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**A BETTER UNDERSTANDING OF ECOLOGICAL CONDITIONS FOR
LEONTOPODIUM ALPINUM IN THE SWISS ALPS**

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Mélanie ISCHER

Directeur : Dr., Pascal, Vittoz

Expert (s) : Dr., Sonja, Wipf

Département d'Ecologie et d'Evolution

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5 Mélanie Ischer¹, Anne Dubuis¹, Antoine Guisan¹ & Pascal Vittoz^{1*}

6 ¹*Department of Ecology and Evolution, University of Lausanne, CH-1015 Lausanne,*
7 *Switzerland.*

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14 * Corresponding author:

15 Pascal Vittoz, Department of Ecology and Evolution, Laboratory of Biological Conservation,
16 University of Lausanne, CH-1015 Lausanne, Switzerland.

17 e-mail: pascal.vittoz@unil.ch
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21 **ABSTRACT**

22 **Questions:** Scientific knowledge about the ecology of the emblematical species
23 *Leontopodium alpinum* is scarce. Although the species is not yet threatened, there are hints of
24 decreasing abundance. In this study, we aimed at answering the following questions: What are
25 the optimal ecological conditions for *L. alpinum* in natural environments? Does sheep pasture
26 affect the presence of *L. alpinum*?

27 **Location:** Swiss Alps.

28 **Methods:** the geographic distribution of *L. alpinum* was modeled using species distribution
29 models. Those models also served as basis to define field sampling. The field vegetation plots
30 were exhaustively inventoried and ecological factors (including soil conditions) were
31 recorded. A redundancy analysis was performed on these data. Published phytosociological
32 relevés completed our own data to perform a correspondence analysis on which ecological
33 indicator values were projected. Those analyses were computed to find out ecological features
34 characterizing the different groups of relevés as well as *L. alpinum*'s ecology.

35 **Results:** *L. alpinum* needs calcareous soils with a pH value varying from alkaline to neutral.
36 This species is not able to grow when grass cover is high. *Seslerion* and *Elyinion* are the two
37 main vegetation types where *L. alpinum* is able to grow, but we found out that the *Caricion*
38 *firmae* is favorable as well, what was actually not indicated in previous literature. We were
39 not able to assess a potential sheep effect in this study.

40 **Conclusions:** In this study, we improved the knowledge about the optimal ecological
41 conditions for *L. alpinum*. We completed the list of the favorable vegetation types for *L.*
42 *alpinum* and we highlighted the important ecological conditions for its growth.

43

44 **KEYWORDS**

45 Alpine grasslands; *Caricion firmae* ; *Elynion*; grazing; *Leontopodium alpinum*; plant cover;
46 *Seslerion*; soil pH; species distribution models;

47

48 **NOMENCLATURE**

49 Aeschimann, D., Heitz, C., Palese, R., Perret, P., Moser, M., 1996. *Index synonymique de la*
50 *Flore de Suisse. Documenta Floristicae Helvetiae 1*, Centre du Réseau Suisse de Floristique,
51 Geneva.

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53 **RUNNING HEAD**

54 Ecology of *Leontopodium alpinum*

55

56 **INTRODUCTION**

57 *Leontopodium alpinum*, the alpine Edelweiss is a perennial herbaceous plant growing on
58 calcareous rocky grasslands, steep rock precipices and alpine pastures (Thompson 1911;
59 Staffebach 2009). It is a 2-12 cm high hemicryptophyte of the Asteraceae family. *L. alpinum*
60 is characterized by its inflorescence, surrounded by white and woolly bracts. The under side
61 of its leaves are also covered by those white and woolly hairs. The flowering season of *L.*
62 *alpinum* ranges from July to September. Edelweiss flowers are visited by a large range of
63 insects belonging to 29 families but only a few of them are responsible for their pollination
64 (Erhardt 1993). In Switzerland, *L. alpinum* is rarely found below 1'300 m a.s.l. It usually
65 ranges from 1'600 m a.s.l. to 3'000 m a.s.l. It is found especially in two distinct plant
66 communities: *Seslerion* and *Elynion* (Delarze & Gonseth 2008). The environment favourable
67 to those communities is characterized by alkaline to neutral calcareous soils. In *Seslerion*,
68 soils are superficial, dry and stony. *Seslerion* is very rich in term of species. Most often, it is
69 found between 1000 m a.s.l. and 2400 m a.s.l. on sunny slopes. Typical species of this

community are *Sesleria cearulea*, *Carex sempervirens*, *Festuca curvula* and *Carex austroalpina* (Delarze & Gonseth 2008). On the other hand, *Elynion* soils are mainly composed of thin, basic particles and are protected from erosion by *Elyna myosuroides* roots (Delarze & Gonseth 2008). This community, characterized by clumps of *Elyna myosuroides*, is less frequent because it colonizes only small area on windy crests, between 2000 m a.s.l. and 3000 m a.s.l. Typical species found in *Elynion* are *Elyna myosuroides*, *Antennaria carpatica* and *Agrostis alpina* (Delarze & Gonseth 2008).

L. alpinum is also well known for its pharmaceutical properties. Indeed, *L. alpinum* is known for its antibacterial (Dobner et al. 2003) and anti-inflammatory (Dobner et al. 2004) properties as well as for its analgesic effects (Speroni et al. 2006). In Switzerland, *L. alpinum* var *Helvetia* has been domesticated by the Agroscope Changins-Wädenswil (ACW). Nowadays, it is cultivated in Val d'Entremont and Val de Bagnes (Carron et al. 2007). It is used to produce anti-aging creams, solar lotions, liquor and chocolates (Martin et al. 2003; Vigneron et al. 2005; Carron et al. 2007).

This species mostly found in alpine areas ranging from the Pyrenees to the Central Balkans in Bulgaria (Hegi, 1965) except for south-eastern Bulgaria and in the Appennini, in Italy (Flora Europea, <http://rbg-web2.rbge.org.uk>). It is native to the Tibetan Plateau, but the exact history of its migration from Asia to Eastern Europe is not solved nowadays. It might have migrated during the Pleistocene, when a continual distribution between Asia and Europe was possible (Blösch et al. 2010). In Europe, only two taxa of the genus *Leontopodium* are observed, which are *L. alpinum* and *L. nivale* (Blösch et al. 2010). *L. nivale* has a much more restricted geographic distribution and can only be found in Bulgaria, Italy and Yugoslavia (Flora Europea, <http://rbg-web2.rbge.org.uk>). As in Switzerland only *L. alpinum* is present, this study will not take *L. nivale* into account.

94 *L. alpinum* has a high symbolic value in alpine countries and is prized by tourists and
95 botanists (Erhardt 1993) to such an extent that Schröter (1926) wrote that more people died by
96 trying to pick it up than by climbing high alpine peaks. Its name is coming from German and
97 “Edel” means “noble” and “weiss” means “white” (Dweck 2004). This attraction for *L.*
98 *alpinum* is probably due its particular shape, its rareness and its legendary inaccessibility.

