

AperTO - Archivio Istituzionale Open Access dell'Università di Torino

Synecology, conservation status and IUCN assessment of *Potentilla fruticosa* L. in the Italian Alps

This is the author's manuscript

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/148733> since 2017-05-26T15:45:25Z

Published version:

DOI:10.1080/12538078.2014.906919

Terms of use:

Open Access

Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)



UNIVERSITÀ DEGLI STUDI DI TORINO

This is an author version of the contribution published on:

Questa è la versione dell'autore dell'opera:

Acta Botanica Gallica: Botany Letters, 161(2), 2014

DOI: 10.1080/12538078.2014.906919

The definitive version is available at:

La versione definitiva è disponibile alla URL:

<http://www.tandfonline.com/doi/abs/10.1080/12538078.2014.906919>

Synecology, conservation status and IUCN assessment of *Potentilla fruticosa* L. in the Italian Alps

Abstract: *Potentilla fruticosa* L. is a self-incompatible clonal shrub, characterized by a wide circumpolar distribution (Asia and North America). In Europe the species has many peripheral isolated populations, and within the Alps it is confined to a restricted area of the Maritime Alps (Italy and France). In alpine environments *P. fruticosa* is affected by a significant lack of information about current population status and little and conflicting information is reported about its potential habitat. Our study investigated *P. fruticosa* populations on the Italian side of the Alps to evaluate its synecology, syntaxonomy, and conservation status. Results showed that six out of the seven populations inventoried in the area during the study, consisted of 20 or fewer individuals, and only one included a high number of plants. The species was observed in the study area within the *Caricetum frigidae* association (*Caricion davallianae* alliance), very close to small creeks characterized by fairly constant water levels. In the Italian Alps *P. fruticosa* has a very restricted geographic range, estimated at around 16 km² (EOO). Isolation of populations affected viable seed production. A continuing decline in the quality and extent of the habitat is expected due to the continuing abandonment of pastures that began 40 years ago in the study area. According to the most recent IUCN categories and criteria the species should be listed at the regional/national level as Critically Endangered (CR).

Keywords: *Caricion davallianae*; endangered species; grazing abandonment; population viability; spatial isolation

Résumé: *Potentilla fruticosa* L. est une espèce arbustive clonale et auto-incompatible qui est caractérisée par une large aire de distribution circumpolaire (Asie et Nord Amérique). En Europe, cette espèce est présente avec plusieurs populations isolées et périphériques et, pour les Alpes, elle se retrouve seulement dans quelques sites des Alpes Maritimes (Italie et France). Les conditions actuelles des populations de *P. fruticosa* dans le milieu alpin ne sont pas réellement connues et les informations en ce qui concerne l'habitat potentiel sont rares et conflictuelles. Au cours de cette étude, on a examiné les populations du versant italien des Alpes Maritimes pour en évaluer la synécologie, la syntaxonomie et l'état de conservation. Seules sept populations ont été inventoriées dans les communes d'Entracque et de Valdieri. Six peuplements étaient caractérisés par un nombre d'individus inférieur ou égal à 20; l'autre population comptait un nombre élevé de plantes. L'espèce a été observée dans l'alliance *Caricion davallianae*, aux alentours de petits ruisseaux avec un niveau plus ou moins constant d'eau. Dans les Alpes italiennes, *P. fruticosa* a montré une aire de distribution très limitée, soit à peu près 16 km² (EOO). L'isolement entre populations a négativement influencé la production de graines viables. On note un déclin de la qualité et de l'extension de l'habitat en raison, également, de l'abandon des activités de pâturage au cours des 40 dernières années. En considérant les plus récentes catégories et critères de l'IUCN, il paraît opportun de classer *P. fruticosa* parmi les espèces «en danger critique d'extinction» (CR) au niveau régional et national.

Mot clé: abandon du pâturage; *Caricion davallianae*; espèce en danger; isolement spatial; viabilité de la population

Introduction

Many studies have shown that spatial isolation and small population size may negatively affect many rare plant species, limiting genetic exchanges between populations, reducing plant fitness and viability, and increasing the risk of extinction (Young, Boyle and Brown 1996; Frankham and Ralls 1998; Lu, Waller and David 2005; Leimu et al. 2006; Aguilar et al. 2008; Kuss et al. 2008). Nonetheless, natural fragmentation is a frequent feature in alpine species, due to the effects of Quaternary history, pronounced mountainous topography and related abiotic heterogeneity (Kuss et al. 2008). Diverse life history traits of different plants may make them more or less vulnerable to fragmentation effects, i.e. stronger negative effects on short-lived species are expected compared to long-lived species (Young, Boyle and Brown 1996). Self-incompatible species are most prone to negative effects of isolation (Leimu et al. 2006).

However the ability of many species to reproduce clonally may limit the negative effects of fragmentation, resulting in a delay of time between generations (Honnay and Bossuyt 2005). Within European taxa, *Potentilla fruticosa* L. represents a very interesting example of a self-incompatible clonal plant characterized by a fragmented distribution range. The species has a wide circumpolar distribution in the northern temperate zone (Asia and North America) with many peripheral isolated populations in Europe. In northern Europe it is recorded in western Ireland, northern England, the Baltic area, and the Ural Mountains (Elkington and Woodell 1963). In southern Europe, very small populations of *P. fruticosa* were observed in the French and Spanish Pyrenees, in the Maritime Alps (France and Italy) and in a single locality in Bulgaria (Elkington 1969).

Many studies have stressed the importance of peripheral isolated populations on species conservation, both for their ecological and genetic importance (Dvornyk 2001; van Rossum et al. 2003; Lesica and McCune 2004; Gapare and Aitken 2005; Lepping and White 2006). Due to the greater physiological stress associated with marginal habitat conditions, peripheral populations may be well adapted to shifting the species range in response to climate change (Hunter and Hutchinson 1994; Garcia-Ramos and Kirkpatrick, 1997; Mott 2010). In addition, they are potentially important for future speciation events (Lesica and Allendorf 1995).

In the Alps, *P. fruticosa* has many peripheral isolated populations with respect to the core distribution. These isolated populations are confined to a restricted area of the Maritime Alps, between the municipalities of Entraque and Valdieri (Piedmont, Italy) and the municipalities of St-Martin-Vésubie, Fontan, Belvédère, and Guillaumes (France) (Pignatti 1982; SILENE 2013). Based on historical and recent observations, only four populations have been documented in the Italian Alps (Burnat, Briquet and Cavillier 1892-1931; Bono 1965; Pascale 2006). According to the only comprehensive Italian Red List of threatened plants (Conti, Manzi and Pedrotti 1997), based on an older version of IUCN categories, *P. fruticosa* is included among Lower Risk (LR) species. Until now it has never been considered for an assessment according to the most recent categories and criteria (IUCN 2001, 2012a) and, at the moment, it is not included within

the new Italian Red List (Rossi, Montagnani, Gargano et al. 2013, Rossi, Montagnani, Abeli et al., 2013).

The knowledge of syntaxonomy and synecology of rare plant species is essential to their conservation, e.g. phytosociological habitat descriptions provide considerable relevant information about habitat quality, syndynamic processes and related management options (Austin 1999; Hölzel 2003; Lonati and Siniscalco 2009a, 2009b, 2010; Lonati, Gorlier and Lombardi 2011). Additionally, IUCN guidelines take into account the reduction of habitat quality during the assessment process (IUCN 2013).

Little and conflicting information about *P. fruticosa* potential habitat in the Alps has been reported. Pignatti (1982) reported the species in the Italian Alps on sunny cliffs, contrasting with the observations of Pascale (2006), who reported the species associated with *Alnus viridis* stands and along alpine streams banks in the same geographic area. Phytosociological data also are not very clear: Aeschimann et al. (2004) indicated the species optimum condition in the Alps in the *Caricion davallianae* alliance, according to observations of Braun-Blanquet (1948) in the Pyrenees. In contrast, the same species is listed by Cavallero et al. (2007) within thermo-xerophilous *Centaureo uniflorae-Festucetum paniculatae* (*Festucion variaae* alliance) in the Italian western Alps.

