, under the highest warming scenario, an extent of suitable habitat similar to its present distribution. *Nardus stricta* and *Silene rupestris* may see no change at first and then similarly lose habitats. Finally, one species, *Pedicularis tuberosa*, may lose habitat in the lowest scenario, then recover it in the medium scenario, and loose it again in the highest.

Amongst the winners, twelve species may gain new surfaces of potential habitats under all scenarios: *Calluna vulgaris* (figure 3), *Galium pumilum*, *Lotus alpinus*, *Phyteuma betonicifolium*, *Plantago alpina*, *Polygala chamaebuxus*, *Pulsatilla vernalis*, *Thymus praecox* subsp. *polytrichus*, *Vaccinium uliginosum* subsp. *microphyllum*, *V. myrtillus*, *V. vitis-idea*, and *Veronica bellidioides*. Only three species would not see any variation in the extent of their potential habitat: *Crepis aurea*, *Phleum alpinum* subsp. *rhaeticum*, and *Cirsium spinosissimum* (neither *amt* nor *perm* is included in their models).

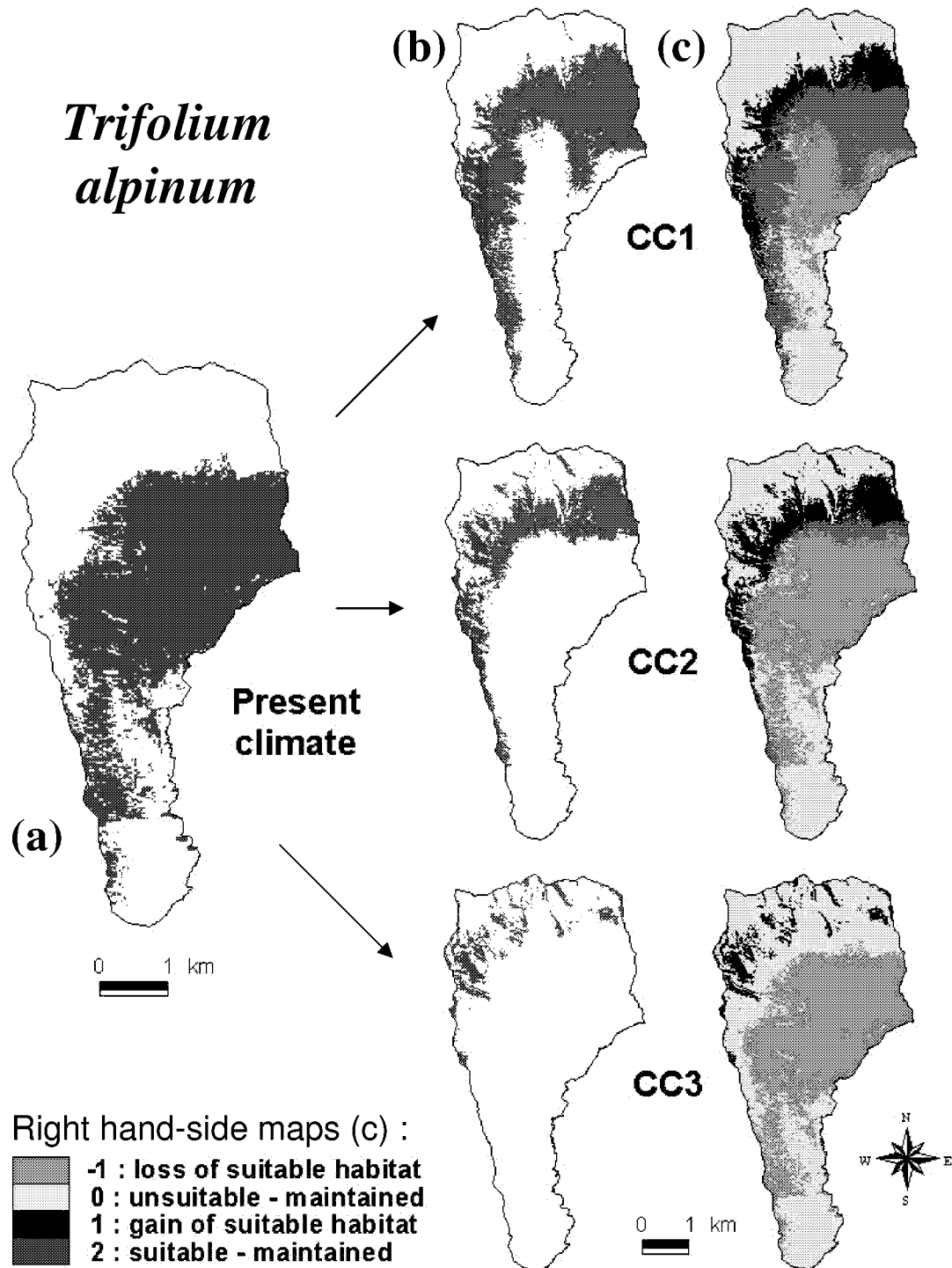


Figure 6. Distribution of the potentially suitable habitats for hosting *Trifolium alpinum* (Fabaceae) under (a) present climate and (b) future climates. Maps in (c) are drawn from combining each climate change map (b) with present distribution (a) to show areas where (i) loss of suitable habitat might occur, (ii) no change would occur, habitat should remain unsuitable for the species, (iii) gain of suitable habitat might occur and (iv) no change would occur, habitat should remain suitable for the species.

4. Discussion

The best models (i.e., those with higher fit and evaluation kappa) were generally obtained for dominant, clonal species such as *Rhododendron ferrugineum*, *Vaccinium myrtillus*, *Carex curvula*, *Nardus stricta*, or *Trifolium alpinum*. The worst models were usually obtained for non-dominant

species with too few occurrences throughout the calibration and, especially, the evaluation data sets (e.g., *Cerastium pedunculatum*, *Veronica bellidioides*), or which have no clear ecological requirements like *Cirsium spinosissimum*, *Luzula alpino-pilosa*, *Ranunculus kuepferi*, or *Sempervivum montanum*.