99 At the beginning of the last century, only alpinists were able to pick up Edelweiss but later
100 on, the Alps became more accessible and it has been picked up by a large part of people,
101 causing a drastic decrease of this species (Jean 1947). The first canton in Switzerland which
102 protected *L. alpinum* was Appenzell Ausserrhoden in 1959 (CRSF website). Fribourg
103 followed this decision in 1973, Valais in 2000 and Vaud only in 2005 (CRSF website).
104 However, these measures were taken without any precise data illustrating clearly the state of
105 *L. alpinum* and actually, the species is considered as Least Concerned (i.e. not threatened) in
106 Switzerland according to Moser et al. (2002). According to Rabinowitz’s seven rarity classes
107 (Rabinowitz et al. 1981), the Edelweiss would be part of the groupe A, a group containing
108 species covering a wide geographic range, able to constitute large local populations but
109 needing a specific habitat. *L. alpinum* has quite a large distribution (Central and Southern
110 European Mountains) and can constitute large local populations. However, one of its specific
111 habitats (*Elynion*) is worthy of protection according to the Swiss ordinance concerning the
112 protection of nature and landscape (OPN 451.1). *L. alpinum* cannot be considered as a
113 common species because it only grows on calcareous areas, which have a restricted
114 distribution in the higher Alps. Furthermore, the acidification of calcareous soils by lixiviation
115 restricts *L. alpinum*’s potential habitat. Finally, Elynion covers only small surfaces (ridges),
116 reducing the possibility for *L. alpinum* to constitute large populations. Hence, not considered
117 as rare and threatened, *L. alpinum* is not a common species with mostly small populations.

Despite *L. alpinum* is an emblematical species in the Alps, particularly in Switzerland, only limited scientific information about its ecology is available.

In general, before deciding of any conservation plan, species conservation status has to be established (IUCN 2001) by getting reliable data on its distribution and detailed knowledge about its ecology. This may be complicated, particularly when species knowledge is weak (Franc et al. in press). The low encounter rate as well as the protection of rare species makes the study more difficult compared to common species. Thus, standard random sampling methods applied to rare species may be totally inefficient (Rushton et al. 2004).

As *L. alpinum* is not a common species, species distribution models (SDMs) were used to increase the sampling success for the fieldwork part. SDMs are efficient tools to quantify the distribution of species in a spatially explicit and statistical way (Guisan & Thuiller 2005). A large number of SDMs varieties are used to study geographic characteristics of plant and animal species distributions (Franklin 1995; Guisan & Zimmermann 2000; Scott et al. 2002; Jeschke et al. 2008; Kery et al. 2010). Different types of SDMs were developed to study various features of individual plant species (Bakkenes et al. 2002) or plant communities (Zimmermann & Kienast 1999). They are used to study the spread of invasive species (Smolik et al. 2010), to predict the distribution and dispersal of a target species under a climate change (Engler & Guisan 2009), and can also be used to improve the sampling of rare species (Guisan et al. 2006). A few successful examples of SDMs applied to rare species were published recently (Engler et al. 2004; Stettler et al. 2007; Hu & Jiang 2010), but rare species distribution modelling is still improving. For example, Wu and Smeins (2010) published a novel approach about the way of studying rare species by using multiple-scale distribution models.

Another way to study the ecology of a target species is to use a phytosociological approach. For a long time, scientists observed that plants precisely reflect the environmental

conditions. However, the use of plants as bio-indicators implies the quantification of such information (Diekmann 2003). A first study done by Ellenberg (Ellenberg 1950) lead to the publication of a list of ecological indicator values (Ellenberg 1974). For Switzerland, Landolt (1977) published an alternative list of ecological indicator values that was updated and completed in 2010 (Landolt et al. 2010). Some studies used phytosociological relevés and ecological indicator values as a tool to find out important environmental factors for a target species (Hermy et al. 1999; Rodriguez-Rojo et al. 2001; Bardat et Hugonnot 2002; Vittoz et al. 2006). In this paper, we used phytosociological relevés and Landolt et al. (2010) ecological indicator values to have a broader view of the ecological conditions where *L. alpinum* can grow in Switzerland and to find out important environmental factors for *L. alpinum*.

However, neither SDMs and nor a phytosociological approach provide information about biotic factors. It is known that herbivores affect species composition of grasslands (Milchunas et al. 1988; Veen et al. 2010). In Switzerland, the number of sheep is still increasing in the Alps (Federal Statistical Office 2010). They tend to graze on the upper part of the pasturage and appreciate staying on released crests (Taylor et al. 1984). Sheep may thus be a potential threat for *L. alpinum*. We wanted to check if sheep pasture has an effect on *L. alpinum* because sheep has a habitat similar to *L. alpinum*'s one. To find out an eventual sheep pasture effect, sampling was stratified using the presence and absence of sheep pasture.

The aim of the present study was to get a better understanding of the ecology of *L. alpinum*, by modelling its geographic distribution in Switzerland and by collecting ecological data including soil features on the field. One initial model was used to predict favourable areas in which to select sampling sites in order to check the model's predictions and to collect reliable data on *L. alpinum*'s ecology. Then a redundancy analysis was performed using data collected during fieldwork to highlight important ecological indicator for *L. alpinum*. Finally

167 a clustering analysis on which Landolt's ecological indicator values were projected was
168 computed to find out in which plant community *L. alpinum* is able to occur.

169 We were expecting that the soil pH is a very important factor for *L. alpinum* to grow (a
170 high pH value preferred over a low one), as well as the topographic position (crests should be
171 more appreciated by *L. alpinum*). Furthermore, we were also expecting to find *L. alpinum*
172 more frequently in *Elynion* and *Seslerion* than in other vegetation types.

173

174 **MATERIAL & METHODS:**

175 **STUDY AREA**

176 Our study area consists of the Swiss Alps, a mountain range occupying 60% of the Swiss
177 territory (fig. 1). The Alps are considered as the most prominent mountain range in Central
178 Europe (Kuhlemann 2007). The Swiss Alps are characterized by their highest summit, the
179 Pointe Dufour, rising to 4'634 m a.s.l., and they have an east-west orientation (Engler et al.
180 2004). Due to this orientation, they stop the rainy clouds coming from the Atlantic Ocean and
181 the North Sea and thus are responsible for the suboceanic climate. Indeed, in Switzerland
182 there is only one floristic unit: the medio-european or subatlantic domain (Ozenda 1982).
183 However, a large climate difference is observed between the outer and inner Alps (see fig.1).
184 The outer Alps are characterized by a humid climate and the inner Alps by a weather due to
185 the dam effect caused by the mountains.

186 Because of time and financial reasons, fieldwork area was restricted to the alpine regions
187 of three cantons, which are Fribourg, Vaud and Valais.

