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Response of Swiss subalpine-alpine végétation to recent climate changes and conséquences on soil organic matter dynamics

Matteodo Magali

Matteodo Magali, 2018, Response of Swiss subalpine-alpine végétation to recent climate changes and conséquences on soil organic matter dynamics

Originally published at : Thesis, University of Lausanne

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Faculté des Géosciences et de l'Environnement
Institut des Dynamiques de la Surface Terrestre
Mention Sciences de l'Environnement

Response of Swiss subalpine-alpine vegetation to recent climate changes and consequences on soil organic matter dynamics

Thèse de doctorat
présentée à la Faculté des Géosciences et de l'Environnement de l'Université de Lausanne
par

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Sous la présidence du Professeur Michel Jaboyedoff

Lausanne, UNIL, 2018

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Master en Biologie de l'environnement
de l'Universita degli Studi di Torino

intitulée

Response of Swiss subalpine-alpine vegetation to recent climate changes and consequences on soil organic matter dynamics

Lausanne, le 18 janvier 2018

Pour le Doyen de la Faculté des géosciences et de l'environnement

Professeur Michel Jaboyedoff

« Combien de mois, combien de vies faut-il pour écrire une phrase qui égale en puissance la beauté des choses? »

1986 - Christian Bobin,
Le huitième jour de la semaine

A ma mère, mio paire e la mia sorellina

Aknowledgements

J’ai écrit ma thèse en anglais pour qu’un public international puisse la comprendre. En suivant le même principe, j’écris ces remerciements en français ou italien, afin d’être sûre que l’expression de mes sentiments parvienne aux personnes concernées.

Eric et Pascal, c’est évidemment vous que je tiens à remercier en premier. En me faisant confiance lors de mon entretien en janvier 2013, et puis tout au long de la thèse, vous avez permis que cette aventure commence et qu’elle se termine dans les meilleures conditions. Je vous ai énormément demandé pendant ces cinq ans, et j’ai reçu beaucoup plus en retour. C’est vraiment un privilège pour moi d’avoir été votre doctorante.

Merci Stéphanie et David : vous n’étiez pas mes superviseurs, mais cette thèse n’aurait pas le même contenu sans vous. Vous m’avez poussée toujours un pas plus loin de ce que j’aurais fait moi-même, et c’est ainsi qu’on avance.

Vous avez été nombreux à m’aider sur le terrain pour faire mes 89 relevés, creuser mes 46 fosses, transporter des kilos de terre et ensuite analyser les 232 échantillons au labo : Loïc, Jessica, Swanee, Aurélie, Ayumi, Yohan et Jérémy, merci infiniment ! Toute analyse au labo a été possible également grâce à l’appui technique de Laurent, Laetitia, Micaela, Thierry et Jean-Claude. Merci à vous tous. Un grand merci Marie-Jo: tu m’as aidée concrètement sur le terrain, au labo, dans la réflexion scientifique, et soutenue moralement quand j’en avais besoin.

Cette thèse contient beaucoup d’analyses statistiques, beaucoup d’heures passées sur R. Pour cela, je tiens à vous remercier Guillaume et Aline ; je vous ai bénis chaque fois que vous m’avez passé un script.

Claire, merci pour avoir été toujours présente, scientifiquement et moralement. Ta bonne humeur n’a jamais manqué pendant les excursions BGS, ce qui en a fait des moments de grand bonheur. Les excursions BGS seront pour moi inoubliables aussi grâce à vous les étudiants ! Grace à votre fraicheur et vos questions toujours stimulantes, vous avez été une véritable source d’énergie pendant toute ma thèse.

Nathalie, Fabienne et Fina, qu’est-ce que je serais sans vous ? Vous m’avez encouragée, rassurée, consolée et supportée pendant cinq ans, tous les jours, constamment. Tout remerciement sur cette page ne suffira pas pour exprimer ma profonde reconnaissance. Mike, tu es arrivé plus tard, mais tu as très vite pris une place fondamentale dans ma vie, en tant qu’ami et collègue. John, si tu n’existais pas, il faudrait t’inventer ; tes massages pendant que je travaille sont un véritable régal.

Une thèse de doctorat est un travail scientifique, certes, mais c’est aussi une expérience de vie. Une vie que je partage depuis quelques années avec les meilleurs êtres vivants sur Terre : vous l’équipe des donkeys ! Merci Nath et Mike (à nouveau), Femi, Benji, Krikri, Mama Giulia, Sté, Gab, Morin, Seb, Leanne, Alexis, Julia, Erika, VV, Nadja, Naomi, Zozo, Ignes, Elfie, Elisa, Nicola, Nico Tabez, Martino, Manu, Monica, Iñigo, Estefania, Gustavo, Eveline, Anders, Mathieu, Thibault, Debra, Moctar, Sassi, Andrea, Renske, Maarten, Lionel, Aline, Christelle, Pascal, Gilles. Merci de m’avoir acceptée telle que je suis et avoir fait de moi une personne heureuse d’être au monde.