According to general predictions on climate warming's ecological impact, alpine species should be at higher risk of local extinction than subalpine species or species distributed down to lower elevations, as the latter have a wider elevation tolerance and thus a lower risk of local extinction. Our results support this hypothesis, with most of the subalpine and alpine species showing a decrease in the extent of their suitable habitats.

Model predictions for the twelve truly alpine species (see table 2 and appendix) suggest that one of them (*Cerastium pedunculatum*) would disappear since the lowest scenario, another one (*Veronica alpina*) would eventually disappear with the highest warming scenario, and eight of them would lose habitat (*Alchemilla pentaphyllea*, *Carex curvula*, *Gnaphalium supinum*, *Leucantheropsis alpina*, *Ranunculus kuepferi*, *Salix herbacea*, *Luzula alpino-pilosa*, and *Phyteuma hemisphaericum*). Except for *Ranunculus kuepferi* which is poorly modeled, scenarios for the other species are plausible. Indeed, when one considers the whole country, physiographic predictors are shown to be unequally distributed with elevation [6], with much fewer gentle slopes being available at higher elevations. As the species concerned occur mainly in snow beds at their lowest distribution, we hypothesize that alpine and nival species may only persist on the edge of habitats colonizable by plants at the highest elevations. They would probably suffer the most from any warming, be it only slight, as there is no possible escape for them upwards.

Although model predictions suggest that two alpine species (*Lotus alpinus* and *Veronica bellidioides*) may gain new surfaces of suitable habitat, the interpretation of these results should be treated with caution, as: (i) these models had only a very poor evaluation and (ii) *L. alpinus* might have been subject to false taxonomic identification, as it is known to intermingles at its lower range with its closest relative *L. corniculatus*, which replaces it completely at lower elevation. Therefore, this model may realistically be a mixture of both species' ecological requirements.