188

189 **SPECIES DATA**

190 Two kinds of data were used. First, to compute a species distribution model and second,
191 to perform the ecological analysis.

Original data used to compute the models were provided by different sources: the Swiss Floristic Network (CRSF), data originating from projects conducted in the spatial ecology group at the university of Lausanne, the vegetation plots of J.L. Richard (not published) and finally various vegetation plots sampled in Zermatt. They were provided as presence data or phytosociological relevés. Only presences having a horizontal accuracy of 100 meters or less were used to compute the model. 405 presences of *L. alpinum* throughout the Swiss Alps were available to build the initial model. However, to avoid spatial autocorrelation, only 206 presences with a minimum distance of 250 m between each other were selected. As no absences were available to compute models, the generation of pseudo-absences was necessary (Engler et al. 2004).

Braun-Blanquet's (Braun-Blanquet 1969), Reinalter's (Reinalter 2004), Schütz's (from Forschungsanstalt für Wald, Schnee und Landschaft (WSL)) and Galland's (Galland 1984) phytosociological relevés were added to the previous available data to perform ecological analyses. 246 *L. alpinum* vegetation records were available for the ecological analyzes.

ENVIRONMENTAL DATA

Occurrence predictors included in the model are quantitative and their description can be found in Table 1. Maps of solar radiations, average moisture index, average slope, the topographic position and the annual degree-days were calculated thanks to the Swiss meteorological network and the 25-m digital elevation model (DEM) (Table 1; see Zimmermann and Kienast 1999 for methodology). Maps were calculated with a resolution of 100 meters.

To reduce the area of model calculation, a mask was created by removing urbanized areas, glaciers, lakes and non calcareous areas (GT_CH layer provided by the Federal

216 Statistical Office) where *L. alpinum* would not be able to grow. Finally, only pixels with an
217 altitude higher than 1'300 m a.s.l. were retained.

218 Sheep pastures distribution was provided as an ArcGIS (ESRI, Inc., Redland, California)
219 layer by the Agricultural office in cantons of Vaud and Fribourg. As no sheep pasture layer
220 was available in the canton du Valais, the Agricultural office of Valais provided us with maps,
221 which were digitalized in ArcGIS.

222

223 SPECIES DISTRIBUTION MODEL

224 Thanks to the “Generate random point” tool of the ArcGis extention Hawth Tools, 10,000
225 pseudo-absences were generated on the whole country. The models were computed using the
226 R library BioMod (Thuiller et al. 2009). Five models were computed to get a reliable
227 probability of *L. alpinum*'s presence. Generalized Linear Models (GLM) (McCullagh and
228 Nelder 1989), Generalized Additive Models (GAM) (Hastie and Tibshirani 1990),
229 Generalized Boosting Models (GBM) (Ridgeway 1999; Friedman et al. 2000; Friedman
230 2001), Multiple Adaptive Regression Splines (MARS) (Friedman 1991) and RandomForest
231 (RF) (Brieman 2001; Brieman 2002) were performed. A polynomial term and a stepwise
232 procedure (computed with a AIC criteria) were used to run the GLM model. 2000 trees were
233 defined to perform the GBM model and the GAM model was run using a spline function with
234 a degree of smoothing of 4. MARS model performed a multivariate adaptive regression spline
235 and the RF run a random forest model. The importance of each variable was calculated by
236 randomizing it, recalculating the model with the randomized variable, correlating this new
237 model with the original one. The importance value was calculated as 1 minus the correlation
238 between the two models (consequently, the higher is the value, the more important is the
239 variable). Each model was repeated five times to assess the variable importance and 20
240 replicates were done with different pseudo-absences on the R library BioMod. The response

241 curves of each predictor variables were computed to understand the link between the
242 presence/absence of *L. alpinum* and the environmental predictors.

243

244 MODEL EVALUATION

245 The Area Under the Receiver Operating characteristic Curve (ROC; Ogilvie and
246 Creelman 1968), the Kappa (Cohen 1960) and the True Skill Statistic (TSS; Doswell et al.
247 1990) index were calculated to evaluate the predictive performance of the previous models.
248 As no independent data were available, data were split randomly into 70/30% parts 20 times.
249 70% was used to perform the model and the 30% left served to evaluate it. Models were
250 evaluated once more after fieldwork (see below) by using presence / absence data collected
251 during fieldwork as independent data to check the reliability of the model's prediction. A
252 contingency table was constructed to compare fieldwork observations to model predictions.
253 The Positive Predictive Power (PPP) and Negative Predictive Power (NPP) (Fielding and Bell
254 1997) were calculated.

255

256 SPATIAL PROJECTION

257 Models were applied with a minimum horizontal accuracy of 100 meters. The Optimized
258 Threshold by ROC was calculated to transform probabilities into presence-absences values.
259 This threshold maximizes the percentage of presences and absences correctly predicted by the
260 models.

261

262 FIELD WORK

263 A stratified sampling was done using sheep pasture layer and predictions of the model.
264 Four strata were defined to check if sheep pasture affects *L. alpinum*'s presence. They are:
265 predicted as favorable for *L.alpinum* with and without sheep, predicted as unfavorable with

266 and without sheep. Based on the above mentioned model, 50 sites per strata were randomly
267 sampled. Sites that were not accessible (very steep slopes, cliffs, etc...) were removed in
268 order to keep 20 sites per strata. The unfavorable sites were sampled randomly in a maximum
269 distance of 1km of a favorable one. Such a distance allowed us to visit an unfavorable site as
270 well as a favorable one during the same day.

271 Fieldwork was done from July to early September 2010. Sites were reached using a
272 Trimble GeoExplorer XM GPS. Once the site was reached, a 50 X 50 m square north oriented
273 was established with a sampling point at the lower left corner. Then *L. alpinum* was searched
274 throughout this plot. If it was found, a 16 m² square centered on the Edelweiss population was
275 delimited and an exhaustive record of the vegetation and its abundance was carried out. If the
276 species was not found and the area classified as favorable, an exhaustive 16 m² record was
277 done on the lower left corner of the 50 x 50 m square; if the area was classified as
278 unfavorable, then no record was carried out. A set of environmental descriptors was noted
279 down during fieldwork to compute the ecological analysis (see Table 2). The pH at eight
280 centimeters under the ground was measured by using a HELLIGE® Soil Reaction pH Tester
281 kit.

282

283 ECOLOGICAL ANALYSES

284 To distinguish groups of phytosociological relevés and their ecological ranges, a
285 clustering analysis was performed and compared to a Correspondence Analysis (CA) on
286 which ecological indicator values (Landolt et al. 2010) were projected on the basis of the
287 correlation between the mean ecological values of the relevés and their position on the axes
288 (Wohlgemuth 2000). This was done using the 246 phytosociological relevés from the
289 literature. An agglomerative hierarchical clustering was done and the Ward method was used.
290 The number of plot groups was fixed to 10 and the number of species groups was fixed to 20.