The present study investigated *P. fruticosa* populations in the Italian Alps to assess their conservation status according to the most recent IUCN criteria and categories (IUCN 2001, 2012a). The specific goals of the work are: (1) to describe actual geographic distribution and assess population size, (2) to define the phytosociological optimum of the species in the Italian Alps, (3) to test whether the vegetative performance and potential reproductive success are related to the isolation of populations, and (4) to identify the factors affecting *P. fruticosa* conservation.

Material and methods

1) Study species

Potentilla fruticosa is a deciduous branched shrub, 50-100 cm high. Both erect and prostrate branches are present in mature plants, the latter being able to easily root adventitiously. Vegetative propagation takes place by means of creeping stems just below the soil surface and may enable the plant to cover a wide area (Elkington and Woodell 1963).

The species is self-incompatible (Innes and Lenz 1991). Flowers are usually produced during the second season when the plants are 40-50 cm high (Elkington and Woodell 1963). Flowers are five-merous, with triangular ovate sepals, are oblanceolate linear epicalyx segments, and orbicular-ovate yellow petals. The whole calyx is persistent in fruit and surrounds the achenes. Achenes are about 1 mm long, dark brown at maturity, and surrounded with a ring of hairs produced from the base.

2) Data collection

To assess the conservation status of *P. fruticosa*, we georeferenced all the existing populations and we quantified the area and the total number of individuals for each population. Identification of populations was based on published sources, herbarium records, personal unpublished observations and extensive field surveys across the entire Italian range of the species during the flowering period (June and July 2010). In most cases plants were easily identified in the field as singular individuals. Due to clonal spread by the external prostate branches, the oldest individuals appeared as polycormic plants with dense canopies and hemi-ellipsoidal crowns, probably corresponding to genets. Individual plants were patchily distributed in the field, forming dense patches of less than 20-25 m². We used a threshold distance of 100 m between patches to differentiate individual populations (Kolb and Lindhorst 2006). Population perimeters were georeferenced using a GPS and the corresponding areas were quantified using Quantum GIS 1.8 (Quantum GIS Development Team, 2012). Five of the seven populations (POP1, POP3, POP4, POP5, POP6) consisted of one single patch; one population (POP2) was comprised of two well separated patches; and one (POP7) included a large number of patches, often close to each other and not easily distinguishable. In all populations except POP7 the size was assessed by direct count of all the individuals (without distinction between mature and immature individuals). In POP7 direct counts of all individual plants were not feasible. Consequently, we estimated the population size by measurement of the area occupied by the patches multiplied by the average plant density (e.g. Pluess and Stöcklin 2004), which was determined by counting all individuals in six 28.3 m² circular plots (3 m radius), randomly arranged inside the area. The population size was assessed during July 2010.

To describe the synecology, structure, and vegetative and reproductive fitness of *P. fruticosa*, in all populations but POP7 we located one or two 28.3 m² circular permanent plots with the plot centre at the centre of each patch. In POP7 surveys were carried out in the same circular plots used to measure plant density. Thirteen plots were surveyed during 2010.

To investigate the species synecology, phytosociological surveys were carried out at each plot during June and July 2010, using the abundance-dominance values proposed by Braun-Blanquet (1932). Percent cover of bare soil, rocks, herbs, lower shrub (height ≤ 1.3 m) and upper shrub (height between 1.3 and 5.0 m) layers were visually estimated. All the woody species, including *P. fruticosa*, were recorded within the lower or upper shrub layer. Floristic nomenclature follows Pignatti (1982).

To describe the population structure we recorded or calculated the following parameters within each circular plot at the end of the growing season (September 2010):

- (i) *P. fruticosa* plant density, by counting all flowering and non-flowering individuals;
- (ii) *P. fruticosa* plant height (from soil level to the tip of the tallest shoot) and diameter (average of two diameters of an approximate ellipse), by measuring all the individuals. Average plant height and diameter were calculated for each plot using data recorded from all individuals;
- (iii) total canopy area of *P. fruticosa* (m² plot⁻¹), summing up all the canopy areas of singular individuals (shape of the canopy crown approximate to an ellipse).

Additionally, to measure the species' vegetative and reproductive fitness, 10 individuals of *P. fruticosa* were randomly selected within each plot except in the smallest population with less than 10 individuals. We measured the following morphological and reproductive traits (September 2010):

- (iv) annual final shoot length (one shoot derived from the terminal bud for each selected individual);
- (v) number of well-developed, potentially viable achenes (total count in 10 flowers randomly selected within each plot, coming from the 10 randomly selected individuals whenever possible). Well-developed fruits (filled) were easily separable from those aborted (unfilled), the latter almost exclusively comprised of the pappus.

To quantify patch isolation we calculated the following indices (Hanski, Kuussaari and Nieminen 1994; Bruun 2000):

- (1) distance from patches *i* to the nearest occupied patch (I_{i1}), calculated using the GPS position of each plot. We also tested the mean distance to the nearest two (I_{i2}), three (I_{i3}) and four patches (I_{i4}), but this did not alter the results as both isolation parameters were strongly correlated (Pearson correlation: $r > 0.99$ and $p < 0.001$ with I_{i2} ; $r = 0.95$ and $p < 0.001$ with I_{i3} ; $r = 0.88$ and $p < 0.001$ with I_{i4});
- (2) overall isolation, henceforth called isolation index (I_n), defined as $I_n = -\sum \exp(-d_{ij})$, where d_{ij} is the distance between patches *i* and *j* in kilometres.

To assess the abiotic factors affecting vegetation at each plot, a number of variables were measured in the field or extracted from available datasets. Topographic variables (elevation, aspect, slope, and distance from the nearest creek) were measured by using topographic measuring devices. Soil pH was measured potentiometrically on air-dried topsoil samples (10 cm) on the > 2 mm soil fraction of a soil/water suspension (soil/water ratio 1:2) using standard techniques (Soil Survey Staff 1999). Aspect was transformed into southness (southness = $180 - |\text{aspect} - 180|$), to provide an interpretable, non-circular variable (Chang et al. 2004). Climate data in the study area were extrapolated for each plot, using UTM coordinates from the Climatologic Atlas of Piedmont (Biancotti et al. 1998).

3) Data analysis

Phytosociological data were transformed into numerical values according to van der Maarel (1979), which were used to classify the 13 plots by cluster analysis (option for clustering: average link; resemblance coefficient: similarity ratio). Each group was assigned an association based on the presence and frequency of phytosociological characteristic species. The syntaxonomical nomenclature follows Grabherr and Mucina (1993), integrated with Mucina, Grabherr and Ellmauer (1993), Oberdorfer (1983) and Theurillat et al. (1994). Nomenclature of associations and related syntaxa was revised according to the International Code of Phytosociological Nomenclature (Weber, Moravec and Theurillat 2000).

We assessed among-group differences of topographic/environmental variables (elevation, southness, slope, soil pH) and *P. fruticosa* performance variables (density, average plant height and diameter, canopy area, shoot length and number of well-developed achenes), by univariate ANOVA. Prior to the analysis, data were tested for homoscedasticity (Levene's test) and three variables (distance from creek, average plant height, and average plant diameter) were \log_{10} transformed to meet this assumption (Supplementary Table 1). ANOVA residuals were also tested for normality using Kolmogorov-Smirnov test (Supplementary Table 2). Group means were compared with Bonferroni post-hoc range test ($p \leq 0.05$), which takes the unbalanced replicates design into account (Soliani 2004; Norusis 2005).

The relationship between the number of filled fruits and patch isolation (I_{r1} and I_n) was analyzed by a regression, using exponential and linear functions, respectively ($p \leq 0.05$). In the linear regression, all variables were tested for normality to meet assumptions of the analysis. Due to wild ungulate damage on flowers and fruits in one plot (POP6), the regression models were performed using 12 plots. The analysis was performed at plot scale (and not at population scale) to utilize a larger dataset in the analysis. All statistical analyses were performed using SPSS 19 (SPSS Inc, Chicago).

In accordance with the IUCN categories and criteria (IUCN 2001, 2012a) and the most recent guidelines for their application (IUCN 2013), species conservation status was assessed using criterion B. We calculated the extent of occurrence (EOO) by measuring the area of the minimum convex polygon including the populations, and the area of occupancy (AOO) superimposing a 2 x 2 km grid to population locations (Gargano 2011). As a first step we applied the IUCN Red List categories and criteria (IUCN 2001, 2012a, 2013) to the Italian populations to determine the preliminary estimate of extinction risk. As a second step, according to the IUCN regional guidelines (IUCN 2012b), we considered the effects of French neighbouring populations on the Italian ones, and the preliminary category was up- or down-listed when appropriate, to determine the final estimate of extinction risk in Italy.