Models for the 34 subalpine-alpine species (see table 2 and appendix) predict that most of them (24) would increasingly lose habitat as warming increase, and one species (*Viola calcarata*) might even disappear under the highest scenario. The predictions may however be exaggerated for some of these species, due to intrinsic limitations in the model parameterization (see below). *Cirsium spinosissimum* and *Crepis aurea* may maintain an area of suitable habitat similar to their present extent. *Luzula lutea* would first lose habitat, but would then recover similar surfaces of suitable habitats, and *Phyteuma betonicifolium*, *Plantago alpina*, and *Vaccinium uliginosum* subsp. *microphyllum* might considerably increase their potential habitat. Predictions for *P. alpina*, a plant occurring mainly in secondary pastures of the upper subalpine and in swards, may be realistic only if present grazing is maintained at a constant rate. In contrast, an extension of *V. uliginosum* subsp. *microphyllum* may only occur if the rate of grazing decreases.

Finally, model predictions for the nine montane to sub-alpine (M-S) species and for the seven species with a larger elevation range (montane to alpine, M-A; see table 2 and appendix), show that these two categories of species may generally be favored by an increasing warming. Seven species would significantly increase their potential extent as compared to their present distribution (*Calluna vulgaris*, *Galium pumilum*, *Polygala chamaebuxus*, *Pulsatilla vernalis*, *Thymus praecox* subsp. *polytrichus*, *Vaccinium myrtillus*, and *V. vitis-idaea*). One species (*Phleum alpinum* subsp. *rhaeticum*) might maintain an extent similar to its present one; three species might benefit from a low to medium warming, but would lose suitable habitat under the highest scenario (*Festuca nigrescens*, *Luzula multiflora*, and *Potentilla erecta*); three species might experience a decrease of their potential habitat in all scenarios (*Aster bellidiastrum*, *Deschampsia flexuosa*, and *Rhododendron ferrugineum*), and two species (*Nardus stricta* and *Silene rupestris*) would certainly do so in the highest scenarios. No species from these two groups would be subject to disappearance. However, the scenarios are probably too pessimistic for *Silene rupestris*, a species growing on shallow, rocky soils, and for *Aster bellidiastrum*, a species linked to neutrophilous-basiphilous fens, as the presence of these species is more likely to depend on edaphic factors than on climate.

However, several limitations, inherent to this modeling approach, call for caution when interpreting the proposed scenarios:

- (1) What is truly modeled here is the probable distribution of potentially suitable habitats for a species, as noticed by d'Oleire-Oltmanns and co-authors [29]. The predicted distribution should not be taken as the real distribution of the species concerned.
- (2) Taxonomic misidentification of species might occur when two species are closely related, with the existence of introgressive individuals, as for instance between *Lotus alpinus* and *L. corniculatus*, or if the species habitus looks very similar when sterile individuals are in concern, e.g., between the two grasses *Agrostis schraderiana* and *Anthoxanthum alpinum*.
- (3) Such a modeling approach does not yet allow to incorporate rules of biotic interactions explicitly (e.g., competition, parasitism, and mycorrhiza), although they may play a key role in the response of organisms to climate change [4,30–32].
- (4) No change in snow cover distribution resulting from climatic change was taken into account in our models, due to the fact that this climatic parameter was obtained directly from spectral information rather than modeled.
- (5) Species might encounter some limitations when migrating upward, because their seed dispersal abilities are limited or because natural or anthropogenic barriers to migration prevent their doing so.