Durant ces cinq ans j'ai aussi eu la chance de participer à la création de l'ACIGE, et pour cela j'ai eu les meilleurs co-pilotes : Benjamin, Gabriel, Antoine, Gwen, Martin, Femi et Davide. Merci à vous tous de m'avoir embarquée dans cette aventure, pour les grillades au bord du lac et les batailles sociales qu'on a menées ensemble.

Un merci spécial va à Marylaure, c'est grâce à ton adresse de Gobat sur un papier cuisine que toute mon aventure suisse a commencé !

Et ensuite il y a un monde en dehors de l'Université qui m'a constamment rappelé que dans la vie il y a autre chose qu'une thèse ! Grazie Chiara, amica mia, sempre al mio fianco con entusiasmo, qualsiasi cavolata io faccia. Carmen ! Perché ho l'impressione di conoscerti da tutta la vita ? Grazie per essere te stessa sempre, per la tua energia e il tuo calore. Tu e Hector siete ormai parte della mia famiglia.

Du côté famille aussi, j'ai une chance énorme. Merci Marie-Madeleine et Christian, vous avez été présents depuis la lettre de motivation pour ce poste de doctorat jusqu'à la fin, toujours avec la même énergie, la même envie de partager et de connaitre. Vous êtes incroyables. Merci à ma maman, mon papa et ma petite sœur. Je vous dédie cette thèse sans la moindre hésitation car c'est surement à vous que je dois le plus. Ce n'était pas facile la distance, les trop courts week-ends à la maison, les centaines de soirées sur Skype avec les ordinateurs qui plantaient. Vous avez supporté tout cela avec amour, convaincus plus que moi que j'étais sur la bonne voie. Merci.

A toutes et tous, qui chacune, chacun à votre place m'avez soutenue dans ce parcours qui restera pour moi une formidable aventure, un très grand merci !

M.M.

Lausanne, 18 Décembre 2017

Abstract

Impacts of current climate change on flora of alpine and nival summits are well known, but they are less understood in subalpine-alpine vegetation types. Moreover, at such elevations, only a few studies are describing soils, humus forms, and factors controlling their distribution. The impact of climate change on the soil organic matter (OM) component is currently under debate. In this context, the identification of ecosystem factors governing OM dynamics in soils is essential. The present research aims to investigate (i) the reaction of main subalpine-alpine vegetation types to recent climate changes, (ii) their associated soil and humus forms, (iii) the ecosystem controls on humus forms and OM stability in the alpine ecosystem.

Three study sites were selected in the Northern Alps and Western Central Alps of Switzerland. Eight vegetation types, typical of the subalpine-alpine belt and spanning a gradient of soil acidity and moisture, were targeted. Recent plant surveys were compared with historical ones (25-50 years), corresponding soils and humus forms were described, and the stability of the OM component was assessed thermally using Rock-Eval pyrolysis.

Both calcareous and siliceous grasslands showed high stability in terms of plant species composition and cover. On the other hand, vegetation types related to long snow cover (snowbeds) changed. Several species, coming from the surrounding grasslands, increased in frequency and cover, likely as a consequence of earlier melting dates and longer growing seasons.

The eight vegetation types displayed a large diversity of soil types and humus forms. But, the plant's community type played a secondary role in the humus form distribution, which was in contrast, mostly determined by the lithology of the soil's parent material, the climate, and the topography. Mull forms were observed all along the whole elevation gradient (1698-2697 m), but mostly at the lowest elevations and on calcareous parent material. Instead, Moder and Mor forms were associated to the highest elevations and siliceous parent materials. The concave topography was determinant for the occurrence of Anmoor forms. Roots were abundant in the investigated soils, particularly on steep slopes. The existing keys for the identification of humus forms proved partly unsuitable for the alpine ecosystem and some adaptations are suggested. Ecosystem controls on soil OM dynamics differed substantially according to the soil layer considered. The vegetation type influenced OM thermal stability in the litter layer, but not in the topsoil and subsoil. Indeed, the supply rate of fresh organic material and the physical and chemical characteristics of the pedogenic environment appeared to control OM stability. This study confirms that factors influencing the outcome of OM in soils are numerous, horizon and soil specific, and highly interconnected. Vegetation shifts, induced by recent climate changes, will likely have limited impact on soil OM dynamics in subalpine-alpine belts.

Résumé

L'impact des changements climatiques sur la flore des sommets alpins est bien connu, mais il l'est beaucoup moins sur la végétation subalpine-alpine. De plus, à ces altitudes, les études décrivant les sols et les formes d'humus, ainsi que les facteurs contrôlant leur distribution, restent très peu nombreuses. L'impact des changements climatiques sur la matière organique (MO) du sol est actuellement débattu dans la littérature scientifique. Dans ce contexte, il est nécessaire d'identifier les facteurs écosystémiques régulant la dynamique de la MO du sol. Le but de cette recherche est d'étudier (i) la réaction des principaux types de végétation subalpins-alpins aux changements climatiques récents, (ii) les sols et les formes d'humus auxquels ces types sont associés, et (iii) les facteurs écosystémiques qui contrôlent la distribution des formes d'humus et la stabilité de la MO dans l'environnement alpin.