For each group, the mean ecological indicator value (Landolt 2010) was calculated. Each group was attributed to a vegetation type according to Derlarze & Gonseth (2008) based on expert knowledge.

A redundancy analysis (RDA) was performed in order to find out important ecological variables for *L. alpinum*. The RDA was done using the 32 phytosociological relevés collected during fieldwork as well as the ecological variables described in table 3. Before computing it, species data were transformed using the Hellinger distance (Beran 1977). This transformation is used with species data to allow computing RDA without considering species common absences as a resemblance (Legendre and Gallagher 2001). Variable significance was calculated with a stepwise function using AIC and permutations in the vegan R package (Oksanen et al. 2010).

RESULTS

VISITED SITES

40 favorable and 40 unfavorable sites were supposed to be visited but due to unfavorable weather conditions, only 32 favorable and 28 unfavorable sites were visited. During fieldwork, *L. alpinum* was found at nine places. It was predicted as present by the model in six locations (sheep were absent in two of them and present in the four remaining) but was predicted as absent in the last three ones (sheep were present in two locations and absent in the remaining one). Presences and absences of *L. alpinum* linked to the model predictions are shown in Table 3.

RESULTS OF THE MODELS

A probability map for presences of *L. alpinum* is shown in Fig. 1. Mean evaluation values resulting from the 70-30% data split as well as the one resulting from the field data

evaluation are displayed in Table 4. The independent dataset did not show a good fit to the model's predictions (PPP= 0.188 and NPP= 0.893).

Variable importance is shown in Fig. 2. The most important variable in our model is the annual degree-days followed by the average moisture index, the average slope, solar radiations and finally by the topographic position. The response curves, showed that *L. alpinum*'s optimal value of degree-days for *L. alpinum* ranges from 400 to 1100 and it corresponds to an altitude between 1700 and 2800 m a.s.l. This species avoided too humid climate and preferred growing on steep slopes with high solar radiations values. The preferred high values of topographic position, which corresponds to crest situation, but it is not a pronounced preference.

CLUSTERING AND CORRESPONDENCE ANALYZES ON PHYTOSOCIOLOGICAL RELEVES

Ten groups of phytosociological relevés and 20 groups of species were defined while computing the clustering analysis (CA) and are shown in Table 5. Results of the correspondance analysis with projection of ecological indicator values (Landolt et al. 2010) are shown in Fig. 3.

The first axis of the CA explained 5.7% of the variance. A gradient of temperatures and light appeared on this axis (see Fig. 3). A thermophilic pole was at the left side of the first axis and a pole of light-dependent relevés was at the right side. The second axis explained 4.7% of the variance. A gradient of soil pH was observable along the second axis. High soil pH values stood at the bottom of the graph.

The first group of relevés (on Fig. 3) was the centre of the CA. Species belonging to the *Seslerion* were the most frequent ones i.e. *Anthyllis vulneraria* s.l., *Aster alpinus*, *Bupleurum*, *ranunculoides*, *Carex sempervirens*, *Galium anisophyllum*, *Gentiana verna*,

341 *Festuca quadriflora*, *Minuartia verna*, *Pedicularis verticillata*, *Phyteuma orbiculare*,
342 *Polygala alpestris*, *Potentilla crantzii*, *Scabiosa lucida*, *Sesleria caerulea*, and *Thesium*
343 *alpinum*. The fifth group also took part at the centre of the AFC but with lower values of soil
344 pH. This group marked the junction between *Seslerion* and *Elynion* but had a clear tendency
345 to rocky and acid soils. This variant of plant community contained species growing on stable
346 soils that are still acidifying.

347 The third and ninth groups contained thermophilic species such as *Koeleria valesiana*,
348 *Poa perconcinna*, *Scabiosa columbaria*, *Dianthus sylvestris*, *Teucrium montanum*, *Galium*
349 *lucidum*, *Astragalus australis* and *Juniperus sabina*. The third group was solely constituted of
350 relevés from Zermatt (south-eastern Valais). Both groups were characterized by species
351 tolerating dry soils. They belonged to *Seslerion* with clear dry and thermophilic trends. The
352 mean ecological value for temperature (T) of the third group was 2.5 and the one for the ninth
353 group was 2.2.

354 The right extreme groups along the first axis were the fourth and seventh groups. They
355 are characterized by light dependent species such as *Artemisia umbelliformis*, *Minuartia*
356 *recurva*, *Minuartia sedoides*, *Silene acaulis*, *Saxifraga exarata*, *Ligusticum mutellinoides*,
357 *Arenaria ciliata*, *Silene exscapa*, *Saxifraga paniculata* and *Sempervivum arachnoideum*. Their
358 mean ecological value for light was 4.5 (for the seventh group) and 4.4 (for the fourth one).
359 Both groups belonged to *Elynion*, with species such as *Elyna myosuroides*, *Gentiana tenella*,
360 *Silene exscapa*, *Arenaria ciliata*. This plant community is growing on windy crests and thus,
361 have plenty of light.

362 The most extreme group along the second axis was the tenth one. It contained only
363 records done in Graubünden (except one in Valais). Species frequently found in this group
364 were *Saxifraga caesia*, *Dryas octopetala*, *Carex firma*, *Carex mucronata*, *Crepis kernerii*, and
365 *Gentiana clusii*. They were typical species of the *Caricion firmae*, a calcareous rocky

grassland mostly found from 2300 m a.s.l. to 2800 m a.s.l. and characterized by rainfall weather alternating with dry periods. This group had extreme ecological values of soil pH (4.1), suggesting a more alkaline soil than in the other groups.

The remaining group presented intermediate composition and ecological conditions.

REDUNDANCY ANALYSIS ON FIELD DATA

The first two constrained axes were significant (p-value of the RDA1 =0.001, p-value of the RDA2 =0.021). The constrained axes explained 37.2% of the variance, and four of the ecological variables were significant: the altitude (p-value = 0.002), the pH at 8cm in the soil (p-value = 0.002), the slope (p-value = 0.018) and the grass cover (p-value = 0.026) (Fig. 4) Sheep pasture (variable trampling) did not appear as important for *L. alpinum* to grow. The pH at eight cm under the ground seems to be the best variable to explain the separation between plots containing *L. alpinum* and plots without it. The mean value of soil pH in plots containing *L. alpinum* was equal to 5.65 ± 1.33 . The minimum pH value in plots containing *L. alpinum* was 4. The grass cover is also related with the presence/absence of *L. alpinum*, suggesting that it does not grow if the grass cover is too dense. The grass covered $59.10 \pm 20\%$ of the 16 m^2 plot containing *L. alpinum* in average. The maximum value of the grass cover in plots containing *L. alpinum* was 90 %. A pattern of plots linked to the altitude and the slope seems to occur, but it does not explain the separation between the plot with and without *L. alpinum*.

