



# Modelling the influence of change in fire regime on the local distribution of a Mediterranean pyrophytic plant species (*Cistus salviifolius*) at its northern range limit

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## ABSTRACT

**Aims** To assess the potential distribution of an obligate seeder and active pyrophyte, *Cistus salviifolius*, a vulnerable species in the Swiss Red List; to derive scenarios by changing the fire return interval; and to discuss the results from a conservation perspective. A more general aim is to assess the impact of fire as a natural factor influencing the vegetation of the southern slopes of the Alps.

**Location** Alps, southern Switzerland.

**Methods** Presence–absence data to fit the model were obtained from the most recent field mapping of *C. salviifolius*. The quantitative environmental predictors used in this study include topographic, climatic and disturbance (fire) predictors. Models were fitted by logistic regression and evaluated by jackknife and bootstrap approaches. Changes in fire regime were simulated by increasing the time–return interval of fire (simulating longer periods without fire). Two scenarios were considered: no fire in the past 15 years; or in the past 35 years.

**Results** Rock cover, slope, topographic position, potential evapotranspiration and time elapsed since the last fire were selected in the final model. The Nagelkerke  $R^2$  of the model for *C. salviifolius* was 0.57 and the Jackknife area under the curve evaluation was 0.89. The bootstrap evaluation revealed model robustness. By increasing the return interval of fire by either up to 15 years, or 35 years, the modelled *C. salviifolius* population declined by 30–40%, respectively.

**Main conclusions** Although fire plays a significant role, topography and rock cover appear to be the most important predictors, suggesting that the distribution of *C. salviifolius* in the southern Swiss Alps is closely related to the availability of supposedly competition-free sites, such as emerging bedrock, ridge locations or steep slopes. Fire is more likely to play a secondary role in allowing *C. salviifolius* to extend its occurrence temporarily, by increasing germination rates and reducing the competition from surrounding vegetation. To maintain a viable dormant seed bank for *C. salviifolius*, conservation managers should consider carrying out vegetation clearing and managing wild fire propagation to reduce competition and ensure sufficient recruitment for this species.

## Keywords

Endangered species, generalized linear model, habitat fragmentation, insubric ecosystems, pyrophilous species, southern Swiss Alps.

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## INTRODUCTION

Fire is one of the major disrupting factors that, in combination with other processes such as climate and land-use changes,

impact on the distribution and composition of vegetation. It thus affects or regulates the functioning of many ecosystems, directly or indirectly influencing plant growth, survival and reproduction and sometimes affecting the dynamics of seeds

and seedlings (Bond *et al.*, 2005). Postfire changes in both plant-species composition and vegetation structure have been studied in several shrubland and forest ecosystems of Europe. In particularly fire-prone regions, such as the Mediterranean area, many plants are fire-adapted (pyrophytes: Trabaud, 2000; Grove & Rackham, 2001). They depend on fire for reproduction or show enhanced flowering, seed germination and seedling recruitments after fire. Fire-recruiting, non-sprouter species are the most sensitive to changes in fire regime. If the time-return interval of fire increases, species the seed-banks of which tend to become exhausted after long intervals without fire show reductions in their population size and fragmented distributions (Holmes & Newton, 2004). In such conditions, the species are exposed to increasing fragmentation, and risk extinction due to stochastic events or the loss of the genetic variability typical of small, isolated populations (Begon *et al.*, 1999).

Tinner *et al.* (1999) suggest that southern Switzerland, including most of the southern slopes of the Alps, is a fire-prone area where fire must be considered an environmental factor that has shaped the vegetation since the Neolithic Age. Many species dramatically decreased following the impact of anthropogenic fires, particularly in the Bronze and Iron Ages (e.g. *Abies alba*, *Fraxinus excelsior*, *Tilia cordata*). Such local extinctions tend to be linked to selective and competition processes, which usually lead progressively to the strong dominance of a few fire-adapted species (e.g. *Pteridium aquilinum*, *Molinia arundinacea*, *Corylus avellana*). In this region, the general outcome appears to be a long-term decrease in species diversity (Delarze *et al.*, 1992; Tinner *et al.*, 2000).

The obligate seeder and 'active pyrophyte' (Naveh, 1974) sageleaf rockrose, *Cistus salviifolius* L., can be seen as representing a typical case. *Cistus salviifolius* is a Eumediterranean plant distributed across the whole Mediterranean area in Europe, from sea level to 1200 m in the Alpes Maritimes (France). It occupies local environmental niches on the southern slopes of the Alps, especially in the lake region of northern Italy and southern Switzerland (Greco, 1997). This pyrophilous pioneer does not appear to be endangered in the fire-prone Mediterranean area, while it shows great vulnerability at the northern edge of its distribution areas on the southern slopes of the Alps, where fires occur irregularly in space and time.

Since the first systematic survey in the early 1990s of the distribution of *C. salviifolius* in southern Switzerland (Ceschi, 1995), the species has continuously regressed, as highlighted by the surveys repeated in 1997 (Greco, 1997), and the following surveys in 1999 and 2002 (G. Greco, unpub. data). In Switzerland, it is therefore listed on the Red List as vulnerable (Moser *et al.*, 2002). During the same decades, fire frequency and the mean burnt area have decreased dramatically in southern Switzerland due to improvements in the organization of fire fighting and to stricter laws (e.g. prohibition of bonfires for burning garden debris). However, whether the fragmentation of the populations of *C. salviifolius* is linked directly to these changes in the fire regime still needs to be tested. What

the consequences of these changes will be for the distribution of this vulnerable pyrophyte species is also unclear.