- (6) This approach does not account for the possible inertia that ecological systems might express when facing an abrupt change of their environment (i.e., the final equilibrium is modeled). For instance, clonal plants forming heaths and swards are likely to be able to resist invading species [33], e.g., alpenrose heaths, or they may persist, e.g., *Carex curvula* [34], at least under a low scenario. In addition, a slow evolution of soil may also allow vegetation to resist colonization, e.g., some alpine meadows on brown soil might prevent invasion by heath species.
- (7) The study was performed above the (anthropogenic) forest limit and, thus, the models cannot correctly predict the potential habitat of species which might persist in a forest understorey (as they are presently found). For instance, models predict a decrease of the *Rhododendron ferrugineum* (alpenrose) or *Homogyne alpina* both of which occur at lower elevations and therefore may not disappear from their present habitat. Yet, the models correctly predict the potential habitats above the forest line, e.g., the distribution of alpenrose heaths.
- (8) Our study included only a limited portion of the full elevation gradient (ranging in Switzerland from less than 200 up to more than 4600 m). As a consequence: (1) the response of some species to elevation can be truncated, and appear linear whereas it should be unimodal, which can have an impact on the final scenarios, and (2) the distribution of potentially invasive species from lower elevations could not be modeled and taken into account in the scenarios.
- (9) The 25 m-resolution digital elevation model used in this study is certainly too coarse to take into account the fine topography and the associated variation in snow cover. Knowing the importance of microtopography for plant distribution in the alpine belt, we could expect that a finer elevation model would also greatly increase the precision in modeling the potential habitat of species.

Bearing these limitations in mind, one can nevertheless consider potential habitat maps (PHM) as a serious basis for further ecological assessments and impact studies, but not as accurate predictions of real species distributions (point 1 above). By providing a visual prognostic of suitable habitat reduction or of expansion of species – or, as a particular case, of species diversity or plant communities (see [23]) – they should help identify the most dramatic trends that

can be expected, such as the predicted disappearance of all suitable habitats for a species. In the latter case, a species might well be able to persist in certain locations, less affected by climate change, but its survival in the long-term would become seriously jeopardized, especially in the case of small, fragmented populations (as reproduction might, for instance, be affected). However, this would probably not be the case for most alpine species if the highest warming scenario should occur, and special consideration should be accorded to the future distribution patterns of these species.

In the future, we recommend including more physiologically meaningful environmental predictors in static distribution models, in order to make them more causal and to render derived climate change scenarios more realistic and interpretable. With this in mind, an effort should be made to obtain better predictors, especially in the field of remotely sensed information applied to model snow cover duration and soil moisture in alpine environments. We also encourage the development of similar studies as the present one, but extended to the entire elevation gradient in Switzerland. Finally, one way to integrate positive or negative species interactions might be to develop systems of simultaneous regression equations, as proposed in [11,14], where each response variable would also be included as predictors in all other equations.

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Appendix

Table A

Liste of modeled species with their acronym, elevation category and response to each scenario of warming.^a

Abreviation	Species name	Groupe	CC1	CC2	CC3
agrup	<i>Agrostis rupestris</i>	S-A	–	–	–
alcpn	<i>Alchemilla pentaphyllea</i>	A	–	–	–
antalp	<i>Anthoxanthum alpinum</i>	S-A	–	–	–
antdio	<i>Antennaria dioica</i>	S-A	–	–	–
arnmont	<i>Arnica montana</i>	S-A	–	–	–
astbel	<i>Aster bellidiastrum</i>	M-A	–	–	–

Table A
(Continued.)