Results

Geographic distribution and population size

We located seven populations of *P. fruticosa* between the municipalities of Entraque and Valdieri. Four populations were confirmed from published and herbarium data and three new populations were found (Table 1, Figure 1).

Populations ranged in size from one to about 18,000 individuals (median = 13 plants). Six of the seven studied populations consisted of 20 or fewer individuals. Only one population (POP7), located in the high Vallone della Meris (Valdieri), consisted of a high number of plants (18,000 estimated individuals). The population area ranged between 0.2 and 27 m², except POP7 which occurred over an area of about 2.6 ha (Table 1).

Based on population locations (Figure 1), we identified two sub-ranges, one for each municipality. Considering all the populations together we calculated an EEO of about 18 km² and an AOO of 16 km².

Populations ranged on average between 1800 and 2280 m a.s.l. (subalpine and alpine belts). They were localized in the intra-alpine zone (Gam's continental index ranged between 54.2 and 63.5°) (Figure 2).

Synecology

The cluster analysis, performed at the plot level, allowed identification of three groups of plots and populations, clearly separated from each other from a phytosociological point of view (Figure 3, Table 2):

1) Group 1 (2 plots; 2 populations) included populations ascribable to thermophilous grasslands dominated by *Festuca paniculata*. These populations could be assigned to the association *Centaureo uniflorae-Festucetum spadiceae*, as confirmed by the presence of many characteristic species of the association and related syntaxa;

2) Group 2 (8 plots, 3 populations) represents over 60% of the plots and included the most important population (POP7). The vegetation could be assigned to the association *Caricetum frigidae* (*Caricion davallianae*), including oligo-mesotrophic communities in basophilous fens with low primary productivity. *Carex frigida* was the most abundant species in the plots. *Potentilla fruticosa* patches were usually close to small creeks with water available throughout the growing season (Table 3);

3) Group 3 (3 plots, 2 populations) included populations characterized by less representative vegetation. However, due to the presence of many characteristic species from basiphilous fens (i.e., *Carex frigida*, *Tofieldia calyculata*, *Pinguicula vulgaris*, *Parnassia palustris*), we included Group 3 within the *Caricetum frigidae*. *Potentilla fruticosa* patches were usually close to small creeks, although in POP3 free water was not usually present, except after periods of very intensive rainfall or recent snowmelt. The plots included in Group 3 were, on average, localized at lower altitudes and on steeper slopes than Group 2 plots (Table 3).

The topsoil reaction was significantly different among the three groups. Nevertheless, the limited range of variation (6.0-6.4 on average) is not very relevant from an ecological point of view.

Several ingressive species (belonging to the classes *Seslerietea albicantis*, *Loiseleurio-Vaccinietea*, *Mulgedio-Aconitetea*, *Quercu-Fagetetea*, *Calluno-Ulicetea*, and *Molinio-Arrhenatheretea*) were observed in all the groups (Table 2), supplying additional information about the synecology (see Discussion).

Vegetative performance and potential reproductive success

Vegetation groups differ significantly in plant size and other traits (Table 3). Within the *Caricetum frigidae* association (Groups 2 and 3), plots located at lower altitude (Group 3)

supported, on average, the significantly largest plant dimensions (diameter and height) and the longest shoot length. The plant dimensions of Group 1 (*Centaureo uniflorae-Festucetum spadiceae*) were similar to Group 2; the length of vegetative shoots was not significantly different from the other two groups.

Plant density did not differ significantly between groups, although the highest values were observed for Group 2. A significant highest number of well-developed achenes was observed in Group 2 (Table 3).

The reproductive success, quantified by the number of well-developed achenes per flower, showed a significant inverse relation with plot isolation (Figure 4). The number of well-developed achenes was significantly fitted by an inverse exponential regression with the minimum distance from the nearest neighbour plots and by an inverse linear regression with the overall isolation index (I_n).

Discussion

Potentilla fruticosa in the Italian Alps has a fairly broad ecological tolerance. We observed the species both in moist and dry conditions (*Caricion davallianae* and *Festucion variaae* alliances, respectively). However, five of the seven known populations were observed in moist conditions in the *Caricetum frigidaae* association in particular (Groups 2 and 3). Consequently, in the study area the *Caricion davallianae* should probably be designated as the optimum condition for the species, which is consistent with reports by other authors in southern Europe (Aeschimann et al. 2004, for the Alps; Braun-Blanquet 1948, for the Pyrenees).

Group 2, observed close to small creeks with water available throughout the growing season, supported the most viable population (POP7), characterized by the highest number of well-developed achenes and the highest demographic turnover, as shown by younger and thus smaller plants. In Group 3, *P. fruticosa* probably grew in less optimal conditions because of irregular water availability, lower altitude, and steeper slopes than Group 2. Steep slopes tend to be well drained thus drier and therefore do not generally favour *P. fruticosa*. Nevertheless, the fact that they support shallow soils (which may result from erosion) limits the re-colonisation by competing trees at low altitudes, which may benefit *P. fruticosa*.

The basophilous characteristics of the *Caricetum frigidaae* were confirmed by the high frequency of several ingressive species belonging to the *Seslerietea albicantis*, indicating the presence of calcareous rocks in the study area or calcium in the soil solution, although topsoil reaction was slightly acidic (according to Soil Survey Staff 1999). The equilibrium in occurrence and abundance between characteristic species of the *Calluno-Ulicetea* (mainly *Nardetalia*) and *Molinio-Arrhenatheretea* classes highlighted a transition between oligotrophic and eutrophic conditions that characterize the communities with low primary productivity included in the *Caricion davallianae* (Hájek and Hájková 2011; Biondi et al 2010).

Potentilla fruticosa occasionally occurred on dry sites (Group 1, *Centaureo uniflorae-Festucetum spadiceae* association), probably due to the presence of nearby populations

established in optimal habitat. The presence of several ingressive species belonging to *Festuco-Brometea* class (e.g., *Stipa pennata*, *Armeria plantaginea*) also indicate very dry conditions. The ecological tolerance of *P. fruticosa* is confirmed by Elkington and Woodell (1963) who observed good growth rates under garden conditions and low rainfall, and in well-drained soil without extra watering. Similarly, in dry conditions (Group 1), we observed vegetative growth (i.e. length of vegetative annual shoots) to be not significantly different from the populations ascribable to the *Caricetum frigidae* (Group 2 and 3).

Many studies have reported negative effects of small population size on species survival (Ouborg 1993; Fisher and Stöcklin 1997). Matties et al. (2004) indicated that the probability of survival for many perennial species increased significantly with population size and that very small populations with less than 26 plants were doomed to extinction. In the study area, six of the seven populations of *P. fruticosa* included a very small number of individuals (equal to or less than 20), and only POP7 could be considered a large viable population (about 18,000 individuals). The high proportion of very small populations likely jeopardizes conservation of *P. fruticosa*. Additionally, in long-lived species like *P. fruticosa*, the negative consequences of reduced population size and increased isolation may not become noticeable for a long time, because established plants often have low mortality (Oostermeijer, Van't Veer and Den Nijs 1994; Colling, Matthies and Reckinger 2002; Matties et al. 2004).