Here we examine the effects of changes in the fire regime in southern Switzerland on the distribution of small populations of pyrophilous species, using *C. salviifolius* as a model organism. Studies of species that occur naturally in small and fragmented populations on the margins of their distribution area may be more promising in this context, since such species may reveal adaptations that have important implications for the management and conservation of endangered species living under similar conditions.

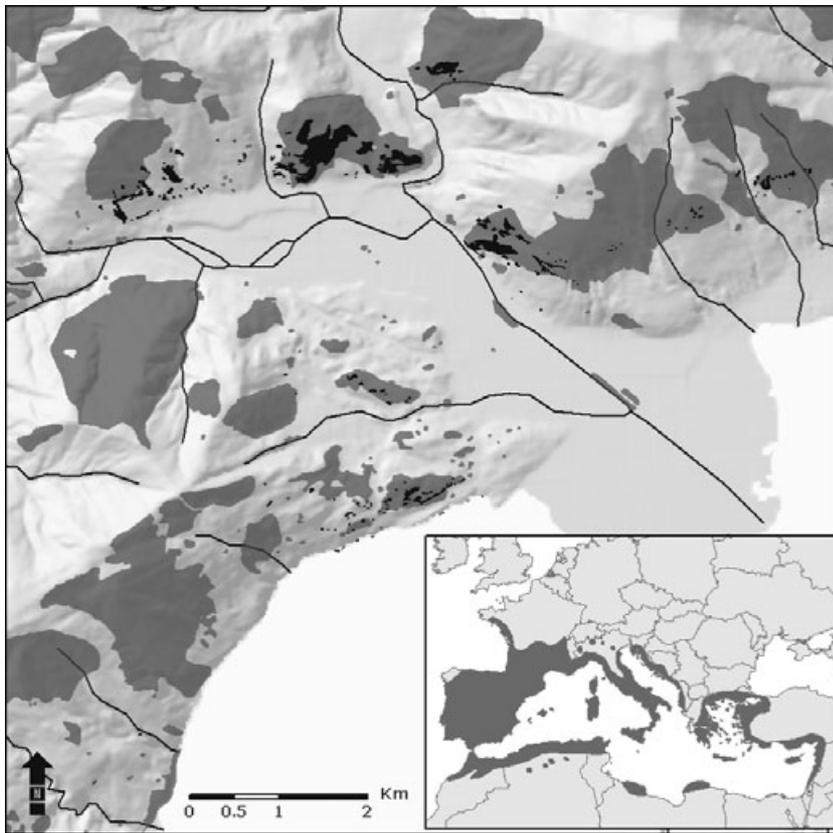
Modelling the distribution of plant and animal species has recently become popular in ecology (Elith, 2000; Guisan & Zimmermann, 2000; Thuiller *et al.*, 2003; Segurado & Araújo, 2004), and is increasingly used for tackling conservation issues (Vaughan & Ormerod, 2003; Guisan & Thuiller, 2005), such as promoting the conservation of rare plants (Dirnbock *et al.*, 2003; Engler *et al.*, 2004; Guisan *et al.*, 2006; Lavergne *et al.*, 2005). In the case of modelling the distribution of *C. salviifolius* in southern Switzerland, a related question is whether fire should be considered a proximal variable as defined by Austin (2002) or if, due to the suboptimal condition of the species at the margin of its area of distribution, other factors (e.g. lack of competitors, extreme climates, etc.) override the role of fire. To address this issue, we tested the following two hypotheses: 1. the distribution of *C. salviifolius* on the southern slopes of the Swiss Alps correlates with the burnt areas – fire is the major factor influencing changes in the occurrence of the species, and 2. the distribution of *C. salviifolius* on the southern slopes of the Swiss Alps is largely in sites that are permanently tree-free; fire plays only a secondary role, by allowing *C. salviifolius* temporarily to extend its occurrence in burnt tree-free spots – if so, *C. salviifolius* should not be considered an obligate pyrophilous seeder any more, at least at the edge of its distributional range.

The results of the modelling approach are discussed in search of an effective strategy for the conservation of the species.

## METHODS

### Study area

The study area is located in the region of Locarno (Ticino, southern Switzerland, 8.70–8.85° E, 46.10–46.20° N; Fig. 1), which corresponds to the main distribution area of *C. salviifolius* in Switzerland. The climate is moist and warm temperate, with a mean annual precipitation of 1600–1700 mm and a mean annual temperature *c.* 12 °C (mean January temperature *c.* 2–3 °C, July *c.* 21–22 °C; Meteorological Station of Locarno-Monti; Spinedi & Isotta, 2004). Precipitation is low in winter (November–February, *c.* 400 mm), but the incidence of summer rain (June–September, *c.* 800 mm precipitation) is characteristic of the so-called Insubrian climate of the region. The warm-temperate and rainy climate, as well as the siliceous soils, favour cultivation of the sweet



**Figure 1** Distribution maps of *Cistus salviifolius* in southern Europe and the Mediterranean (Walter, 1954), and in the study area (black patches, G. Greco, unpubl. data, 2002) together with forest fires (grey patches) during the period 1968–2002.

chestnut (*Castanea sativa*), which is cultivated as coppices and represents the dominant forest tree, followed by oak (*Quercus* sp.) and other deciduous tree species.