DISCUSSION

In this study, we modeled the distribution of the emblematical species *L. alpinum*. As it is neither a rare nor a common species, the model served as base for improving the sampling, to ensure finding *L. alpinum* populations. Some studies already assessed the model-

based sampling efficiency to find rare species (Engler et al. 2004; Edwards et al. 2005; Guisan et al. 2006). We found different vegetation types in which *L. alpinum* is able to grow. As expected, the most frequent were *Seslerion* and *Elyinion* according to Delarze & Gonsseth (2008) but we highlighted the fact that *L. alpinum* is also frequent in the *Caricion firmae*, particularly in the Graubünden. We demonstrated that soil pH, as well as grass cover, were important factors for the growth of *L. alpinum*.

MODEL

Data collected during fieldwork did not show a good fit to the model's predictions. The positive predicting power (PPP) was low compared to the negative predicting power (NPP). That means that our model did not provide reliable presence predictions. However, it better predicted the absence than the presence (NPP>PPP). *L. alpinum* was found only nine times. We suppose these disappointing results are due to the fact that the geological map used as filter to retain only calcareous areas, did not have a sufficient resolution. Often visited sites were in fact set on siliceous rocks. Such a result may also be due to the low resolution of the model projection. 100m-pixels are too large if we assume that *L. alpinum* often grows on ridges. A too low resolution may hide the "ridge effect" and pixels containing a ridge are not detected as favorable areas if the remaining part of the pixel is flat, for example.

The model of the geographic distribution of *L. alpinum* showed good evaluations for ROC and TSS indices with the 70-30 data split (Table 4). The mean evaluation values resulting from the 70-30 data split were much higher than the ones computed on the data collected during fieldwork. This may be explained by the upper-mentioned reasons. Another reason explaining the low evaluations of the model with fieldwork data is that the number of points that were likely to be visited was too low to get a reliable evaluation of the models.

415 Furthermore, it is important to keep in mind that our “independent” data is not absolutely
416 independent from the models because the sampling was realized based on the model.

417 Only five ecological variables were used to build the model. Thus an important
418 variable may have not been considered. As so few literature about *L. alpinum*’s ecology was
419 available, we chose ecological variables we thought important. The most important ecological
420 variable included in our model was the degree-days. This variable is always important when
421 working in mountains because of the large elevation range in the study area (Anne Dubuis,
422 personal communication). *L. alpinum* had an optimal degree-days value that ranged between
423 500 and 1000 which corresponds to altitudes ranging between 1700 and 2800 m a.s.l. The
424 response curves also showed that *L. alpinum* prefers growing on steep slopes with high solar
425 radiation. Indeed, this is often where *Seslerion* is found. This species seems to avoid humid
426 climate but tolerate low humidity values and it is probably due to the fact that it grows in
427 relatively dry environments interrupted by periods of bad weather. By observing the response
428 curves, it is possible to see a tiny preference for high values of topographic position. It
429 corresponds to crests. This weak preference is due to the fact that one of the favourable
430 environments *Elynion* (found on windy crests) but that the two other ones, which are
431 *Seslerion* and *Caricion firmae*, are found on south facing slopes.

432 According to fig. 1, *L. alpinum* is more frequently predicted as present in the Inner
433 Alps. Furthermore, it grew on ridges, steep slopes with high solar radiations and avoided too
434 humid climate. These results suggested that this species is better adapted to dry climate.

435

436 ECOLOGICAL ANALYSES

437 A lot of phytosociological relevés were done in Europe (Schaminee et al. 2009).
438 Getting such data from the literature is a way of studying a target species or communities (see
439 Ewald 1999; Deil 2005; Vittoz 2006; Bergmeier & Dimopoulos 2008). In this study,

440 phytosociological relevés coming from the literature and containing *L. alpinum*, were used to
441 complete the ones done during fieldwork to better encompass the whole ecological amplitude
442 of *L. alpinum*'s distribution.

443 The relevés situated at the center of the chart belonged clearly to the *Seslerion*
444 (Delarze & Gonseth 2008). This vegetation type is mostly found in subalpine-alpine, south-
445 facing slopes, on shallow, calcareous soils. Species contained in phytosociological relevés at
446 the left side of the chart are thermophilious, or even sub-continental species belonging to
447 steppe communities (most of the data came from Zermatt, the mountain town with the most
448 continental conditions in Switzerland). However, altogether, these relevés are still to classify
449 in the *Seslerion*, in a thermophilic and continental wing of the community. Relevés containing
450 light-dependent species are found at the right side of the first axis. They belong to *Elynion*,
451 which corresponds to windy ridges. This environment is much colder than south-facing slopes
452 because of the wind effect and the absence of snow in winter that exposes plants to lower
453 temperatures (Delarze & Gonseth 2008). The characteristic plant of *Elynion*, *Elyna*
454 *myosuroides*, is one of the species, which is the most resistant to cold temperatures (Delarze
455 & Gonseth 2008). These climatic conditions imply relatively open vegetation mats allowing
456 sunlight reaching the soil. The two vegetation types described upper (*Seslerion* and *Elynion*)
457 are the ones already known as favorable for *L. alpinum* (Delarze & Gonseth 2008).

458 In the present paper, we highlighted the fact that *L. alpinum* grows in a plant
459 community that was actually not indicated as favorable for it to constitute populations: the
460 *Caricion firmae*, according to Delarze & Gonseth (2008). It is a sparse and open grassland
461 mostly found in Graubünden for Switzerland with *Carex firma* as dominant species. Soil is
462 calcareous and alkaline, shallow, poor in fine particles but may be rich in humus (Delarze &
463 Gonseth 2008). It ranges mainly from 2300 to 2800 m a.s.l.. The growing season is very short
464 with succession of rain and edaphic drought. Species frequently found in this community are

465 *Carex firma*, *Carex sempervirens*, *Dryas octopetala* and *Festuca quadriflora*. The *Caricion*
466 *firmae* is not considered as needing a particular protection according to the Swiss ordinance
467 concerning the protection of nature and landscape (OPN 451.1) but Delarze & Gonseth (2008)
468 considered it as a fragile environment. As plants grow extremely slowly, it is sensitive to any
469 deterioration. In the case where the equilibrium is broken, *Caricion firmae* may regress in an
470 irreversible way to the benefit of landslide communities.