Trois sites d'étude ont été sélectionnés en Suisse dans les Alpes du Nord et les Alpes internes occidentales. Huit types de végétation, représentatifs de l'étage subalpin-alpin et couvrant un gradient d'acidité et d'humidité du sol, ont été sélectionnés. Des relevés floristiques récents ont été comparés avec des relevés historiques (25-50 ans), les sols et les formes d'humus correspondantes ont été décrits, et la stabilité de la MO a été étudiée thermiquement (pyrolyse Rock-Eval).

La composition et le recouvrement spécifique des pelouses calcaires et acides sont restés très stables. En revanche, les communautés dépendantes d'un long enneigement (combes à neige) ont changé. Plusieurs espèces, arrivant des pelouses avoisinantes, ont augmenté en fréquence et recouvrement, probablement en raison des fontes des neiges progressivement plus précoces et des saisons végétatives plus longues.

Une grande diversité de sols et de formes d'humus caractérise les huit types de végétation. Cependant, la distribution des formes d'humus reste surtout contrôlée par le matériel parental du sol, le climat, et la topographie. La végétation ne jouerait donc qu'un rôle mineur. Les formes d'humus de type Mull ont été observées sur tout le gradient altitudinal (1698-2697 m), mais plus spécifiquement aux altitudes inférieures, sur calcaire. Les Moders et Mors, par contre, sont associés aux altitudes élevées et aux matériaux parentaux siliceux. Une topographie en cuvette est déterminante pour la présence des formes Anmoor. Les racines sont abondantes dans les sols étudiés, surtout sur les pentes raides. Les clés de détermination des formes d'humus actuellement disponibles se sont montrées en partie inappropriées pour le milieu alpin et des adaptations sont suggérées. Les facteurs écosystémiques qui contrôlent la dynamique de la MO sont apparus comme dépendants de l'horizon considéré. Le type de végétation influencerait la stabilité thermique de la MO dans la litière mais pas dans les autres horizons du sol. Dans les horizons organo-minéraux et minéraux, le taux d'approvisionnement en matériel organique frais et les caractéristiques physico-chimiques du milieu pédologique contrôleraient la stabilité thermique de la MO. Cette étude confirme que les facteurs affectant le destin de la MO du sol sont nombreux, spécifiques au type d'horizon et de sol considérés, et hautement interconnectés. L'évolution de la végétation induite par les changements climatiques récents va probablement avoir un impact limité sur la dynamique de la MO des sols aux étages subalpins-alpins.

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1 Introduction

1.1 State of the art

1.1.1 The alpine climate

The term *alpine*, even if originated from the mountain range of the European Alps, refers to the life zone occurring above the natural treeline on mountains worldwide. In the European Alps, the natural treeline is located between 1900 (Northern Alps) and 2400 m (Inner Alps) and defines the uppermost limit of the *subalpine* vegetation belt (Favarger, 1995; Körner, 2003), naturally dominated by phanerophytes (woody plants higher than 50 cm). Above the treeline elevation, climatic conditions become physiologically too harsh to allow tree growth and only low stature vegetation develops. This vegetation, dominated by swards, low heaths, cushion plants, and with sporadic annual plants, is defined as *alpine* (Theurillat *et al.*, 1998). The uppermost boundary of the alpine life zone is represented by the occurrence of permanent snow cover on flat ground ("snowline"; Ozenda, 1985; Schröter, 1926). The closed alpine vegetation progressively turns into fragmented plant cover (Körner, 2003), mostly concentrated in favourable rocky places (Theurillat *et al.*, 1998). This transition is observed between 2600 and 3100 m (Northern and Inner Alps, respectively) and determines the lower boundary of the *nival* zone (Theurillat *et al.*, 1998).

During the Atlantic period (7.5-5 ka BP), climate was warmer and wetter than today, allowing for the uppermost tree limit to be 250 ± 100 m higher than today's potential treeline (Carnelli *et al.*, 2004; Favilli *et al.*, 2010; Holtmeier and Broll, 2005). A combination of decreasing temperatures since 6.9 ka BP (Tinner *et al.*, 1996), and the beginning of extensive clearing and grazing at the Bronze period (ca 4 ka BP), followed by important deforestations during the Middle Age, led the alpine grasslands to extend downwards (Favilli *et al.*, 2010; Gobet *et al.*, 2003; Tinner *et al.*, 1996). The process of forest opening continued until the middle of XIXth century and substantially lowered the treeline (Favilli *et al.*, 2010). In the Swiss Central Alps, the present treeline elevation is around 12 to 180 m lower than the natural treeline during the Holocene (Tinner and Theurillat, 2003). Thus, the alpine vegetation belt expanded downwards and now occupies a space that would climatically correspond to the upper subalpine vegetation belt.

In the present chapter, climatic conditions characterizing the alpine belt are discussed. The following considerations are valid also for the upper-subalpine belt that, despite less severe climatic conditions, shows very similar trends to the alpine belt.

The alpine climate results from two main components (Ozenda, 1985): (1) the elevation gradient that modulates a series of parameters similarly on many mountain ranges and (2) the complexity of the Alpine chain and its geographical position determining local precipitation regimes and wind currents. The present chapter focuses on the first component (the effect of elevation), while the local climates characterizing the study sites are discussed separately in Chapter 2.