Because of these climatic conditions, the area is prone to fast-spreading surface fires during the period of vegetation dormancy (December–April). Until the 1990s the area was particularly susceptible to rapidly spreading surface fires during winter, which created a mosaic of intact and burnt areas at different successional stages, depending on fire frequency and the time elapsed since the last fire (Delarze *et al.*, 1992). Since 1990, fire frequency and the mean burnt area have been dramatically reduced, dropping from 91 fires and 910 ha per year in the period 1968–90 to 57 fires and 357 ha in the period 1991–2002 (Conedera & Pezzatti, 2005).

### ***Cistus salviifolius***

The sageleaf rockrose, *C. salviifolius* is a diploid, insect-pollinated shrub displaying an obligatory seeding reproductive strategy that makes it particularly well adapted to disturbances such as recurrent fires (Troumbis & Trabaud, 1986; Hanley & Fenner, 1998; Farley & McNeilly, 2000). *Cistus salviifolius* is therefore a pyrophilous pioneer shrub that is not particularly tolerant of competition, but that has an ability to colonize rapidly disturbed and freshly burnt sites consisting of poor, acid soils (Trabaud, 1995). This ecological

feature can be seen as a combination of opportunism, heliophytism and pyrophytism (Legrand, 1992). *Cistus salviifolius* usually has a relatively short life span (15 years, Troumbis & Trabaud, 1986; Roy & Sonié, 1992) and is considered an obligatory pyrophilous seeder (Troumbis & Trabaud, 1986). Seeds have a primary dormancy imposed by an impermeable, hard seed coat, which can be released by the heat of a wild fire, enabling the species to produce massive quantities of seedlings shortly after the first rain (Roy & Sonié, 1992; Thanos *et al.*, 1992). *Cistus salviifolius* germinates after moderate-intensity heat shocks (Nadal *et al.*, 2002; Chamorro-Moreno & Rosua-Campos, 2004) and is even able to withstand temperatures > 100 °C. The best germination success rate appears to be attained by a fine balance between temperatures high enough to facilitate germination, and low enough to maintain seed viability (Hanley & Fenner, 1998). According to Lloret *et al.* (2003), seeders such as *Cistus* need more time to regenerate than large grasses, such as *Ampeodesmos mauritanica*. The presence of such fast resprouters may leave *Cistus* in their shadow, inhibiting its growth. Only a small percentage (4–25%) of seeds display a soft, thin or ruptured coat and are therefore able to germinate without any heat shock, although they are delayed in time (Thanos *et al.*, 1992; Trabaud, 1995; Nadal *et al.*, 2002). A further condition for the species to germinate well is the availability of full light; under cover the germination rate is reduced dramatically (Roy & Sonié, 1992; Trabaud, 1995). In general,

the presence of adult individuals is essential for the colonization of burnt or disturbed areas, as the seed-dispersal distances of *Cistus* are very limited (maximum 0.5 m: Troumbis & Traubad, 1986).

In southern Switzerland, where the species reaches its northern distribution limit and populations are sparse, it appears to colonize steep, south-facing slopes that have recently burned, or where competing resprouting pioneer herbaceous and shrub species such as bracken (*Pteridium aquilinum*), purple moor-grass (*Molinia arundinacea*), Scotch broom (*Cytisus scoparius*) and heather (*Calluna vulgaris*) are scarce. Along an altitudinal gradient, light and heat become increasingly limiting factors. In the study area, the altitudinal limit of *Cistus* is 1000 m a.s.l. (Greco, 1997).