Several studies have shown that isolation and habitat fragmentation can decrease seed production as a result of pollination limitation in both self-incompatible and self-compatible species (Aizen and Feinsinger 1994; Cunningham 2000; Aguilar and Galetto 2004; Kolb 2005). In *P. fruticosa*, a strong decrease in potentially viable seed production was observed in isolated patches, probably due to the combined effects of small numbers of individuals (Kolb and Lindhorst 2006) and the self-incompatibility that characterized hermaphroditic accessions (Innes and Lenz 1991). The regression analyses showed that starting at a distance of 300-500 m from the nearest patch, potentially viable seed set was reduced to zero, but a more detailed experimental approach is probably needed to identify pollination limiting distances. However, clonality may promote vegetative reproduction, thereby decreasing population extinction risk and promoting long-term persistence even in isolated populations (Stöcklin and Fischer 1999). Under favourable environmental conditions, clonal reproduction in *P. fruticosa* enabled small populations and individual genets to persist for a very long time. Spread of *Alnus viridis*, particularly at low altitude populations (subalpine belt), may be a possible threat for *P. fruticosa* survival, due to its intolerance to shade (Elkington and Woodell 1963). A number of ingressive species belonging to the *Mulgedio-Aconitetea* class indicated close dynamic relations to *A. viridis* stands. In addition, the presence of many characteristic species of the *Querco-Fagetea* (mainly belonging to *Fagetalia sylvaticae*) evidenced potential tree invasion processes, particularly at the lower altitudes. Conversely, at high altitudes the local dominance of the dwarf shrub *Juniperus nana* limited the vegetative spread of *P. fruticosa* from its external prostate branches. *Juniperus nana* was locally abundant within studied populations and was frequently

observed together with other woody ingressive species belonging to *Loiseleurio-Vaccinietea* class.

Since the presence of *P. fruticosa* is related to the openness of vegetation, the positive effects of grazing on shrub control (Ascoli et al. 2013; Probo et al. 2013) may be very important for *P. fruticosa* conservation. In Britain and Ireland, *P. fruticosa* is generally avoided by grazing stock, particularly where more palatable species are available (Elkington and Woodell 1963). During our study, we observed only minor damage to fruits in a plot grazed by wild ungulates. Only POP7 was located in an area grazed by sheep, and the high number of *P. fruticosa* plants seems to indicate a positive effect of extensive grazing. All other populations were located in abandoned grasslands, where trees and shrubs have extensively recolonised open herbaceous habitats. A continuing decline in the quality and extent of habitat is therefore expected and may be a potential threat for *P. fruticosa* conservation. General trends showed that on the Italian side of the Maritime Alps, socioeconomic changes have affected traditional livestock farming systems over the last 40 years, with the number of livestock farms and the pasture area decreasing by 70% between 1970 and 2010 (Valle 2013). This pastoral abandonment has probably compounded the fragmentation of *Caricetum frigidae*, which was already naturally very fragmented in the study area, due to its dependence on proximity to small streams.

IUCN assessment and implication for species conservation

The geographical range of *P. fruticosa* in the Italian Alps is very restricted, estimated at around 16 km² (EOO). According to the IUCN categories and criteria (IUCN 2001, 2012a) and the most recent guidelines for their application (IUCN 2013), taking the criterion B1ab(iii) into account (EOO < 100 km², taxon severely fragmented and continuing to decline in habitat quality due to grazing abandonment), we preliminarily categorized *P. fruticosa* into the Critically Endangered (CR) IUCN category. At regional/national levels, due to the isolation from the neighbouring French populations caused by the orography of the Alps, immigration of propagules from neighbouring regions is not expected to be significant. Under this criterion, the category was not up- or down-listed at regional/national levels [CR B1ab(iii)] (IUCN 2012b). A future revision of the old comprehensive Italian Red List of threatened plants (Conti, Manzi and Pedrotti 1997) that categorized the species in the LR – Lower Risk category, should consider moving *P. fruticosa* to a higher threat category (CR - Critically Endangered).

Actions that could be implemented for the conservation of *P. fruticosa* in the Italian Alps include:

- (i) shrub clear cutting close to actual known populations, especially at low altitudes;
- (ii) defining a favourable stocking rate and monitoring grazing effects. Extensive grazing is expected to have a positive effect on nutrient balance if herbage removal exceeds dung deposition, with a slight decrease in nutrient availability favourable to the oligotrophic species belonging to the *Caricion davallianae* alliance (Hájek and Hájková 2011). On the contrary, the presence of night pens could increase nitrophilous species and contribute to habitat loss.

Additionally, trampling and seed transport may have contrasting effects depending on the grazing intensity (Ascoli et al. 2013; Probo et al. 2013; Tocco et al. 2013);
(iii) *ex-situ* conservation, which might be facilitated by the species adaptability to garden conditions at low altitude (Elkington and Woodell 1963; M. Pascale and M. Lonati, pers. obs.);
(iv) restocking of small isolated populations, where seed production is inconsistent (IUCN 2012c, Pérez, Anadón and Díaz 2012).

References

- Aeschimann, D., K. Lauber, M. D. Moser, and J. P. Theurillat. 2004. *Flora alpina*. Bologna: Zanichelli.
- Aguilar, R., and L. Galetto. 2004. "Effects of forest fragmentation on male and female reproductive success in *Cestrum parqui* (Solanaceae)." *Oecologia* 138: 513–520.
- Aguilar, R., M. Quesada, L. Ashworth, Y. Herrerias-Diego, and J. Lobo. 2008. "Genetic consequences of habitat fragmentation in plant populations: susceptible signals in plant trait and methodological approaches." *Molecular Ecology* 17: 5177–5188.
- Aizen, M. A., and P. Feinsinger. 1994. "Forest fragmentation, pollination, and plant reproduction in a chaco dry forest, Argentina." *Ecology* 75: 330–351.
- Ascoli, D., M. Lonati, R. Marzano, G. Bovio, A. Cavallero, and G. Lombardi. 2013. "Prescribed burning and browsing to control tree encroachment in southern European heathlands." *Forest Ecology and Management* 289: 69–77.
- Austin, M.P. 1999. "The potential contribution of vegetation ecology to biodiversity research." *Ecography* 22 (5): 465–484.
- Biancotti, A., G. Bellardone, S. Bovo, B. Cagnazzi, L. Giacomelli, and C. Marchisio. 1998. *Distribuzione regionale di piogge e temperature* [Regional distribution of rainfall and temperature]. Torino: Cima Icam.
- Biondi, E., C. Blasi, S. Burrascano, S. Casavecchia, R. Copiz, E. Del Vico, D. Galdenzi, et al. 2010. *Manuale italiano di interpretazione degli habitat Direttiva 92/43/CEE* [Italian handbook for the interpretation of the habitats 92/43/EEC]. Roma: Progetto Artiser.
- Bono, G. 1965. "La Valle Gesso e la sua vegetazione (Alpi Marittime). La Flora [The Valle Gesso and its vegetation. The Flora]." *Webbia* 20 (1): 1–216.
- Braun-Blanquet J. 1948. *La végétation alpine des Pyrénées orientales*. Manresa: Imp. Ramon Torra S.C.
- Braun-Blanquet, J. 1932. *Plant sociology*. New York and London: McGraw-Hill Book Company.
- Bruun, H. H. 2000. "Deficit in community species richness as explained by area and isolation of sites." *Diversity and Distribution* 6: 129–135.
- Burnat, E., J. Briquet, and F. Cavillier. 1892–1931. *Flore des Alpes Maritimes* [Flora of Maritimes Alps]. Genève: H. Georg.
- Cavallero, A., P. Aceto, A. Gorlier, G. Lombardi, M. Lonati, B. Martinasso, and C. Tagliatori. 2007. *I tipi pastorali delle Alpi piemontesi* [Pasture vegetation types of Piemontese Alps]. Bologna: Alberto Perdisa Editore.
- Chang, C., P. Lee, M. Bai, and T. Lin. 2004. "Predicting the geographical distribution of plant communities in complex terrain: a case study in Fushian Experiment Forest, northeast Taiwan." *Ecology* 27: 577–588.
- Colling, G., D. Matthies, and C. Reckinger. 2002. "Population structure and establishment of the threatened long-lived perennial *Scorzonera humilis* in relation to environment." *Journal of Applied Ecology* 39: 310–320.