1.1.1.1 Atmospheric pressure

Atmospheric pressure decreases almost linearly with increasing elevation. As an example, the atmospheric pressure at the sea level is around 1013 hPa (average for a standard atmosphere), while it is 750 hPa (26% lower) at 2600 m (Körner, 2003). A decrease in pressure is supposed to increase molecular diffusivity and therefore stimulate evapotranspiration (De Saussure (1779-1796) in Barry 1978). However, the concomitant decrease in temperatures at higher elevations reduces the rate of molecular diffusion and thus hamper evapotranspiration. The partial pressure of CO_2 and oxygen are reduced with increasing elevation by the same amount as the total pressure (Körner, 2003). Nevertheless, alpine plants evolved towards high photosynthetic efficiency of CO_2 utilization per unit leaf area (Körner, 2003) and the low CO_2-pressure occurring at the alpine belt does not result in decreased photosynthesis rates.

1.1.1.2 Temperature

Mean air temperature declines, in average, by 0.57°C per 100 m increment in the European Alps (Schröter, 1926). This year average gradient is however higher in summer (0.7 °C per 100 m) than in winter (0.4 °C per 100 m; Ozenda 1985). The elevation lapse rate of temperature is influenced by the slope aspect as well, being around 0.1°C higher on South-facing slopes than on North-facing slopes (Ozenda, 1985). The annual temperature amplitude (temperature difference between the warmest and the coldest month) declines with elevation (Ozenda, 1985): according to Schröter (1926) is around 13,8°C at 2500 m, while it reaches 19,4°C at 460 m.

The difference between the actual water vapour pressure and the saturation water vapour pressure (the "vapour pressure deficit") is positively linked to the temperature and, therefore, decreases with elevation. This means that in the alpine belt, the capacity of the air to take more moisture is very limited and the saturation vapour pressure is more easily reached than at lower elevations (Körner, 2003).

Therefore, the absolute atmospheric water content at higher elevations is generally lower than in the lowlands (Körner, 2003).

1.1.1.3 Solar radiation

As a consequence of decreased atmospheric pressure, the solar radiation is intense in the alpine belt.Moreover, as air turbidity declines with elevation, the solar radiation undergoes little diffusion by the air particles and reaches directly the soil. This determines high thermic contrasts between sun and shadow exposed surfaces (Sauberer and Dirmhirn, 1958 in Körner, 2003), and between day and night. The radiative heat losses during clear nights are indeed high in the alpine belt (Körner, 2003) and soil may freeze even in summer (Taschler and Neuner, 2004). The intensity of solar radiation is also modulated by the snow, which increases radiation by reflection but, at the same time, reduces it under its cover. However, the relative frequency of local cloud cover also increases with elevation and it might counteract the radiation effect (Körner, 2003).

The UV fraction, highly absorbed by the atmosphere at low elevations, represents an important fraction of total solar radiation at high elevations as the atmosphere thickness is lower than in lowlands. The UV intensity in the alpine belt may be up to 1,5-2 times higher than in lowlands in summer, and 3-4 times in winter (Favarger, 1995). This high intensity may have important effects on alpine plant morphogenesis (Körner, 2003).

1.1.1.4 Precipitations

Mountain ranges act as barriers to air flow and force it upwards. At higher elevations, temperature and vapour pressure deficit both drop leading to the formation of clouds and precipitations. The precipitation gradient increases by 50 to 200 mm per 100 m in elevation (Favarger, 1995). Contrary to temperature, the elevation precipitation gradient presents high local variability determined by the relative position on the mountain (windward vs leeward) and especially the wind direction. Oceanic air flows from the West and North-West or from the Mediterranean sea and continental winds from North-East, importantly shape the local precipitation regimes of the European Alps (Favarger, 1995).

As temperature decreases with elevation, the proportion of precipitation in the form of snow increases proportionally. At ca. 2000 m, snow represents between 50 and 60 % of annual precipitations and it represents their totality above 3600 m (Ozenda, 1985). The abundance of snow falls, combined to low air temperature, results in long snow cover periods in the alpine belt. The growing season of alpine plants is consequently very short and it is reduced by ca. 7 days per 100 m increment on north aspect (ca. 6 days on south aspect; Gesler, 1946 in Favarger, 1995). The growing season period in the alpine belt varies from 147 days at 2440 m in the Valais Alps (Körner, 2003 p. 46) to 184 days at the lower alpine belt (2463 m) in the Dolomites (Erschbamer *et al.*, 2009).

1.1.2 The climate plants experience

Elevation per se, and the associated variation of climatic parameters, are poor predictors of life conditions of alpine plants (Gottfried *et al.*, 1998; Körner, 2003). Despite of "hostile" climatic conditions occurring at high elevations, microclimatic conditions can be favourable to the growth of alpine plants. During clear sky days, air temperature, wind speed and relative humidity measured at 2 m above the surface and within compact leaf canopy at 1-2 cm high are largely decoupled (Körner, 2003). This decoupling depends on two main factors: the topography (slope and exposure) and the stature of the plants themselves.