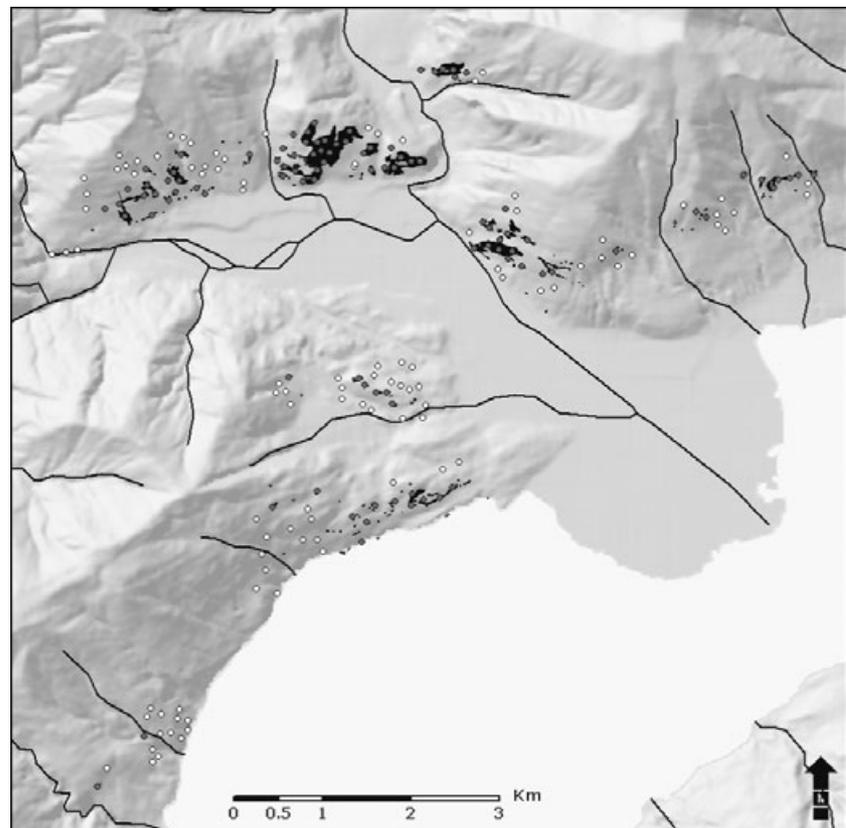
### Species distribution data

Data on the presence and absence of *C. salviifolius* were obtained from the most recent field mapping done by G. Greco in 2002. A systematic survey was carried out over 376 ha during the flowering period of the species in spring. *Cistus salviifolius* was recorded in an area of 54 ha, while in 322 ha the species was not observed (Fig. 1). We assume Greco's survey is reliable, and considered areas where *C. salviifolius* was not observed to be absent (as did Guisan & Hofer, 2003), thereby avoiding the generation of pseudo-absences (Zaniewski *et al.*, 2002).

From the overall mapped area (376 ha), we randomly selected 100 points of *Cistus* presence and 100 points of *Cistus* absence (Fig. 2). This ensured a neutral prevalence of 0.5, as unbalanced prevalence in the species data has been shown to affect some accuracy metrics (McPherson *et al.*, 2004). To avoid spatial autocorrelation in the response variable, which can bias the estimation and selection of model parameters (Guisan & Zimmermann, 2000), target points were further separated by a minimum distance of 100 m. Based on the known ecology of the species, this measure was considered sufficient, particularly due to the short seed-dispersal distance of tens of centimetres (Troumbis & Traubad, 1986), up to 40 m on sloping sites (Legrand, 1992).

### Environmental predictors

A large set of climatic maps was obtained from Zimmermann & Kienast (1999) (Table 1). These authors mapped the climatic parameters of Switzerland on a 25 × 25-m grid by interpolating values from the national network of meteorological weather stations (MeteoSwiss), additionally taking into account the relief and local lapse rates of changes in climatic parameters. From their original set, we retained three predictors that were uncorrelated in our data set and considered physiologically meaningful for plants: annual mean temperature (AMT); annual potential evapotranspiration (PET; formula of Turc, 1961); and annual precipitation (PREC).



**Figure 2** Sampling sites (grey, presence; white, absence of *Cistus salviifolius*).

**Table 1** List of climatic, topographic and derived predictors forming the initial pool of predictors used to model the distribution of *Cistus salvifolius* in the study area

Abbreviation	Description	Unit
PREC	Annual mean precipitation (1961–90)	mm year <sup>-1</sup>
AMT	Annual mean temperature (1961–90)	1/100 °C
PET	Annual potential evapotranspiration*	mm day <sup>-1</sup>
TOPO	Topographic position	unitless
SLOPE	Average slope of each quadrat	degrees
FROC	Neighbourhood statistics of rock coverage, circle with radius 25 m	frequency
TFIRE	Time elapsed since last fire (1969–2002)	year
TCUT	Time elapsed since last clear cut (1985–2002)	year

All bioclimatic predictors are described in more detail by Zimmermann & Kienast (1999).

\*Potential evapotranspiration was calculated with the Turc (1961) formula:  $PET = 0.4 \times [T/(T + 15)] \times (R_s + 50)$ , where  $T$  is the annual mean temperature (°C);  $R_s$  is the sum of solar radiations (cal cm<sup>-2</sup>).

Predictors representing topography and geomorphology consisted of a measure of topographic position and slope. The topographic position (TOPO) was calculated in a GIS by applying circular-moving windows with increasing radii to a digital elevation model (Zimmermann & Roberts, 2001). Positive values express relative ridges, hilltops and exposed sites; negative values stand for gullies, valleys or toe slope. Elevation and aspects were not included, as these are highly correlated with the climatic predictors (temperature and radiation). The average slope of each quadrat (SLOPE) was included as a potentially important factor for the gravitational dispersal of seed.

The predictor related to rock distribution in the study area (FROC) was calculated by running a circular moving window (focal function) of 25 m radius on a base map of rock coverage. The 25-m circle was based on the results of exploratory analyses testing other geometrical forms and radii. The circular shape and 25-m radius accord well with the ecology of the species. The focus was initially on forest coverage, based on data from the Swiss National Topographic Map (scale 1 : 25,000), but preliminary analyses showed that this predictor had a poor response, and it was not used in further analyses.

Both disturbance by fire and coppicing of the chestnut forests greatly influence reproduction by seed germination and resprouting, as they temporarily reduce competition from the other plant species (Troumbis & Trabaud, 1986). Thus we included predictors related to fire and forest management. ‘Time elapsed since the last fire’ (TFIRE) in the past 35 years was obtained from the Wildfire Database of southern Switzerland (Conedera *et al.*, 1996). The time elapsed since last coppicing (TCUT) was derived from the archives of the local Forest Service.

The final set of descriptors – hereafter called predictors – used to fit the model (Table 1) was selected from a larger set of

quantitative environmental descriptors, so that all pairwise correlations between predictors were < 0.6. This was done to prevent the potential problems caused by multicollinearity in GLM (Menard, 2002). All Spearman pairwise correlations between predictors were calculated on a matrix of all environmental predictors sampled from 10,000 points selected randomly within the study area. These were obtained or calculated from existing raster or vector maps, or from the digital elevation model (DEM) at a resolution of 25 × 25 m (DEM25, swisstopo, 2002) in ArcMAP GIS (ESRI, Redlands, CA, USA).