- Conti, F., A. Manzi, and F. Pedrotti. 1997. *Liste rosse regionali delle piante d'Italia* [Regional Red List of Italian plants]. Camerino: Università di Camerino.
- Cunningham, S. A. 2000. "Depressed pollination in habitat fragments causes low fruit set." *Proceedings of the Royal Society B* 267: 1149–1152.
- Dvornyk, V. 2001. "Genetic variability and differentiation of geographically marginal Scots pine populations from Ukraine." *Silvae Genetica* 20: 64–65.
- Elkington, T. T., and S. R. J. Woodell. 1963. "Biological Flora of the British Isles: *Potentilla fruticosa* L." *Journal of Ecology* 53: 769–781.
- Elkington, T. T. 1969. "Cytotaxonomic variation in *Potentilla fruticosa* L." *New Phytologist* 68: 151–160.
- Fischer, M., and J. Stöcklin. 1997. "Local extinctions in remnants of extensively used calcareous grassland 1950–1985." *Conservation Biology* 11: 727–737.
- Frankham, R., and K. Ralls. 1998. "Conservation biology – inbreeding leads to extinction." *Nature* 392: 441–442.
- Gapare, W. J., and S. N. Aitken. 2005. "Strong spatial genetic structure in peripheral but not core populations of sitka spruce [*Picea sitchensis* (Bong.) Carr.]." *Molecular Ecology* 14: 2659–2667.
- Garcia-Ramos, G., and M. Kirkpatrick. 1997. "Genetic models of adaptation and gene flow in peripheral populations." *Evolution* 51: 21–28.
- Gargano, D. 2011. "Verso la redazione di nuove Liste Rosse della flora d'Italia: una griglia standard per la misura dell'Area of Occupancy (AOO) [Towards the preparation of a new Red List of Italian flora: a standard grid to measure the Area of Occupancy (AOO)]." *Informatore Botanico Italiano* 43: 455–458.
- Grabherr, G., and L. Mucina. 1993. *Die Pflanzengesellschaften Österreichs 2, Natürliche waldfreie Vegetation* [The plant communities of Austria 2, Natural vegetation]. Jena: G. Fischer.
- Hájek, M., and P. Hájková. 2011. *Caricion davallianae Klika 1934*. In *Vegetace České republiky. 3. Vodní a mokřadní vegetace* [Vegetation of the Czech Republic. 3. Aquatic and wetland vegetation], edited by M. Chytrý, 619–623. Praha: Academia.
- Hanski, I., M. Kuussaari, and M. Nieminen. 1994. "Metapopulation structure and migration in the butterfly *Melitaea cinxia*." *Ecology* 75 (3): 747–762.
- Hölzel, N. 2003. "Re-assessing the ecology of rare flood-meadow violets (*Viola elatior*, *V. pumila* and *V. persicifolia*) with large phytosociological data set." *Folia Geobotanica* 38: 281–298.
- Honnay, O., and B. Bossuyt. 2005. "Prolonged clonal growth: escape route or route to extinction?" *Oikos* 108: 427–432.
- Hunter Jr, M. L., and A. Hutchinson. 1994. "The virtues and shortcomings of parochialism: conserving species that are locally rare, but globally common." *Conservation Biology* 8: 1163–1165.

- Innes, R. L., and L. M. Lenz. 1991. "A genetic analysis of self-incompatibility and double flowers in *Potentilla fruticosa* L." *Euphytica* 51: 241–248.
- IUCN. 2001. *IUCN Red List categories and criteria: version 3.1*. Gland and Cambridge: IUCN Species Survival Commission.
- IUCN. 2012a. *IUCN Red List categories and criteria: version 3.1. Second edition*. Gland and Cambridge: IUCN Species Survival Commission.
- IUCN. 2012b. *Guidelines for application of IUCN Red List criteria at regional and national levels: version 4.0*. Gland and Cambridge: IUCN Species Survival Commission.
- IUCN. 2012c. *IUCN Guidelines for reintroductions and other conservation translocations*. Cambridge: IUCN Species Survival Commission.
- IUCN. 2013. Guidelines for using the IUCN Red List categories and criteria: version 10.1. IUCN Accessed 10 September 2013. <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>
- Kolb, A. 2005. "Reduced reproductive success and offspring survival in fragmented populations of the forest herb *Phyteuma spicatum*." *Journal of Ecology* 93: 1226–1237.
- Kolb, A., and S. Lindhorst. 2006. "Forest fragmentation and plant reproductive success: a case study in four perennial herbs." *Plant Ecology* 185: 209–220.
- Kuss, P., A. R. Pluess, H. H. Ægisdóttir, and J. Stöcklin. 2008. "Spatial isolation and genetic differentiation in naturally fragmented plant populations of the Swiss Alps." *Plant Ecology* 1(3): 149–159.
- Leimu, R., P. Mutikainen, J. Koricheva, and M. Fisher. 2006. "How general are positive relationships between plant population size, fitness and genetic variation?" *Journal of Ecology* 94: 942–952.
- Leppig, G., and J. W. White. 2006. "Conservation of peripheral plant populations in California." *Madroño* 53 (3): 264–274.
- Lesica, P., and F. W. Allendorf. 1995. "When are peripheral populations valuable for conservation?" *Conservation Biology* 9: 753–760.
- Lesica, P., and B. McCune. 2004. "Decline of arctic-alpine plants at the southern margin of their range following a decade of climatic warming." *Journal of Vegetation Science* 15: 679–690.
- Lonati, M., A. Gorlier, and G. Lombardi. 2011. "Syntaxonomy and synecology of *Hedysarum brigiaticum* communities in the western Italian Alps." *Acta Botanica Gallica* 158 (4): 473–486.
- Lonati, M., and C. Siniscalco. 2009a. "Populations status, syntaxonomy and synecology of *Scopolia carniolica* Jacq. in the Western Alps (Piedmont, Italy)." *Acta Botanica Gallica* 156 (2): 245–258.
- Lonati, M., and C. Siniscalco. 2009b. "Syntaxonomy, synecology and conservation of *Pseudostellaria europaea* Schaeftlein communities in NW Italy in comparison with Eastern Alps populations." *Plant Biosystem* 143 (1): 120–136.

- Lonati, M., and C. Siniscalco. 2010. "Syntaxonomy and synecology of *Erica cinerea* L. communities in the Alps (north-western Italy)." *Acta Botanica Gallica* 157 (3): 493–504.
- Lu, Y., D. M. Waller, and P. David. 2005. "Genetic variability is correlated with population size and reproduction in American wild-rice (*Zizania palustris* var. *palustris*, Poaceae) populations." *American Journal of Botany* 92 (6): 990–997.
- Matthies, D., I. Braüer, W. Maibom, and T. Tschardt. 2004. "Population size and the risk of local extinction: empirical evidence from rare plants." *Oikos* 105: 481–488.
- Mott, C. L. 2010. "Environmental constraints to the geographic expansion of plant and animal species." *Nature Education Knowledge* 3 (10): 72.
- Mucina, L., G. Grabherr, and T. Ellmauer. 1993. *Die Pflanzengesellschaften Österreichs 1, Anthropogene Vegetation* [The plant communities of Austria 1, Anthropogenic vegetation]. Jena: G. Fischer.
- Norusis, M.J., 2005. *SPSS 13.0 Statistical Procedures Companion*. Chicago: SPSS Inc.
- Oberdorfer, E. 1983. *Pflanzensoziologische ExcurSIONflora* [Phytosociological Flora]. Stuttgart: E. Ulmer.
- Oostermeijer, J. G. B., R. Van't Veer, and J. C. M. Den Nijs. 1994. "Population structure of the rare, long-lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in the Netherlands." *Journal of Applied Ecology* 31: 428–438.
- Ouborg, N. J. 1993. "Isolation, population size and extinction: the classical and metapopulation approaches applied to vascular plants along the Dutch Rhine system." *Oikos* 66: 298–308.
- Ozenda, P. 1985. *La végétation de la chaîne alpine dans l'espace montagnard européen* [The vegetation of the Alps within the European mountains]. Paris: Masson.
- Pascale, M. 2006. "Nuove stazioni di alcune specie di Fanerogame rare nelle Alpi cuneesi (Piemonte, Italia Nord-occidentale) [New finds of some rare Angiosperms in the Alps of Cuneo, Piedmont, north-western Italy]." *Bollettino Museo Regionale Scienze Naturali Torino* 23: 730–731.
- Pérez, I., J. Anadón, and M. Díaz. 2012. "What is wrong with current translocations? A review and a decision-making proposal." *Frontiers in Ecology and the Environment* 10: 494–501.
- Pignatti, S. 1982. *Flora d'Italia*. Bologna: Edagricole.
- Pluess, A. R., and J. Stöcklin. 2004. "Population genetic diversity of the clonal plant *Geum reptans* (Rosaceae) in the Swiss Alps." *American Journal of Botany* 91 (12): 2013–2021.
- Probo, M., A. Massolo, M. Lonati, D. W. Bailey, A. Gorlier, L. Maurino, and G. Lombardi. 2013. "Use of mineral mix supplements to modify the grazing patterns by cattle for the restoration of sub-alpine and alpine shrub-encroached grasslands." *Rangeland Journal* 35 (1): 85–93.
- Quantum Gis Development Team. 2012. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. Accessed 15 June 2012. <http://qgis.osgeo.org>
- Rossi G., C. Montagnani, D. Gargano, T. Abeli, S. Ravera, A. Cogoni, G. Fenu, et al. 2013. *Lista rossa della Flora italiana. 1. Policy species e altre specie minacciate* [Red List of