471 We got a better understanding of *L. alpinum*'s ecology thanks to data collected during
472 fieldwork. The pH at 8 cm under the ground seems to be the best indicator used in this study
473 to explain the presence of *L. alpinum*. We were expecting that high soil pH values would be
474 important for *L. alpinum* to grow and our results confirmed this hypothesis. We recorded a
475 minimum value of 4 for soil pH in plot containing *L. alpinum*. This is due to the fact that in
476 some places, the soil was heterogeneous and *L. alpinum* was found on a small blocks
477 calcareous rock where it was not possible to establish a soil profile. The fact that *L. alpinum* is
478 not able to grow on acid soils may reduces its potential habitat because calcareous soils tend
479 to acidify. The acidification may be due to different reasons such as the natural evolution after
480 lixiviation of the bases (Poss 1993; Vittoz & Gmür 2009; Gobat et al. 2010). It may also be
481 due to acid deposition as it is the case in forests (Ulrich & Pankrath 1983) and cultivated
482 fields (Poulain 1967) or due to acid rainfalls (Breemen et al. 1982) for example. The principal
483 sources of soil acidification in high mountain grasslands are the acidification due to cattle
484 nitrate deposition (Simpson 1962; Ball & Ryden 1984), to atmospheric nitrogen deposition
485 (Horswill et al. 2008; Bobbink et al. 2010) and the lixiviation of carbonate particles.
486 According to our result, a soil acidification may reduce the potential habitat of *L. alpinum*.

487 The grass cover also seemed to be an important variable to explain the presence of *L.*
488 *alpinum*. As it is a short herbaceous plant (2 to 12 cm) and that it needs a high light level
489 (ecological value for light of 4; Landolt et al. 2010), our results highlighted the fact that *L.*

490 *alpinum* is not able to compete for light. It grows in open grasslands, where the average
491 vegetation's height is low. This is indeed the case in *Seslerion*, *Elyinion* and *Caricion firmae*
492 communities.

493 The altitude and the slope appeared to explain significantly a pattern of plots.
494 However, as shown on Fig. 4, these ecological factors did not separate records containing *L.*
495 *alpinum* from the ones in which it was not present.

496 In this study, no sheep pasture effect was assessed because of insufficient occurrences
497 and non-reliable grazing data. Indeed, information about sheep pasture was insufficiently
498 precise. Sheep pasture layer was available but we never had any information about the grazing
499 management (rotational or permanent, livestock number, etc...). Furthermore, the number of
500 sheep is still increasing in the Alps and it involves that some pasture are occupied only for a
501 few years. Actually, the summering is more variable and its influence is perhaps not always
502 perceptible immediately. So for the previous reasons, it was not possible to assess any sheep
503 pasture effect but it would still be interesting to answer this question with a better and larger
504 data set.

505 We identified places that correspond to ecological conditions necessary for *L. alpinum*
506 to constitute populations but where it was not present. Indeed, our model predicted them as
507 favorable areas, the species growing on those places were apparently similar to places
508 containing *L. alpinum* and the ecological conditions were the ones needed by this species to
509 grow. It would be interesting to get more data to investigate if there are any dispersion
510 problems preventing *L. alpinum* to colonize new favorable areas or if any negative factors
511 were not considered.

512 These findings about *L. alpinum*'s ecology highlighted the fact that it cannot be
513 considered as a common species. Indeed, its geographic distribution mainly consisted of the
514 Inner Alps, where the climate is dry. Furthermore it colonized only small surfaces such as

windy ridges. The actual conservation status of *L. alpinum* in Switzerland is Least Concerned (i.e. not threatened) according to Moser et al. (2002). However, its actual habitat may be reduced by several threats such as soil acidification or the sensitivity to any deterioration of the plant communities where *L. alpinum* is found. As it was not possible to assess the sheep pasture effect on *L. alpinum*'s population, it is not known if sheep have to be considered as threat for this species. According to that, we suggest to pay attention to the evolution of *L. alpinum*'s populations.

522

523 CONCLUSION

524 In this study, we got a better understanding of the alpine species, *L. alpinum*. As
525 expected, *Seslerion* and *Elynion* are two plant communities that are favorable for this species.
526 We found a new vegetation type where *L. alpinum* is able to grow: the *Caricion firmae*. We
527 highlighted the fact that this species grows on calcareous soils with a pH varying from
528 alkaline to neutral. Furthermore, *L. alpinum* cannot grow in an environment where the
529 vegetation is dense. We were unable to assess a potential sheep pasture effect because of
530 insufficient and non-reliable data.

531

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TABLES

Table 1: Abbreviations, descriptions and units of quantitative geographic information system predictors used to model the distribution of *Leontopodium alpinum*. They were prepared at a 100 m resolution.

Table 2: Abbreviations, descriptions and units of qualitative and quantitative descriptors recorded during fieldwork. The first five variables are quantitative, the trampling is semi-qualitative, the topography is binary and the last two variables are qualitative.

Table 3: Contingency table containing fieldwork observations (presence/ absence of *L. alpinum*) linked to the model's predictions (Favorable and Unfavorable areas).

Table 4: Mean evaluation values of the models computed by using two different methods: at first 30% of the original data were used to perform the model's evaluation and then a dataset collected during fieldwork was used for the same goal.

Table 5: Synthetic table based on the results of the clustering analysis. Ten groups of phytosociological relevés were defined as well as 20 groups of species. Mean ecological values (Landolt et al. 2010) per group are shown at the top. Only species being present in at least 40% of the plots of a specific group were retained. The order of the groups follows the first axis of the correspondence analysis (Fig. 3). Only species with a high discriminant value for one of the groups were retained in the upper part of the tableau. Roman numerals are related to the species frequency in the 10 groups: I = 1 to 20%, II = 21 to 40%, III = 41 to 60%, IV = 61 to 80% and V = 81 to 100%.

780

781 **Fig. 1:** Map of the Swiss Alps and our study area which is constituted by the cantons de Vaud,
782 Valais and Fribourg. Pixels where *Leontopodium alpinum* is predicted as present by the
783 models are printed out with a darker colour than pixel were it is predicted as absent.

784

785 **Fig. 2:** Importance of variables entered in the model. It was computed by randomizing it,
786 recalculating the model with the randomized variable and correlating this new model with the
787 original one.

788

789 **Fig. 3:** Correspondence Analysis with projection of ecological indicator values (Landolt et al.
790 2010). Each group of plots (computed during the clustering analysis) is printed out with a
791 different symbol (see Table 5).