Finally, the altitude above 1000 m a.s.l., corresponding to the highest elevation physiologically sustainable for the species in this area, was used separately in a last step to filter predictions made by the models.

### Model fitting

Generalized linear models (GLM; McCullagh & Nelder, 1989) with a binomial variance function and a logistic link were used to fit all models. Models were fitted in s-PLUS (ver. 6.2; Insightful Corp., Seattle, WA, USA), using the LRM (logistic regression model) function of the Design library (Harrell, 2001), including only linear and quadratic forms of the predictors. One advantage of GLMs is that they can be readily implemented in GIS (Guisan *et al.*, 2002; Rushton *et al.*, 2004). The advantage of LRM over GLM is to provide a large series of goodness-of-fit metrics that are valid for logistic models (Harrell, 2001), including the Nagelkerke (adjusted)  $R^2$  coefficient of determination and area under the curve (AUC; see Model evaluation).

The final model was obtained by applying a backward step-down variable deletion based on the Akaike information criterion (AIC; McCullagh & Nelder, 1989) to find the combination of predictors that yielded the greatest reduction in deviance (similar to variance in maximum-likelihood techniques).

### Model evaluation

Unfortunately, too few observations were available to use the split-sample approach, that is, to put aside a portion of the original data set for an independent evaluation of the model. Therefore the validation was performed using two resampling techniques. We first used a jackknife resampling technique to obtain pseudo-independent predictions for each observation; this is a particular case of cross-validation (leave-one-out CV; Manly, 1997; Jaberg & Guisan, 2001) for small sample sizes. This procedure consists of fitting the model with all but one observation at a time, and predicting a value for the response at the excluded point. The latter is considered to be ‘independent’ of the model calibration. The step is repeated as many times as there are observations, each time removing a different observation and fitting a distinct model. We additionally performed a bootstrap with  $N = 200$  resampling runs using the validate LRM function in the Design library (Harrell, 2001). Through resampling with replacement the rows of observations, the bootstrap allows one to estimate the

optimism in any measure of predictive accuracy, and then subtract the estimate of optimism from the initial apparent measure to obtain a corrected estimate (Efron & Tibshirani, 1993). With LRM, for instance, corrected values of  $R^2$ , and Somers'  $D_{xy}$  and other statistics can be obtained this way (Table 3). When the difference between apparent and corrected value is too high, sometimes referred to as 'optimism from overfitting', the stability of the model should be seriously questioned (Harrell, 2001).

For validating the models using the pseudo-independent predictions obtained with the jackknife procedure, we used the AUC measures of prediction success, based on confusion matrices of predicted vs. observed presence-absence data. This threshold-independent measure is obtained by calculating the AUC of a receiver operating characteristic (ROC) plot (Swets, 1988; Fielding & Bell, 1997). The AUC can take values between 0 and 1, where 0.5 indicates that the model has no predictive power (no different from random); 1 signifies a perfect model; and values  $< 0.5$  indicate a relationship worse than expected by chance (that errors were better predicted than correct predictions). According to Swets (1988), models providing values  $> 0.9$  are considered highly accurate; those providing values in the range 0.7–0.9 useful; and those  $< 0.7$  poorly accurate.

The Cohen (1960) coefficient, maximized on the training set (Huntley *et al.*, 1995), was finally used to define the optimal threshold for deriving binary presence-absence maps from probabilistic predictions (Manel *et al.*, 2001).

### Spatial predictions

All multiple models were implemented in the ArcINFO GIS (ver. 8.3) by combining the predictor grids as defined by replacing the values of their LRM estimate (coefficient) in the model formula. This procedure generates grids with floating values between 0 and 1, indicating the probability that *C. salviifolius* occupies a grid cell (1 = presence; 0 = absence). As we were mainly interested in the higher suitability values, we reclassified the grid into three classes: (1)  $< 0.6$ , (2) 0.6–0.8, and (3)  $> 0.8$ . The threshold value  $P = 0.6$  indicates the species' presence ( $\geq 0.6$ ) or absence ( $< 0.6$ ), as determined by maximizing Kappa on the training set, while the other two classes represent two categories of increasing habitat suitability for the species (0.6–0.8 = potential habitat is suitable for the species;  $> 0.8$  = potential habitat is highly suitable for the species). By reclassifying the grids into these three classes, we produced a map representing classes of increasing habitat suitability for the species.

### Altered fire regime scenarios

To estimate the impact of fire on the distribution of *C. salviifolius*, the model was then recalculated using two modified maps of the predictor 'Time elapsed since the last fire' (TFIRE): (1) no fire in the past 15 years (15-year scenario, setting TFIRE values to  $\geq 15$ ), (2) no fire in the past 35 years (35-year scenario, setting TFIRE by default to 35).