- Italian Flora. Policies and threatened species]. Comitato Italiano IUCN e Ministero dell'Ambiente e della Tutela del Territorio e del Mare. Roma: Stamperia Romana.
- Rossi, G., C. Montagnani, T. Abeli, D. Gargano, L. Peruzzi, G. Fenu, S. Magrini, et al. 2013. "Are Red Lists useful for plant conservation? The New Red List of the Italian Flora in the perspective of National Conservation policies." *Plant Biosystems*. DOI:10.1080/11263504.2013.868375.
- SILENE. 2013. Système d'Information et de Localisation des Espèces Natives et Envahissantes – Cartographie. Accessed 10 Septembre 2013. <http://flore.silene.eu/index.php?cont=accueil>
- Soil Survey Staff. 1999. *Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys*. Washington: US Government Printing Office
- Soliani, L. 2004. *Manuale di statistica per la ricerca e la professione* [Handbook of Statistics for research and profession]. Parma: Uni Nova.
- Stöcklin, J., and M. Fischer. 1999. "Plants with longer-lived seeds have lower local extinction rates in grassland remnants 1950-1985." *Oecologia* 120: 539–543.
- Theurillat, J. P., D. Aeschimann, P. Küpfer, and R. Spichiger. 1994. "The higher vegetation units of the Alps." *Colloques Phytosociologiques* 23: 190–239.
- Tocco, C., M. Probo, M. Lonati, G. Lombardi, M. Negro, B. Nervo, A. Rolando, and C. Palestini. 2013. "Pastoral practices to reverse shrub encroachment of sub-alpine grasslands: dung beetles (Coleoptera, Scarabaeoidea) respond more quickly than vegetation." *PLoS ONE* 8 (12): e83344. doi:10.1371/journal.pone.0083344.
- Valle, M., 2013. *Spazio transfrontaliero Maritime Mercantour. La diversità naturale e culturale al centro dello sviluppo sostenibile e integrato del territorio*. Beinasco: AGIT MARIOGROS.
- van der Maarel, E. 1979. "Transformation of cover-abundance values in phytosociology and its effects on community similarity." *Vegetatio* 39: 97–144.
- van Rossum, F., X. Vekemans, E. Gratia, and P. Meerts. 2003. "A comparative study of allozyme variation in peripheral and central populations of *Silene nutans* L. (Caryophyllaceae) from western Europe: implications for conservation." *Plant Systematics and Evolution* 242: 49–61.
- Weber, H. E., J. Moravec, and J. P. Theurillat. 2000. "International code of phytosociological nomenclature." *Journal of Vegetation Science* 11: 739–768.
- Young, A., T. Boyle, and T. Brown. 1996. "The population genetic consequences of habitat fragmentation for plants." *Trends in Ecology & Evolution* 11: 413–418.

Figure captions

Figure 1. Location of the studied populations and potential species range. EOO: extent of occurrence; AOO: area of occupancy.

Figure 2. Relationship between altitude (m) and yearly precipitation (mm) for the located seven populations of *P. fruticosa*: (progressive numbers according to Table 1). Lines show Gams' continentality index thresholds (Gams' angle) and define the ecological districts according to Ozenda (1985).

Figure 3. Dendrogram of phytosociological surveys (Ward's method, similarity ratio). Plot codes (PL01÷13), population codes (POP1÷7) and their repartition in clusters (GR01÷3) are shown below the dendrogram.

Figure 4. Univariate relationships between the number of well-developed achenes and isolation, quantified as (a) minimum distance from the nearest occupied plot, and (b) overall isolation (Isolation index, I_n). * $p < 0.05$; *** $p < 0.001$.

Appendix I. Date and accidental species of relevés (Table 1)

PL01: 29/06/2010; *Asphodelus albus* (1), *Aster alpinus* (1), *Astragalus monspessulanum* (1), *Alchemilla alpina* s.l. (+), *Arabis brassica* (+), *Arabis hirsuta* (+), *Centaurea triumfettii* (+), *Cerastium arvense* (+), *Cruciata glabra* (+), *Dianthus sylvestris* (+), *Erysimum jugicola* (+), *Hieracium sylvaticum* (+), *Laburnum alpinum* (+), *Leucanthemum coronopifolium* (+), *Lychnis flos-jovis* (+), *Myosotis alpestris* (+), *Sempervivum montanum* (+), *Silene rupestris* (+). PL02: 19/07/2010; *Alchemilla alpina* s.l. (+), *Astragalus monspessulanum* (+), *Gnaphalium norvegicum* (+), *Myosotis alpestris* (+), *Platanthera chlorantha* (+), *Ranunculus montanus* (+), *Sedum annuum* (+), *Silene rupestris* (+). PL03: 26/07/2010; *Achillea erba-rotta* (+), *Aster alpinus* (+), *Rubus fruticosus* (+), *Saxifraga aspera* (+), *Saxifraga stellaris* (+), *Sedum annuum* (+), *Silene rupestris* (+), *Viola rupestris* (+). PL04: 26/07/2010; *Agrostis alpina* (+), *Saxifraga stellaris* (+). PL05: 26/07/2010; *Polystichum lonchitis* (+), *Potentilla crantzii* (+), *Soldanella alpina* (+). PL06: 26/07/2010; *Cirsium spinosissimum* (+), *Potentilla crantzii* (+), *Sedum anacampseros* (+), *Soldanella alpina* (+). PL07: 26/07/2010; *Silene rupestris* (1), *Agrostis alpina* (+), *Aster alpinus* (+), *Luzula sylvatica* (+), *Melica nutans* (+), *Potentilla crantzii* (+), *Sempervivum aracnoideum* (+). PL08: 11/08/2010; *Alchemilla alpina* s.l. (+), *Athyrium filix-foemina* (+), *Cirsium spinosissimum* (+), *Polystichum lonchitis* (+). PL11: 29/06/2010; *Carex flacca* (2), *Cruciata glabra* (+), *Leucanthemum coronopifolium* (+), *Linum catharticum* (+), *Silene rupestris* (+), *Solidago virgaurea* (+), *Sorbus aucuparia* (+). PL09: 11/08/2010; *Athyrium filix-foemina* (+), *Polystichum lonchitis* (+), *Potentilla crantzii* (+), *Ranunculus montanus* (+), *Sempervivum aracnoideum* (+), *Solidago virgaurea* (+). PL10: 10/08/2010; *Potentilla crantzii* (1), *Ranunculus montanus* (1), *Agrostis tenuis* (+), *Alchemilla alpina* s.l. (+). PL12: 29/06/2010; *Carex flacca* (1), *Lamium garganicum* (1), *Asphodelus albus* (2), *Alchemilla alpina* s.l. (+), *Arabis brassica* (+), *Cerastium arvense* (+), *Cruciata glabra* (+), *Fragaria vesca* (+), *Geum rivale* (+), *Hieracium sylvaticum* (+), *Leucanthemum coronopifolium* (+), *Linum catharticum* (+), *Lychnis flos-jovis* (+), *Mentha longifolia* (+), *Pulmonaria picta* (+), *Saxifraga stellaris* (+), *Senecio fuchsii* (+). PL13: 13/07/2010; *Clematis alpina* (1), *Carex flacca* (+), *Lonicera* sp. (+), *Saxifraga aspera* (+), *Sedum anacampseros* (+), *Solidago virgaurea* (+), *Tulipa australis* (+).

Table 1. Code, location and size [number of total individuals (= genets)] of the studied populations.