792

793 **Fig. 4:** Redundancy Analysis plot of phytosociological relevés containing *L. alpinum* (printed
794 out as triangles) and phytosociological relevés that do not contain *L. alpinum* (printed out as
795 circles). See table 2 for ecological variables

Table 1

Abbreviation	Description	Unit
Slope	Average slope computed for each pixel	%
Sumrad	Sum of solar radiation during June, July and August	kJ day ⁻¹
Mmind	Average moisture index during June, July and August	1/10mm / mth
Topo	Topographic position and other topography related variables	Mostly unitless
Ddeg	Annual degreedays with a threshold of 0 degree	day*deg

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Table 2

Abbreviation	Description	Unit
Altitude	Altitude of the phytosociological relevés.	Meters
Slope	Average slope of the mountainside.	Degrees
Expo	Exposition of the phytosociological relevés (transformed using the cosinus function).	Degrees
GrassCover	Percentage of grass cover in a 16 m ² square.	%
pH8	Soil pH value at eight cm under the ground.	Unitless
Trampling	Semi-quantitative variable : 0 = No Trampling, 1 = few trampled, 2= trampled, 3= very trampled	Unitless
Topo	Noted down as a binary variable. 1 =crest, 0 = anything else.	Unitless
Texture8	Soil texture at a depth of 8 cm; classified as clays, silts or sands.	Unitless
Coarse8	Coarse particles, classified as a few coarse particles, very coarse particles	Unitless

Table 3

		Field observation	
		(N=60)	
		presence	absence
Predictions	Favorable	6	26
	Unfavorable	3	25

Table 4

Mean Evaluation Values	30/70 data split	Independent data
Kappa	0.287	0.200
ROC	0.915	0.545
TSS	0.708	0.163

Table 5

Mean ecological indicator values		G3	G9	G1	G5	G8	G10	G6	G2	G4	G7
T		2.5	2.2	2.0	1.9	2.2	1.8	1.7	1.8	1.7	1.5
K		3.8	3.9	3.6	3.6	3.7	3.6	3.7	3.6	3.5	3.6
L		4.1	4.3	4.2	4.3	4.3	4.3	4.5	4.4	4.4	4.5
F		2.1	2.0	2.5	2.3	2.2	2.5	2.4	2.4	2.5	2.5
R		3.5	3.7	3.5	3.2	3.7	4.1	3.4	3.6	3.3	3.1
N		2.2	2.1	2.1	2.1	2.1	2.0	1.9	1.9	1.9	1.9
H		2.7	2.4	2.8	2.7	2.4	2.6	2.4	2.5	2.9	2.5
D		3.4	3.9	3.3	3.5	3.7	3.5	3.9	3.7	3.4	3.7
Number of records per group		25	9	51	47	22	20	11	24	25	12
Species		G3	G9	G1	G5	G8	G10	G6	G2	G4	G7
Astragalus leontinus Wulfen	2	IV	II	I	I	I					
Briza media L.	2	IV		I							
Dactylis glomerata L.	2	IV									
Anthoxanthum odoratum L.	2	III		I	I					I	
Carex caryophyllea Latourr.	2	III		I		I				I	
Leucanthemum adustum (W. D. J. Koch) Gremli	2	III		II		II					
Trifolium montanum L.	2	III		I							
Trifolium pratense L. s.l.	2	III		I							
Silene nutans L. s.str.	2	II	III	I	I						
Helianthemum nummularium (L.) Mill. s.l.	4	V	III	IV	III	IV	I	I	II	I	
Thymus serpyllum aggr.	4	V	V	IV	IV	IV	I	I	III	I	II
Festuca ovina aggr.	4	V	III	II	III	II			I	I	
Oxytropis campestris (L.) DC. s.l.	4	V	V	II	III	I		II	I	II	
Senecio doronicum (L.) L.	4	IV	IV	V	III	II		III	I		II
Galium pumilum Murray	4	III		III	IV	I	I	V	I	I	I
Galium anisophyllum Vill.	4	IV	II	III	IV	II		V	I	III	
Helianthemum alpestre (Jacq.) DC.	4	III	V	III	III	I	V	I	II	II	
Thalictrum foetidum L.	7	III	I	I		I					
Minuartia mutabilis (Lapeyr.) Bech.	11	I	IV		I	I					
Taraxacum laevigatum aggr.	11	I	IV	I	I			I	I		
Astragalus sempervirens Lam.	11	I	III		I						
Koeleria vallesiana (Honck.) Gaudin	20	I	IV								
Scutellaria alpina L.	20		IV			I					
Helictotrichon parlatorei (Woods) Pilg.	20		III								
Onobrychis montana DC.	20		III								
Bupleurum ranunculoides L. s.l.	3	V	V	II	I	III					I
Koeleria macrantha (Ledeb.) Schult.	3	V	II		I	I					
Lotus corniculatus aggr.	3	V	I	III	II	I					
Plantago serpentina All.	3	V	III	I	I	I					
Acinos alpinus (L.) Moench	3	IV	III	II	I	III					
Carduus defloratus L. s.l.	3	IV		III	II	II	I		I		I
Carex humilis Leyss.	3	IV		II		III					
Carlina acaulis L. s.l.	3	IV		II	I	II			I		
Dianthus sylvestris Wulfen	3	IV	IV	I	I	III				I	
Euphorbia cyparissias L.	3	IV	IV	II	II	III		I			
Teucrium montanum L.	3	IV		I	I	III	I		I		
Erysimum rhaeticum (Hornem.) DC.	3	III	III	I	I	II					
Galium lucidum All.	3	III		I		II					
Astragalus australis (L.) Lam.	3	II	IV	II	I	II		I			I
Euphrasia salisburgensis Hoppe	3	I		III	I	III	II		I	I	
Sempervivum arachnoideum L.	10	IV	III	I	V			I	I	II	III
Euphrasia alpina Lam.	10	IV		I	II			I		I	I
Hieracium pilosella L.	10	IV	II	I	II	I					
Pulsatilla halleri (All.) Willd.	10	IV	V	I	I						