## RESULTS

### Model fitting

The final model (Table 2) includes five predictors and accounts for 56.9% of the null deviance (Nagelkerke  $R^2$ ; bootstrap-corrected  $R^2 = 0.542$ ). Thus the model has a fairly good calibration, and also a good discrimination ability ( $D = 0.55$ , corrected 0.51). As expected from the position of the species at the extreme of environmental gradients, no square term was retained. Predictors positively related to the species are: annual potential evapotranspiration (PET), neighbourhood statistics of rock coverage (FROC), average slope of each quadrat (SLOPE), and topographic position (TOPO). The only significant predictor retained with a negative correlation is the time elapsed since the last fire (TFIRE). Figure 3a shows the resulting potential habitat distribution map obtained for *C. salviifolius*.

### Model evaluation

The evaluation of the final model provides a value of 0.89 for the AUC on the training set (resubstitution; a measure of how well the model was fitted to the observations), falling in the upper range of 'useful' models (0.7–0.9) according to the scale of Swets (1988). This is a satisfying value if one considers the very fine resolution and small extent considered by the study, because in many cases the larger the spatial scale, the easier it is to detect significant species-environment relationships (such as large climatic gradients). In addition, the model remains reasonably robust when evaluated with the pseudo-independent jackknife-resampling procedure (AUC = 0.86), as the evaluation values decrease only slightly in comparison with the AUC for the training set. The bootstrap procedure further reveals low values of optimism, yielding corrected values very close to the original calibration and discrimination indices (Table 3), thus supporting the view that our model is fairly robust.

**Table 2** Predictors selected in the logistic regression model with their regression coefficients, standard errors, Wald Z statistics and associated significance levels ( $P$  value)

Predictor	Regression coefficient	Standard error	Wald Z	$P$ (Wald)
Intercept	-14.8855	3.3314	-4.47	0.0000
PET	0.001	0.0002	4.56	0.0000
FROC	7.7647	1.9792	3.92	0.0001
SLOPE	0.0956	0.0276	3.47	0.0005
TOPO	0.0063	0.0019	3.37	0.0007
TFIRE	-0.0647	0.02153	-3.01	0.0026

PET, annual potential evapotranspiration; FROC, neighbourhood statistics of rock coverage, circle with radius 25 m; SLOPE, average slope of each quadrat; TOPO, topographic position and other topographical variables; TFIRE, time elapsed since last fire (1969–2002).  $R^2 = 0.569$ ; bootstrap-corrected  $R^2 = 0.542$ ; area under the curve (AUC) = 0.886; Somers'  $D_{xy} = 0.773$ .

**Table 3** Resampling validation (bootstrap, 200 loops) of a logistic regression model, with backward step-down variable deletion

	Index, original	Training	Test	Optimism	Index, corrected
$D_{xy}$	0.773	0.776	0.760	0.015	0.757
$R^2$	0.568	0.580	0.553	0.026	0.542
Intercept	0	0	0.011	-0.011	0.011
Slope	1	1	0.905	0.095	0.905
$E_{max}$	0	0	0.024	0.024	0.024
$D$	0.551	0.567	0.531	0.036	0.515

Original values and their correction for over-optimism are shown for Somers'  $D_{xy}$  rank correlation;  $R^2$  index; intercept and slope of an overall logistic calibration equation; maximum absolute difference in predicted and calibrated probabilities ( $E_{max}$ ); and discrimination index,  $D$ . Overall, both calibration ( $R^2$ ) and discrimination ( $D$ ) are rather satisfying and the values of optimism are fairly low, revealing a robust model.  $N = 200$ .

### Response of *C. salviifolius* to different fire regimes

Figure 3b,c and Table 4 show the results of running the model when it is assumed there had been no fires for the past 15 years (15-year scenario) and 35 years (35-year scenario). According to the predictions, *C. salviifolius* would preserve between 70% and 81% of its distribution with the probability class considered in the 15-year scenario, and between 60% and 74% with the class considered in the 35-year scenario.

## DISCUSSION

### Modelling the potential distribution of *C. salviifolius*

The final AIC-based models emphasize the important role of topographic and geomorphological predictors in explaining the distribution of *C. salviifolius* in the study area (SLOPE and TOPO). The only significant predictor related to disturbance is the time elapsed since last fire (TFIRE). As expected, it shows a negative correlation with the distribution of *C. salviifolius* and therefore tends to confirm the relative importance of fire for *C. salviifolius*, especially in the early stage of the succession. The only predictors related to climatic characteristics in the model is annual potential evapotranspiration (PET; positive relation). PET is not correlated to annual temperature (AMT) in the study area (although it is at the Swiss scale), probably due to the rugged topography, as the calculation of this variable additionally takes into account solar radiation, which becomes particularly important on steep and exposed slopes, as is the case here. Both resampling evaluations additionally confirm that the model is robust and has a good predictive power in the study area.

Annual precipitation (PREC) was not, in the end, related to the distribution of *C. salviifolius*, which suggests that it is not a good predictor for such a Mediterranean species in the climate of the southern Alps, where precipitation is abundant overall.