Abreviation	Species name	Groupe	CC1	CC2	CC3
calvul	<i>Calluna vulgaris</i>	M-A	+	+	+
cambar	<i>Campanula barbata</i>	S-A	+	–	–
camsch	<i>Campanula scheuchzeri</i>	S-A	–	–	–
carcur	<i>Carex curvula</i>	A	–	–	–
carres	<i>Cardamine resedifolia</i>	S-A	–	–	–
carsem	<i>Carex sempervirens</i>	S-A	–	–	–
cerped	<i>Cerastium pedunculatum</i>	A	Ex	Ex	Ex
cirspi	<i>Cirsium spinosissimum</i>	S-A	nc	nc	nc
creaur	<i>Crepis aurea</i>	S-A	nc	nc	nc
desfle	<i>Deschampsia flexuosa</i>	M-S	–	–	–
eupmin	<i>Euphrasia minima</i>	S-A	–	–	–
fesnig	<i>Festuca nigrescens</i>	M-A	+	nc	–
galpum	<i>Galium pumilum</i>	M-S	+	+	+
genaca	<i>Gentiana acaulis</i>	S-A	–	–	–
geumon	<i>Geum montanum</i>	S-A	–	–	–
gnasup	<i>Gnaphalium supinum</i>	A	–	–	–
helver	<i>Helictotrichon versicolor</i>	S-A	–	–	–
homalp	<i>Homogyne alpina</i>	S-A	–	–	–
leohel	<i>Leontodon helveticus</i>	S-A	–	–	–
leualp	<i>Leucanthemopsis alpina</i>	A	–	–	–
ligmut	<i>Ligusticum mutellina</i>	S-A	–	–	–
loipro	<i>Loiseleuria procumbens</i>	S-A	–	–	–
lotalp	<i>Lotus alpinus</i>	A	+	+	+
luzalp	<i>Luzula alpino-pilosa</i>	A	+	–	–
luzlut	<i>Luzula lutea</i>	S-A	–	–	nc
luzmul	<i>Luzula multiflora</i>	M-A	+	+	–
luzmut	<i>Luzula spicata subsp. mutabilis</i>	S-A	+	–	–
narstr	<i>Nardus stricta</i>	M-S	nc	–	–
pedtub	<i>Pedicularis tuberosa</i>	S-A	–	nc	–
phlrha	<i>Phleum alpinum subsp. rhaeticum</i>	M-A	nc	nc	nc
phyhem	<i>Phyteuma hemisphaericum</i>	A	–	–	–
phytbet	<i>Phyteuma betonicifolium</i>	S-A	+	+	+
plaalp	<i>Plantago alpina</i>	S-A	+	+	+
poalpi	<i>Poa alpina</i>	S-A	–	–	–
polcha	<i>Polygala chamaebuxus</i>	M-S	+	+	+
polviv	<i>Polygonum viviparum</i>	S-A	–	–	–
potaur	<i>Potentilla aurea</i>	S-A	–	–	–
potere	<i>Potentilla erecta</i>	M-S	+	+	–
pulver	<i>Pulsatilla vernalis</i>	M-S	+	+	+
rankue	<i>Ranunculus kuepferi</i>	A	–	–	–
ranvil	<i>Ranunculus villarsii</i>	S-A	–	–	–
rhofer	<i>Rhododendron ferrugineum</i>	M-S	–	–	–
salher	<i>Salix herbacea</i>	A	–	–	–
sedalp	<i>Sedum alpestre</i>	S-A	–	–	–
sedmon	<i>Sempervivum montanum</i>	S-A	–	–	–
silrup	<i>Silene rupestris</i>	M-S	nc	–	–
solalp	<i>Soldanella alpina</i>	S-A	–	–	–
solmin	<i>Solidago virgaurea subsp. minuta</i>	S-A	–	–	–
thympol	<i>Thymus praecox subsp. polytrichus</i>	M-A	+	+	+
trialp	<i>Trifolium alpinum</i>	S-A	–	–	–
vacmic	<i>Vaccinium uliginosum subsp. microphyllum</i>	S-A	+	+	+
vacmyr	<i>Vaccinium myrtillus</i>	M-S	+	+	+
vacvit	<i>Vaccinium vitis-idaea</i>	M-A	+	+	+
veralp	<i>Veronica alpina</i>	A	–	–	Ex
verbel	<i>Veronica bellidioides</i>	A	+	+	+
viocal	<i>Viola calcarata</i>	S-A	–	–	Ex

^a A = alpine, S-A = subalpine to alpine, M-S = montane to subalpine, M-A = montane to alpine.
+ = extension of present species habitat is increased, – = extension of present species habitat is decreased,
– – = extension of present species habitat is decreased of more than 90%, nc = no change, Ex = extinct in
the study area. CC1 = warming of 1.5 K, CC2 = warming of 3 K, CC3 = warming of 4.5 K.

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