1.1.2.1 The role of slope and exposure

The action of solar radiation and wind is strongly shaped by slope and exposure of the alpine terrain. Slope modulates the equatorial solar incidence angle and the duration of snow cover (Körner, 2003). Indeed, exposure being equal, snowmelt is anticipated on steeper slopes, while it will be delayed in depressions (Michalet *et al.*, 2002).

The micro-habitat exposure strongly participates to the decoupling between air and leaf surface temperatures (Körner, 2003). Moser *et al.* (1977, in Körner, 2003) measured the temperature on leaves of *Ranunculus glacialis* at contrasting exposures at 3184 m in the Tyrolean Alps during a clear day (Figure 1.1). Leaf temperatures were always higher than air temperature at any exposure, but the difference was much higher on south than north slopes. While leaf temperatures on the north slope were mainly in the -5 to 0 °C range for most part of the day, those on the south slope were mainly (61,5 % of hours) in the 0 to 15 °C range. Leaf temperature reached the highest values on ridges around noon, when solar incidence is at its maximum on a flat terrain.

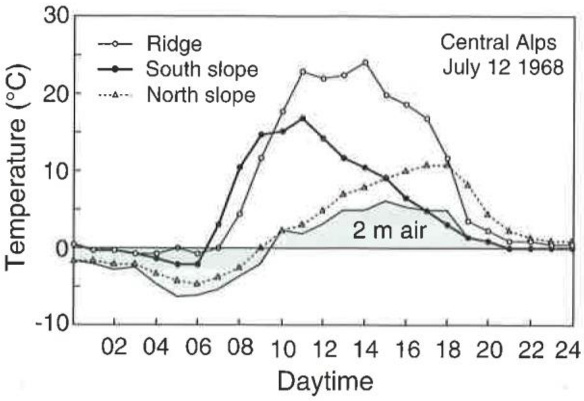

Figure 1.1 - Influence of microhabitat exposure on leaf temperature**.** Variations of air temperature and *Ranunculus glacialis* leaf temperatures at microhabitats differing in slope exposure during a clear day at 3184 m (July 12th, 1968; Moser et al. 1977, in Körner, 2003 p. 33).

Moreover, exposure also influences the time of snowmelt and, consequently, the length of the growing season. According to soil temperature measurements at 10 cm deep on a lower alpine summit (2463 m) in the Southern Alps, Erschbamer *et al.* (2009) found that south-exposed slope displayed significantly longer growing seasons than north-exposed slopes. By defining the growing season as the period with mean daily soil temperature above 2 °C, this varied from 134 to 172 days from north to south exposure, respectively (3 years average).

When cloud cover inhibits direct sun, as it is very often the case in the Alps, or during night, leaf temperature rapidly drops and reaches similar values to the air temperature (Körner, 2003). The importance of exposure on temperature experienced by plants is therefore limited to clear sky days.
Not only exposure, but also the interaction between wind and relief strongly determines the pattern of snow distribution in alpine terrains (Figure 1.2).

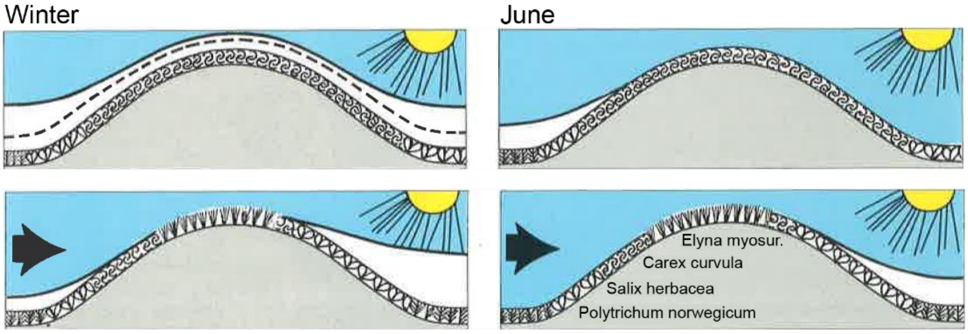

Figure 1.2 - Influence of relief and wind on the snow cover distribution in winter and at snowmelt. Arrows represent the wind direction. The most representative alpine plant species for each topographic situations are displayed in the bottom-right figure and they are indicated by different symbols (Reisigl and Keller, 1987; modified).

Strong winds can remove snow from a windward slope and accumulate it on the leeward side and depressions. Windward- and leeward-snow patterns may change considerably according to wind direction and therefore show high inter-annual variability. On the contrary, snow accumulation in depressions and on north-exposed slopes is a quite conservative process and determines spatially constant snowmelt figures in the alpine landscape (Figure 1.3). Such places covered by high amounts of winter snow for much of the year are called snowbeds and are generally associated to species-poor and low productive plant communities (Bjork and Molau, 2007).