Code	Municipality	Location	Finding	Altitude(m a.s.l.)	Population area(m²)	Population size (n. of individuals)
POP1	Entracque	Piano del Praiet	confirmed	1825	4.5	11
POP2	Entracque	Piano del Praiet	confirmed	1807-1812	24	13
POP3	Entracque	Vallone di Pantacreus	confirmed	2103	27	10
POP4	Entracque	Vallone delle Rovine	newfind	2050	0.2	1
POP5	Valdieri	Vallone della Meris	newfind	2072	20	20
POP6	Valdieri	Vallone della Meris	newfind	1900	2	2
POP7	Valdieri	Vallone della Meris	confirmed	2211-2320	~ 26000	~ 18000

Table 2. Phytosociological surveys.

Plot code	PL01	PL02	PL03	PL04	PL05	PL06	PL07	PL08	PL09	PL10	PL11	PL12	PL13		
Cluster groups	GR1		GR2								GR3				
Altitude (m a.s.l.)	1825	2050	2072	2316	2286	2270	2261	2302	2211	1900	1812	1807	2103		
Aspect (°N)	124	168	136	100	94	84	102	90	60	322	108	104	84	Presence	Frequency
Slope (°)	34	40	47	25	35	27	27	26	33	18	46	38	70		
Upper shrub cover (5 m < height < 1.3 m) (%)	0	0	0	0	0	0	0	0	0	0	0	0	20		
Lower shrub cover (height < 1.3 m) (%)	10	2	25	45	20	10	20	5	10	10	10	5	75		
Herbaceous cover (%)	40	70	50	40	45	40	55	35	65	80	70	70	25		
Bare ground (%)	10	10	5	5	15	10	10	3	5	10	5	10	10		
Rock cover (%)	40	20	30	10	20	40	15	55	20	15	15	15	10		
Charact. species of <i>Centaureo-Festucetum spadiceae</i>															
<i>Hypericum richeri</i>	+	.	.	+	+	+	+	+	+	.	.	+	+	9	IV
<i>Centaurea uniflora</i>	+	+	+	+	.	.	+	.	+	+	+	.	.	8	IV
<i>Silene nutans</i>	1	1	+	3	II
<i>Lilium bulbiferum</i> subsp. <i>croceum</i>	.	+	+	.	2	I
<i>Trifolium montanum</i>	+	1	I
Charact. species of <i>Festucion varia</i>															
<i>Festuca scabriculum</i>	.	2	1	1	.	+	2	.	2	.	.	.	2	7	III
<i>Potentilla grandiflora</i>	+	1	.	.	.	+	.	.	+	.	+	+	.	6	III
<i>Potentilla valderia</i>	1	1	I
Charact. species of <i>Festucetalia spadiceae</i>															
<i>Plantago serpentina</i>	+	.	.	.	+	+	+	+	+	+	+	.	.	7	III
<i>Festuca paniculata</i>	2	3	+	1	4	II
<i>Veronica fruticans</i>	+	+	2	I
<i>Erigeron alpinus</i>	.	.	1	1	I
<i>Geum montanum</i>	+	1	I
Charact. species of <i>Caricetea curvulae</i>															
<i>Dianthus neglectus</i>	.	+	+	+	.	+	.	.	+	+	.	.	.	7	III
<i>Phyteuma betonicifolium</i>	+	1	+	+	.	.	.	+	.	5	II
<i>Pedicularis kernerii</i>	.	.	.	+	+	+	.	+	4	II
<i>Juncus trifidus</i>	.	1	+	2	I
<i>Euphrasia alpina</i>	.	+	+	2	I
<i>Gentiana kochiana</i>	+	.	.	.	+	.	.	2	I
<i>Luzula lutea</i>	.	+	1	I
<i>Leontodon helveticus</i>	+	1	I
<i>Hieracium glanduliferum</i>	+	1	I
<i>Agrostis rupestris</i>	+	1	I
Charact. species of <i>Caricetum frigidae</i> and <i>Caricion davallianae</i>															
<i>Potentilla fruticosa</i>	2	1	2	3	2	2	2	2	1	1	2	1	4	13	V
<i>Carex frigida</i>	.	.	2	2	2	3	2	2	+	1	+	+	1	11	V
<i>Tofieldia calyculata</i>	.	.	+	+	+	+	+	+	.	.	+	+	.	8	IV
<i>Trichophorum alpinum</i>	.	.	2	1	1	.	.	+	4	II
<i>Carex davalliana</i>	+	1	I
Charact. species of <i>Caricetalia davallianae</i>															
<i>Parnassia palustris</i>	.	.	+	+	.	+	+	+	.	+	+	.	.	7	III
<i>Pinguicula vulgaris</i>	.	.	1	+	.	.	.	+	.	.	+	+	.	5	II
<i>Juncus alpino-articulatus</i>	.	.	+	1	I
Charact. species of <i>Scheuchzerio-Caricetea fuscae</i>															
<i>Bartsia alpina</i>	.	.	+	+	1	1	+	+	.	.	+	.	.	7	III
<i>Eriophorum angustifolium</i>	.	.	.	+	1	I
<i>Carex capillaris</i>	+	1	I
<i>Carex panicea</i>	+	.	1	I
Companion species															
Ingr. species of <i>Seslerietea albicantis</i>															
<i>Carduus carlinaefolius</i>	+	1	.	.	.	+	+	+	+	+	+	2	.	8	IV
<i>Festuca violacea</i>	.	+	.	2	2	2	2	.	2	7	III
<i>Carex ornithopoda</i>	+	.	.	.	+	+	.	+	.	.	+	.	+	5	II
<i>Pedicularis gyroflexa</i>	.	+	+	.	+	.	+	4	II
<i>Biscutella laevigata</i>	+	1	+	.	.	.	+	.	3	II
<i>Senecio doronicum</i>	+	+	2	I
<i>Bupleurum ranunculoides</i>	+	+	+	2	I
<i>Scabiosa vestita</i>	+	1	I
<i>Acinos alpinus</i>	+	+	1	I
<i>Stachis pradica</i>	.	+	1	I
<i>Dianthus furcatus</i>	.	+	+	1	I
<i>Thesium alpinum</i>	+	1	I
Ingr. species of <i>Asplenietea trichomanis</i>															
<i>Rhodiola rosea</i>	.	.	+	.	+	+	+	.	1	2	.	.	.	6	III
<i>Epilobium collinum</i>	.	.	+	+	+	3	II
<i>Saxifraga paniculata</i>	.	.	.	+	+	2	I
<i>Primula latifolia</i>	.	.	+	1	I
<i>Silene cordifolia</i>	+	1	I
<i>Asplenium trichomanes</i>	+	1	I
<i>Primula marginata</i>	+	.	.	1	I
<i>Valeriana tripteris</i>	+	.	1	I
Ingr. species of <i>Quercio-Fagetea</i> and <i>Rhamno-Prunetea</i>															
<i>Daphne mezereum</i>	.	.	.	+	+	+	.	+	1	+	.	.	.	6	III
<i>Luzula nivea</i>	+	.	1	+	1	.	4	II