		G1	G2	G3	G4	G5	G6	G7	G8	G9	G10
Cerastium arvense subsp. strictum (W. D. J. Koch) Schinz & R. Keller	10	III	IV	I	IV	I		III		I	
Veronica fruticans Jacq.	10	III	I	I	III			I		I	II
Pedicularis tuberosa L.	10	III		I	II						
Potentilla crantzii Fritsch	10	II	III	II	III					II	
Viola rupestris F. W. Schmidt	10	I	III	I	III				I	I	
Poa perconcinna J. R. Edm.	10	I	IV		II						
Pulsatilla vernalis (L.) Mill.	10		II	I	III			I	I	II	I
Saxifraga caesia L.	8			I			V		I	I	
Dryas octopetala L.	8			II			IV	I	I	II	
Carex firma Host	8			I			III		I		
Carex mucronata All.	8	I	III	I	I	I	III		I		
Crepis kernerii Rech. f.	8						III				
Gentiana clusii E. P. Perrier & Sonjeon	8			II			III		I	I	
Draba aizoides L.	12	I	IV	I	V	I	I	V	IV	II	I
Herniaria alpina Chaix	12	I	II	I	IV	II		V	IV	I	I
Saxifraga oppositifolia L.	12			II	II		I	V	IV	III	II
Artemisia glacialis L.	12	I	IV	I	III	I		V			
Gentiana schleicheri (A. Vacc.) Kunz	12			I	II		I	IV	IV	I	III
Oxytropis helvetica Scheele	12			I	III			III	I		I
Carex curvula All. s.l.	12		II		V			II	I	III	II
Senecio incanus L. s.str.	1			I	I	I		III			
Artemisia umbelliformis Lam.	1			I	I			I	I	I	III
Elyna myosuroides (Vill.) Fritsch	9	II		III	III	I	I	I	IV	V	II
Polygonum viviparum L.	9			IV	I		II		II	V	I
Arenaria ciliata L.	9			I	I		I	I	II	IV	II
Ligusticum mutellinoides (Crantz) Vill.	9			I	II			II	II	IV	III
Carex capillaris L.	9								I	III	II
Gentiana tenella Rottb.	9			I	I		I			III	I
Oxytropis lapponica (Wahlenb.) J. Gay	9			I	I		I		I	III	
Pedicularis verticillata L.	9			II			I		I	III	
Silene acaulis (L.) Jacq.	9			I			I			III	I
Silene exscapa All.	9			I	II	I		I	II	III	IV
Carex rupestris All.	9			I	I		II		V	II	
Carex sempervirens Vill.	9	I		V	I	I	II			II	I
Gentiana campestris L. s.l.	9			III	I	I				II	II
Poa alpina L.	9		III	II	III	I	I		I	II	I
Saxifraga paniculata Mill.	9	I	III	III	III	I			I	II	III
Saxifraga exarata Villars s.l.	9		I	I	II	I		II	I	I	V
Festuca halleri aggr.	19	I			I	I			I	II	III
Minuartia recurva (All.) Schinz & Thell.	5		II		I						III
Minuartia sedoides (L.) Hiern	5					I			I	I	III
Primula hirsuta All.	5			I			I		I	I	III
Non discriminant species											
Leontopodium alpinum Cass.	4	V	V	V	V	V	V	V	V	V	V
Sesleria caerulea (L.) Ard.	4	IV	II	V	IV	IV	V	IV	III	IV	I
Festuca quadriflora Honck.	4	II	IV	III	V	III	III	V	IV	V	V
Minuartia verna (L.) Hiern	4	III	IV	III	V	III	III	III	V	V	II
Agrostis alpina Scop.	4	III	III	III	IV	II	III	I	III	V	V
Aster alpinus L.	4	V	V	IV	V	III	II	III	III	IV	V
Gentiana verna L.	4	III	IV	III	V	I	I	II	II	III	I
Anthyllis vulneraria L. s.l.	4	IV	II	IV	IV	III	IV	III	II	II	I
Campanula cochleariifolia Lam.	1	I		I	I	I	I	III	III	I	I
Campanula scheuchzeri Vill.	9	II	II	IV	III	I	I	II		IV	I
Gypsophila repens L.	3	III	II	II	I	II	II		III		I
Juniperus communis L. s.l.	3	III	II	II	I	II	I		I		I
Euphrasia minima Schleich.	9	I		II	II	I		I	I	III	II

		G1	G2	G3	G4	G5	G6	G7	G8	G9	G10
Botrychium lunaria (L.) Sw.	9	I		I	III	I		I	I	II	I
Salix serpyllifolia Scop.	9			I	I		I	II	II	III	II
Hippocrepis comosa L.	18	I	III	I	I	I	I			I	
Globularia cordifolia L.	3	II	II	II		III	II		II		
Sedum atratum L.	9			I	I		I		II	II	III
Erigeron uniflorus L.	9			I	I		I		II	III	I
Leontodon hispidus L. s.l.	3	I	II	II	I	III			I		
Campanula rotundifolia L.	3	III	II	I		II			I	I	
Erigeron alpinus L.	10	II		II	III	I			I		I

Fig. 1



Fig. 2

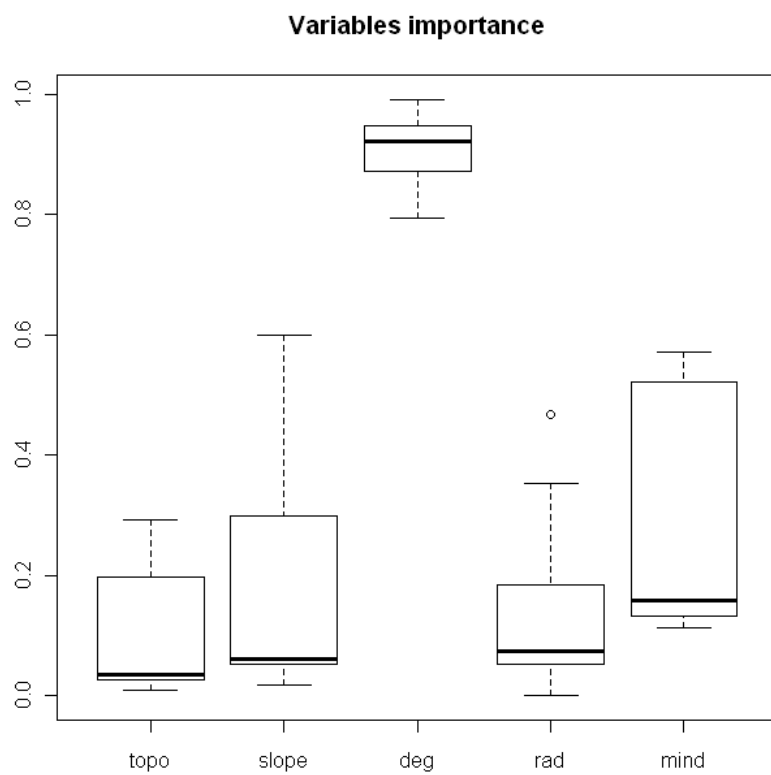


Fig. 3

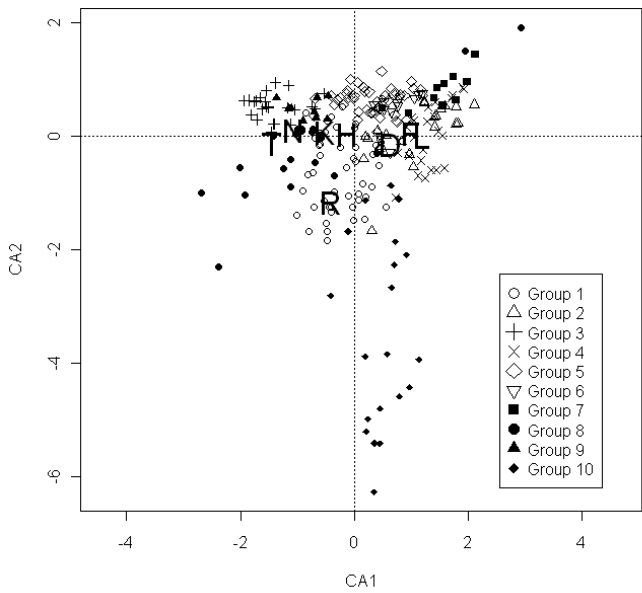


Fig. 4