Wind may influence life conditions of alpine plants also by transporting ice pellets and snow that physically damage plant tissues (Ozenda, 1985). For this reason, plants occurring on windy ridges are often prostrate (Körner, 2003). Moreover, wind affects the aerodynamic boundary layer enhancing the convective heat loss and evaporative cooling. The consequent dehydration may be lethal for some plant species that therefore concentrate in sheltered spots formed by the micro-reliefs.

Figure 1.3 - Snow cover distribution shaped by topography and exposure at the alpine – subnival belt of the Réchy Valley (July 1st 2015).

The high micro-topography diversity, typical of the alpine terrain, induces large gradients of soil moisture, leaf temperature, wind exposure, snow cover and timing of snowmelt on a very short space scale. As the alpine plant species distribution is tightly coupled to the micro-climatic conditions (Michalet *et al.*, 2002), the variation of slope and exposure induces a mosaic of plant communities within the same elevation range (Scherrer and Körner, 2011).

1.1.2.2 The role of plants themselves

Under similar conditions of slope and exposure, a prostrated dwarf shrub and a rosette plant show higher leaf temperatures than a taller shrub or an herbaceous plant with leaves along the stem (Körner, 2003). Thus, the more plants are in contact with ground, the higher their leaf temperature and the decoupling with atmospheric temperature. With an air temperature of 22 °C, the centre of the rosette of a common alpine crassulacean plant, as *Sempervivum montanum*, were shown to warm up to 54 °C (Larcher, 1977 in Körner, 2003). The heat accumulation provides advantages for plant development, photosynthesis and especially reproduction, which largely depends on warm temperatures (Körner, 2003). The compact life form, which also protects from strong winds and excessive evapotranspiration, is therefore characteristic of the alpine environment. Tussock grasses, dominant life form in the alpine grasslands, do not reach the same high leaf temperatures as in prostrate plants because of their taller size. However, the presence of standing dead leaves at their stem basis represents a protection against freezing, controls the nutrient cycling and avoids space occupancy by other plants (Körner, 2003). Such a litter trap life strategy can also avoid litter removal and transport by strong winds (Gavazov, 2010). It has been showed that strong wind and snowdrift are responsible for important litter redistribution in arctic landscapes, removing it from ridges and accumulating in depressions as snowbeds (Fahnestock *et al.*, 2000).

1.1.3 The alpine soils and humus forms

1.1.3.1 General features

Mountain soils generate a significant diversity of ecosystem services, including physical support to plants, nutrient and organic carbon (C) cycling, biodiversity and biological activity (FAO, 2015). The formation and evolution of alpine soils is deeply connected to the nature of the parent material, the relief, the biosphere, the climate, and the time passed since the parent material deposition (Jenny, 1941). Contrarily to lowland environments, these factors present large variations in a very short space scale in the Alps, leading to a remarkable edaphic variability (Baruck *et al.*, 2016).

The steep topography and the harsh climatic conditions proper to the alpine environment lead to morphodynamic and cryogenic processes that are important drivers of alpine soils genesis (Körner, 2003). However, the air temperature and its diurnal and annual variations are mostly reflected in the topsoil layer (5 cm deep), but are nearly completely damped at 50 cm deep (Schaetzl and Thompson, 2015) Therefore, soil freezing may occur especially at surface, in diurnal or seasonal cycles, according to the slope exposure, the snow cover properties and the plant canopy (Körner, 2003). As alpine soils are mostly covered by snow in winter, topsoil freezing is more likely to occur in summer. During a freeze-thaw cycle, the topsoil and the above vegetation are heaved and the substrate becomes periodically loose (Körner, 2003). This process, combined with sufficient moisture, leads to solifluction along steep slopes, or frost hummock formation, polygon soils, garland and stripe formations (Körner, 2003). Solifluction and active erosive processes on steep slopes commonly result in topsoil erosion, profile truncation, and burying of A horizons.

The thermal conditions and the moisture availability not only play a role in cryogenic processes, they are also essential drivers of physical and chemical weathering of parent material (Egli *et al.*, 2014) and organic matter (OM) decomposition (Ponge, 2013). Freeze-thaw cycles are important drivers of physical weathering in high-elevation soils, especially in late fall, before the first important snowfall (Dahlgren *et al.*, 1997). Chemical weathering has often been assumed to be strictly related to temperature, and therefore to display low rates in cold high elevations sites. However, many studies evidence that weathering in cold regions may be similar or even higher than in warmer regions (Follmi *et al.*, 2009; Hall *et al.*, 2002). Instead of temperature, moisture availability seems to be particularly crucial for chemical weathering in the alpine regions (Egli *et al.*, 2006).

Moreover, the age of material, on which the soil develops, influences the weathering rates. Young geomorphic surfaces (10 to 10^4 years old) weather up to 3-4 orders of magnitude faster than older surfaces (10^5 to 10^6 years old; Egli *et al.*, 2014). Thus, the abundance of fresh mineral surfaces and fine-grained sediments provided by glacier erosion furtherly participate to the enhancement of the alpine weathering rates (Riebe *et al.*, 2004).