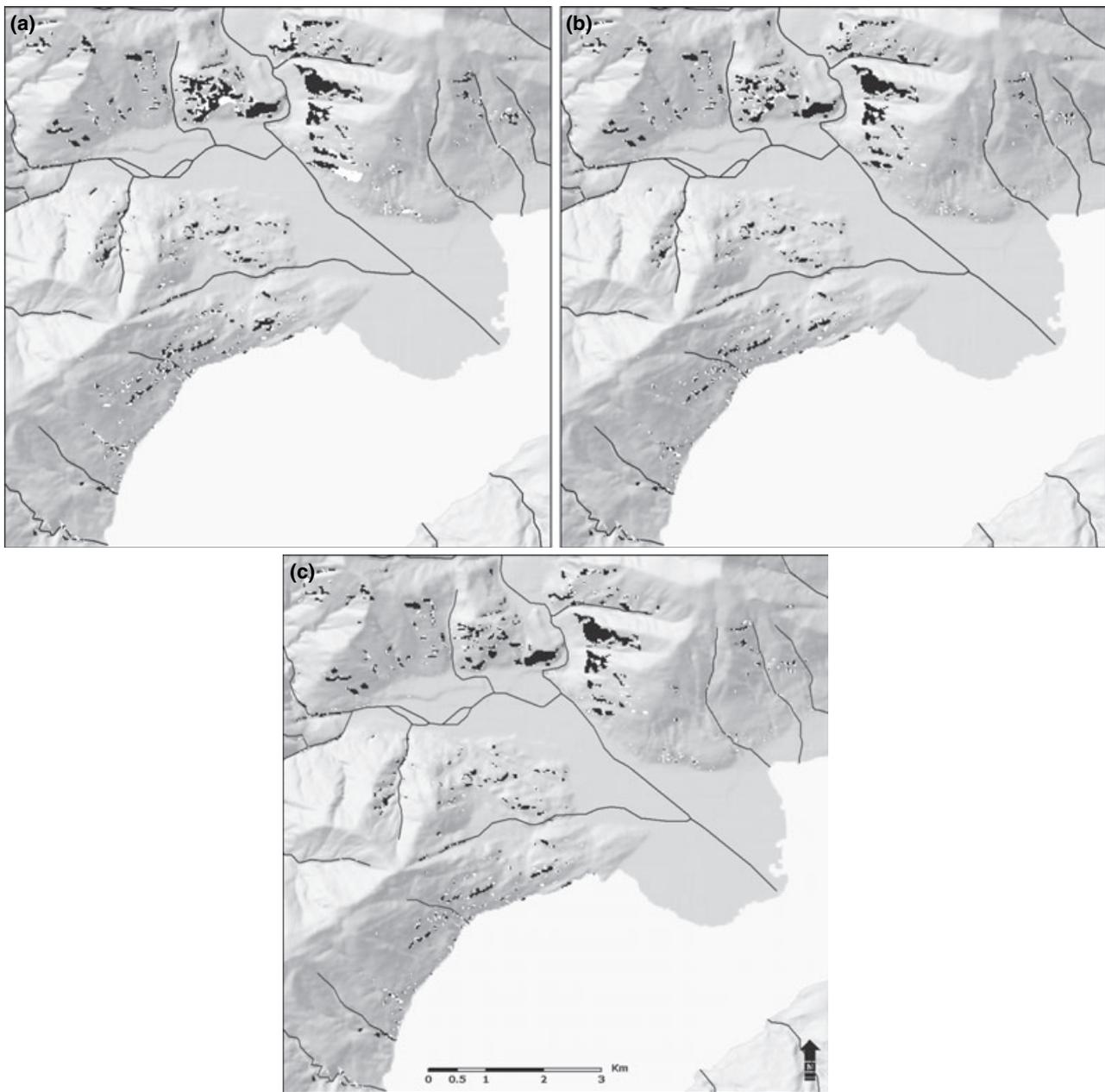
But sites characterized by a dry summer season cannot be properly expressed by an annual index. Forest roads, paths and coppice strips beneath power lines are also potentially important factors that might affect the regeneration of *C. salviifolius* locally, for example by regularly eliminating competitive species, but it was not possible to include them in the model. Nevertheless, they usually have only a local and limited relevance (Sini, 2003).

The spatial prediction of *C. salviifolius* is also coherent with our knowledge of the species' distribution in the area. There are areas where no occurrences of *C. salviifolius* are known, while the model predicts its occurrence (Fig. 3). These areas are on very steep and impervious rock outcrops that are hardly accessible: the habitats are probably suitable for the species, but its occurrence was difficult to sample in the field. As we believed that the model predicted the occurrence of *C. salviifolius* correctly, we went back to the field to check the most accessible of these sites, and successfully observed the species there.

### Role of fire vs. topography

Our results suggest that the present distribution of *C. salviifolius* appears to be largely in a permanently tree-free area. As suggested by the model, the unsuitable conditions for tree growth are mainly due to particular geomorphological conditions, such as emerging bedrock, ridge location or steep slopes. The rather limited decrease in predicted *C. salviifolius* habitat with reduced fire frequency (15- and 35-year scenarios) highlights the short-term effect of fire: *C. salviifolius* is only positively affected by fire for a few years after the event. This confirms the results of the distribution model fitted on the data from 2002 (which are based on real fires), and is in good agreement with the findings of Roy & Sonié (1992), who found that a related *Cistus* species reduced its recruitment after the fifth postfire year. In the specific situation of southern Switzerland, *C. salviifolius* also has to face competition from postfire chestnut resprouts that are particularly fast-growing. Under such conditions, the effects of fire may last for even less time than in the Mediterranean regions. According to this interpretation, fire would play a secondary role in allowing *C. salviifolius* temporarily to extend its occurrence in burnt areas by increasing germination rates (Nadal *et al.*, 2002), and by reducing the competition from the surrounding vegetation.