<i>Dryopteris filix-mas</i>	+	+	+	.	3	II
<i>Avenella flexuosa</i>	.	+	+	2	I
<i>Viola riviniana</i>	.	.	+	+	2	I
<i>Poa nemoralis</i>	+	+	2	I
<i>Cotoneaster integerrimus</i>	+	+	2	I
<i>Rhamnus alpina</i>	+	1	I
<i>Convallaria majalis</i>	.	.	+	1	I
<i>Euphorbia dulcis</i>	1	.	1	I
<i>Luzula albida</i>	+	1	I
Ingr. species of <i>Trifolio-Geranietea sanguinei</i>															
<i>Thalictrum minus</i>	.	.	1	+	1	+	.	+	+	1	III
<i>Anthericum liliago</i>	+	+	+	3	II
<i>Trifolium alpestre</i>	+	+	2	I
<i>Peucedanum oreoselinum</i>	+	1	I
<i>Vincetoxicum hirsutiflorum</i>	1	1	I
<i>Clinopodium vulgare</i>	+	1	I
<i>Viola hirta</i>	.	+	1	I
<i>Seseli libanotis</i>	.	.	+	1	I
Ingr. species of <i>Vaccinio-Piceetea</i>															
<i>Juniperus nana</i>	+	.	1	2	+	+	1	+	.	2	.	.	.	8	IV
<i>Rhododendron ferrugineum</i>	.	.	.	1	1	+	+	+	+	+	.	.	.	7	III
<i>Vaccinium gaultherioides</i>	.	.	+	1	+	+	1	+	6	III
<i>Vaccinium myrtillus</i>	+	+	1	.	+	.	4	II
Ingr. species of <i>Calluno-Ulicetea</i> and <i>Nardetalia</i>															
<i>Potentilla erecta</i>	+	.	1	1	1	1	+	.	.	.	2	1	1	9	IV
<i>Nardus stricta</i>	.	+	+	.	+	1	.	+	.	2	+	+	.	8	IV
<i>Festuca nigrescens</i>	.	.	+	.	+	1	.	.	.	2	.	.	2	5	II
<i>Meum athamanticum</i>	.	+	.	.	.	+	.	+	3	II
<i>Botrychium lunaria</i>	.	.	+	+	.	.	+	3	II
<i>Hieracium pilosella</i>	+	+	2	I
<i>Polygala vulgaris</i>	+	+	.	.	2	I
<i>Carex pallescens</i>	+	.	+	.	2	I
<i>Ajuga pyramidalis</i>	+	1	I
<i>Antennaria dioica</i>	+	.	.	.	1	I
<i>Coeloglossum viride</i>	+	.	.	.	1	I
Ingr. species of <i>Mulgedio-Aconitetea</i>															
<i>Veratrum album</i> subsp. <i>lobelianum</i>	.	+	+	1	1	1	1	+	1	.	1	1	.	10	IV
<i>Geranium sylvaticum</i>	.	.	+	+	+	.	+	.	+	.	.	+	.	7	III
<i>Viola biflora</i>	.	.	.	+	+	+	+	+	+	.	.	.	1	7	III
<i>Calamagrostis villosa</i>	.	.	3	2	.	3	4	3	.	5	II
<i>Alnus viridis</i>	.	.	2	+	1	+	4	II
<i>Rosa pendulina</i>	+	.	.	+	.	.	+	3	II
<i>Peucedanum ostruthium</i>	.	.	+	+	+	.	3	II
<i>Agrostis schraderana</i>	+	+	.	+	3	II
<i>Polygonatum verticillatum</i>	+	+	.	2	I
<i>Aconitum variegatum</i>	+	1	2	I
<i>Aconitum vulparia</i>	+	1	2	I
Ingr. species of <i>Festuco-Brometea</i>															
<i>Galium obliquum</i>	+	+	+	+	1	5	II
<i>Carlina acaulis</i>	+	+	.	.	+	+	.	.	.	+	.	.	.	5	II
<i>Hippocrepis comosa</i>	+	+	.	.	.	+	+	.	.	5	II
<i>Festuca curvula</i>	1	2	+	.	+	+	.	.	.	5	II
<i>Stachis recta</i>	1	+	+	.	3	II
<i>Bunium bulbocastanum</i>	+	+	+	3	II
<i>Asperula aristata</i>	+	.	.	.	+	.	.	2	I
<i>Briza media</i>	1	+	.	2	I
<i>Primula veris</i> subsp. <i>columnae</i>	+	+	.	2	I
<i>Armeria plantaginea</i>	+	1	I
<i>Stipa pennata</i>	+	1	I
<i>Brachypodium rupestre</i>	+	1	I
<i>Teucrium chamaedrys</i>	.	.	+	1	I
<i>Allium sphaerocephalon</i>	+	.	1	I
<i>Carex caryophyllaea</i>	+	.	1	I
<i>Sanguisorba minor</i>	+	.	1	I
Ingr. species of <i>Molinio-Arrhenatheretea</i>															
<i>Lotus corniculatus</i>	+	.	.	.	+	.	+	.	+	.	+	+	.	7	III
<i>Trollius europaeus</i>	.	.	1	.	.	+	1	.	.	.	+	1	.	5	II
<i>Trifolium pratense</i> subsp. <i>nivale</i>	+	+	.	+	+	+	.	.	.	5	II
<i>Rumex acetosa</i>	+	+	1	1	.	.	.	4	II
<i>Leontodon hispidus</i>	+	.	1	.	.	.	+	+	.	4	II
<i>Achillea stricta</i>	+	.	+	+	.	.	+	.	4	II
<i>Poa alpina</i>	+	.	.	+	+	.	.	.	3	II
<i>Crepis paludosa</i>	.	.	+	+	.	2	I
<i>Crocus albiflorus</i>	+	1	I
<i>Leontodon autumnalis</i>	+	.	.	.	1	I
<i>Trisetum flavescens</i>	+	.	.	.	1	I
<i>Dactylis glomerata</i>	2	.	1	I
<i>Arrhenatherum elatius</i>	+	.	1	I
Other companion species															
<i>Carex sempervirens</i>	1	2	+	1	2	+	2	2	2	.	+	.	.	10	IV
<i>Astrantia minor</i>	.	.	1	+	1	1	1	+	+	.	+	+	.	9	IV
<i>Orchis maculata</i>	.	.	+	+	1	1	+	+	.	.	1	+	+	9	IV
<i>Thymus serpyllum</i> s.l.	+	1	.	.	1	.	+	+	+	.	.	+	.	8	IV
<i>Alchemilla vulgaris</i> s.l.	+	.	.	.	1	+	.	+	+	2	.	+	+	8	IV
<i>Campanula scheuchzeri</i>	.	+	+	+	+	.	+	+	+	+	.	.	.	8	IV
<i>Saxifraga aizoides</i> L.	.	.	+	+	+	+	1	+	.	2	.	.	.	7	III

<i>Allium schoenoprasum</i>	.	.	+	2	2	1	1	1	+	7	III
<i>Anthoxanthum alpinum</i>	+	+	.	.	+	+	+	+	6	III
<i>Aster bellidiastrum</i>	+	.	.	.	+	+	+	+	.	.	+	.	.	6	III
<i>Leucanthemum ceratophylloides</i>	.	.	.	+	+	+	1	1	+	6	III
<i>Rubus idaeus</i>	+	+	+	1	.	3	II

See Appendix I for accidental species

Table 3. Differences in environmental, structural and growth/reproductive performance variables within groups, tested by univariate ANOVA (F = F-test value; p = significance; significantly different variables at $p \leq 0.05$ in bold). Group means were compared with Bonferroni post-hoc range test ($p \leq 0.05$), sites with no letters in common were significantly different. Means \pm standard error are shown.

Variables	GROUP 1	GROUP 2	GROUP 3	F	p
Topographic/environmental variables					
Elevation (m a.s.l)	1938 \pm 112.5 ab	2202 \pm 51.1 b	1907 \pm 97.8 a	5.4	0.026
Southness (°)	146 \pm 22	101 \pm 9.5	99 \pm 7.4	2.8	0.109
Slope (°)	37 \pm 3.0 ab	30 \pm 3.1 a	51 \pm 9.6 b	4.6	0.037
Distance from creek (m)	56.0 \pm 50.0 b	0.5 \pm 0.20 a	5.0 \pm 0.40 a	10.8	0.031
Soil pH	6.2 \pm 0.10 ab	6.4 \pm 0.07 b	6.0 \pm 0.09 a	5.1	0.030
<i>Potentilla fruticosa</i> structure					
Density (individuals plot ⁻¹)	6.0 \pm 5.00	24.1 \pm 6.12	4.3 \pm 0.88	2.6	0.121
Average plant height (cm)	26.0 \pm 6.00 a	27.8 \pm 1.59 a	56.0 \pm 10.34 b	4.2	0.003
Average plant diameter (cm)	45.3 \pm 9.70 a	42.7 \pm 4.40 a	103.7 \pm 34.61 b	5.0	0.031
Total canopy area (m ² plot ⁻¹)	2.1 \pm 1.81	5.2 \pm 1.77	4.0 \pm 1.70	0.4	0.675
<i>Potentilla fruticosa</i> traits					
Length of vegetative shoots (cm)	14.5 \pm 1.67 ab	12.5 \pm 0.74 a	18.0 \pm 1.48 b	6.8	0.013
N° of achenes per flower	0.7 \pm 0.55 a	14.5 \pm 3.10 b	6.1 \pm 30.31 a	4.9	0.036