The alpine soils are not always the result of the *in situ* bedrock weathering, but very often they originate from surficial deposits made of terrestrial sediments reworked during Quaternary glaciations (Martignier *et al.*, 2013). Present and past aeolian dusts belong to these deposits (Martignier *et al.*, 2015) and, given their wide distribution in the Alpine chain and their present-day high deposition rates (up to

102 g m^{-2} yr^{-1}; Kufmann, 2003), they can play a major role in alpine pedogenic processes (Martignier *et al.*, 2013).

Alpine vegetation is affected *by* soil type and, at the same time, it has an effect *on* soil and, notably, OM properties. Acidic soils are characterized by high solubility of several potential toxic ions, such as Al^{3+}, Mn^{2+}, and Fe^{3+}, and by deficiencies of important plant nutrients, such as PO_4^{3-}, Ca^{2+}, Mg^{2+}, and K^+. Calcareous soils are dominated by Ca^{2+} and HCO_3^- ions instead, while they present low availability of Fe^{3+} (Lee, 1999). Plants tolerating high levels of Al^{3+} are able to grow on strongly acidic soils ("acidophilic" species), while those inhibited by Al^{3+} but tolerating deficiencies of Fe^{3+} and Ca^{2+} saturation levels are thus mainly found on alkaline soils ("calcicole" species; Clymo, 1962; Lee, 1999; Rorison, 1986). By turn, vegetation influences the soil OM content and its vertical distribution through the root system (Jobbagy and Jackson, 2000). Furthermore, organic acids produced by litter, root exudates and root decomposition are likely involved in the chemical weathering of the parent material (Egli *et al.*, 2008b) as well as in some processes of soil formation, such as podzolisation (Lundstrom *et al.*, 2000).

The role of the biosphere in the soil formation includes also the contribution of soil fauna and microorganisms. These organisms are responsible for litter fragmentation, mineralisation, and incorporation into the mineral soil, as well as soil structure, porosity, and water infiltration (Schaetzl and Thompson, 2015). Macrofauna comminuters, such as earthworms and large arthropods, however are considered to be absent in alpine soils due to the harsh climatic conditions (Jiang *et al.*, 2015; O'Lear and Seastedt, 1994). Instead, microarthropods (oribatid mites and springtails) dominate in alpine tundra (O'Lear and Seastedt, 1994), as well as bacteria, fungi and some archaea (Hofmann *et al.*, 2016). Moreover, according to a study of Blagodatskaya *et al.* (2010) in a forest ecosystem, the slope exposure influences the fungal-bacterial ratio: fungi would dominate on north-east facing slopes, colder and wetter, and bacteria would dominate instead on south-west facing slopes, warmer and drier.

Climate is among the crucial parameters that determine rates of litter decomposition (De Deyn *et al.*, 2008) and rates of nutrient transfer from the parent material to the soil system (White and Blum, 1995). Given the harsh climatic conditions of the alpine ecosystem, both processes are expected to be slow and the alpine soils to be nutrient-poor (Körner, 2003). According to Seastedt *et al.* (2001), the full structural decomposition of high alpine forbs may take 2 years, 5 years for sedge leaves, and more than 10 years for evergreen dwarf shrubs.

Alpine plants developed adaptations to the low availability of nutrients by reducing their growth rate and their aboveground biomass and developing important root systems (Körner, 2003). The litter produced by these slow-growing species is considered highly concentrated in organic C forms and poor in nutrients (Aerts and Chapin, 2000; De Deyn *et al.*, 2008). As a result, these litters present high C/N ratio, which is generally considered as an indicator of poor quality and low potential degradability. Resistance forms, such as sclerophylly, succulence, and evergreen foliage make the litter recalcitrant to decomposition (Ponge, 2013), and furtherly enhance the nutrient limitation.

Besides vascular plants, cryptogams can also play a major role in the soil nutrient cycling. Bryophytes, and some lichen groups, can increase the soil nutrient content by hosting nitrogen-fixing bacteria or, in contrast, can decrease it by the accumulation of recalcitrant polyphenols (bryophytes notably; Cornelissen *et al.* 2007).

Different decomposition rates according to the litter nutrient content might be the result of different microbial community composition. Barta *et al.* (2010) demonstrated that fungi (slow decomposer; Wardle *et al.*, 2004) dominate when litter is rich in phenolics and poor in phosphorus (P), while bacteria (rapid decomposer) are prevalent in opposite conditions.

Moreover, alpine plants develop an important root system, probably to supply the lack of nutriments and a reduced mycorrhization (Körner, 2003). Alpine forbs produce 62 m of fine roots per g of dry root matter in average, while comparable forbs at low elevations produce 41 m g^{-1} (Körner and Renhardt, 1987). In terms of root biomass, Hitz *et al.* (2001) measured an increase from 7 to 13 t ha^{-1} (0-5 cm) from 1665 m up to 2525 m in the Swiss Alps. The C investment in alpine plant species is therefore largely unbalanced in favour of belowground structures (Figure 1.4). Indeed, the annual C input from aboveground phytomass and roots in a Haplic Podzol at 2525 m amounted to 17.9 and 91.1 g m^{-2} $year^{-1}$, respectively (Hitz *et al.*, 2001). Similarly, a root : shoot ratio of 5.8 has been estimated in alpine grasslands of the Qinghai-Tibetan plateau (Yang *et al.*, 2009).