The progressive fragmentation of the *C. salviifolius* population over recent decades in southern Switzerland is probably due to a decrease in fire frequency and mean burnt area. The lack of disturbance induces a forest succession, starting with the very competitive early stages of *P. aquilinum* and *M. arundinacea*. Lloret *et al.* (2003) obtained similar results for *Cistus* species among a Mediterranean plant community. By similarly modelling the behaviour of the species under different fire regimes, these authors found that their *Cistus* species showed a peak of occurrence at intermediate fire frequency.



**Figure 3** Three distribution models of *Cistus salviifolius* in the study area on the southern slopes of the Swiss Alps: (a) potential distribution in 2002; (b) 15-year scenario model, no fire in the past 15 years; (c) 35-year scenario model, no fire in the past 35 years (probability of being a suitable habitat for the species: white, 60–80%; black, 81–100%).

**Table 4** Presence of *Cistus salviifolius* (number of  $25 \times 25$ -m grid points) as predicted by the model with different fire scenarios

Probability of presence (%)	Original model, <i>n</i> (%)	15-year scenario, <i>n</i> (%)	35-year scenario, <i>n</i> (%)
> 80	3008 (100)	2431 (80.8)	2236 (74.3)
60–80	2033 (100)	1413 (69.5)	1226 (60.3)
> 60	5041 (100)	3844 (76.3)	3462 (68.7)

Our comparison between the present distribution of *C. salviifolius* and the scenarios with reduced fire regimes highlights the increased importance of vegetation-free sites, such as rocky habitats, ridge locations and steep slopes during long periods without fire. Under these conditions, rocky habitats with high radiation at elevations between 200 and 800 m are likely to play a key role as a shelter for this vulnerable species in the southern part of the Swiss Alps, and should therefore be considered in conservation plans.

### Can *C. salviifolius* survive without fire in the Alps?

The results of the model raise questions about the flexibility of *C. salviifolius* when fire frequency varies. The populations of *C. salviifolius* on the southern slopes of the Swiss Alps are likely to become tolerant to long periods without fire. The definition of *C. salviifolius* as an obligate pyrophilous species is thus questionable, at least in our study area. A lack of fire-induced regeneration may promote local adaptation through positive selection of the non-dormant seeds that can germinate without heat from fire (Thanos *et al.*, 1992; Trabaud, 1995; Nadal *et al.*, 2002), while hard seeds – which seem better adapted to regular fires – may decrease. This process could influence the stand ageing pattern, population structure and dispersion potential, as well as the survival rate of *C. salviifolius* (Bastida & Talavera, 2002; Quintana *et al.*, 2004). During times with no fire disturbances, germination of non-dormant seeds will be favoured. In this context and with potentially long-term change in fire regimes, an important factor limiting the survival of *C. salviifolius* populations in the Alps will be the persistence of the dormant seed bank in the soil. Cerabolini *et al.* (2003) classified *C. salviifolius* as a 'long-term persistent species being able to persist for at least 5 years without fire'. We have, however, found no precise estimate in the literature of its persistence, or of how long it takes the dormant seeds of this species to decay in the soil. As it is a widespread species in the Mediterranean basin, where fire occurs regularly, we do not expect it to have seeds with very long longevity (Troumbis, 1996).

Under such conditions, *C. salviifolius* populations could lose their self-regulatory properties and become more exposed to the negative effects of single, dramatic events, according to the event-dependent hypothesis of Bond & van Wilgen (1996). Population persistence is thus more likely to be driven by stochastic events than by fire-induced processes. We are not able to predict, given our present state of knowledge, whether the seed bank of *C. salviifolius* in southern Switzerland will tend to become exhausted after long intervals without fire. It may be that target populations will have insufficient reproductive potential after the next severe fire. If we assume that the next fire will almost completely destroy any living individuals (Hofer, 1965), persistent seed banks will play a particularly important role in ensuring the survival of species with life spans shorter than the average fire cycle (Holmes & Newton, 2004). For *C. salviifolius* plants, a maximum longevity of about 15 years is usually assumed (Troumbis & Trabaud, 1986; Roy & Sonié, 1992).

### Practical implications

Our results also open up new conservation options for environmental managers and decision-makers interested in the conservation of *C. salviifolius* in the southern Swiss Alps. For example, mechanical intervention can reduce the spread of the competing vegetation, and adequate wild-fire propagation management can help to maintain a dormant seed bank that is

viable in the long term. Without such conservation measures, the long-term future of *C. salviifolius* in southern Switzerland cannot be guaranteed.

### CONCLUSIONS

In this study we used a spatial modelling approach to assess whether fire controls the distribution of *C. salviifolius* by first fitting a distribution model for the species, then testing the influence of changes in the fire regime by altering the pyrological parameters in the model. The results provide new information on the ecology of *C. salviifolius* in southern Switzerland: it is now clear that the distribution of *C. salviifolius* on the southern slopes of the Swiss Alps is strongly related to the availability of competition-free sites, which are mostly determined by topography. Fire is thus likely to play a secondary role in allowing *C. salviifolius* temporarily to extend its occurrence though seed germination and seedling recruitment in the surrounding, vegetation-free, burnt areas. This finding provides us with a different view of the role of fire in shaping the distribution of species in such extra-Mediterranean ecosystems. Being strictly correlative, our study only provides support for our interpretation of the role played by fire in determining the distribution of *C. salviifolius* in the area. In future studies, these results should ideally be confirmed by experimental work, for example on the effect of fire on the seeds and seedlings of these populations.

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