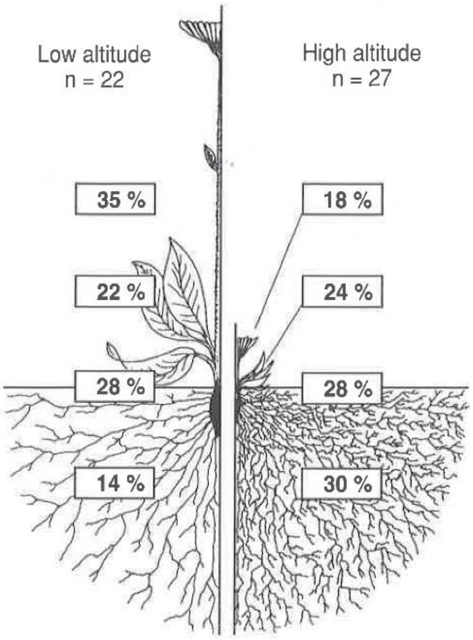

Figure 1.4 - Dry matter allocation in perennial herbaceous plant species from low and high elevations in the Alps in four plant compartments: stem plus flower, leaves, storage organs plus thick roots, fine roots. (Körner and Renhardt, 1987 in Körner, 2003).

Decomposability of roots has been poorly studied so far, but it appears to be lower than that of shoots, and thereby, roots represent a source of recalcitrant C pool (Craine *et al.*, 2005; Tjoelker *et al.*, 2005). However, high root production is also accompanied by higher concentrations of root exudates, which represent a source of labile C and stimulate the activity of some soil decomposers (priming effect; Kuzyakov, 2002).

1.1.3.2 Humus forms

Most of the plant-soil interactions take place within the humus form, i.e. the ensemble of organic layers and the organo-mineral horizon (usually the A horizon) of a soil profile. Being at the interface between vegetation, soil organisms, parent material, and under the control of climatic parameters (Ponge, 2003), the humus forms have been suggested as synthetic indicators of environmental variable interactions (Bonifacio *et al.*, 2017).

Soil parent material has been identified as a major determinant of humus forms at large scale to the same level as climate (Ponge *et al.*, 2011). Indeed, in forest ecosystem of France, moder and mor forms were prevalently associated to neutral to acid soils, while eumull forms (the more active form among the mulls) were dominant in alkaline warmer soils (Ponge *et al.*, 2011).

Alpine soils and humus forms have been poorly studied compared to their lowland counterparts. Indeed, with the exception of Austria who developed its soil classification system in the Alpine environment, other Nations of the Alp chain did not take into account the specifics of high-elevation soils (Baruck *et al.*, 2016). Similarly, humus form classifications originated in forest ecosystems and are only recently opening their identification keys to include other ecosystems (e.g. Zanella *et al.*, 2017).

In light of present knowledge, Moder and Mor humus forms are expected in the alpine life zone because of the low temperatures, the poor litter degradability and the absence of macrofauna comminuters, (Ponge, 2003). Mull forms would be limited to low elevations (Ascher *et al.*, 2012; Bonifacio *et al.*, 2017) and south facing slopes (Zanella *et al.*, 2017). However, a description of alpine humus forms diversity, and of their relationship with vegetation, climate and soil parent material is still lacking for the alpine ecosystem.

1.1.4 Effects of snowpack

Alpine soils can be covered by snow for more than half of the year, up to ten months in depressions or north-exposed sites (snowbeds). The snow layer plays fundamental roles in alpine ecology, going from protection against low temperature extremes, winter desiccation, ice blast, solar radiation, and control on nutrient cycling (Körner, 2003).

During winter, the soil temperature is highly dependent on the snow cover timing, thickness, density, and duration (Maurer and Bowling, 2014; Zhang, 2005). A snowpack thickness of 30-40 cm is sufficient to maintain near zero temperatures at the topsoil (Brooks and Williams, 1999; Cline, 1995), even if the air temperature is -22 °C (Eckel and Thams, 1939 in Körner 2003). The snow insulation potential is inversely proportional to thermal conductivity, which, in turn, increases with high snow density (Zhang, 2005). For instance, a fresh fallen, low density snow (0.1 g cm^{-3}) displays a thermal conductivity tenfold lower than a compacted snow (density of 0.4 g cm^{-3}, Körner 2003). In turn, the thermal conductivity of a dense ripened snow layer is 5 to 20 times lower than a mineral soil (Zhang, 2005). The thermal insulation by snow cover may avoid soil freezing for all winter season, provided that the snow cover is constant, thick, and occurs early enough in winter.

1.1.4.1 On plants

The snow cover allows the penetration of a certain amount of solar radiation to the ground, selecting for the less photosynthetically active part of the spectrum (blue-green range, Richardson and Salisbury, 1977 in Körner, 2003). The fraction of total radiation reaching the ground is negligible under thick snow cover and it increases gradually during winter, with the decline of snowpack thickness and the increase of solar radiation (Körner, 2003). This process, accompanied by the thermal insulation, and the large water availability, permits some plants to be physiologically active and to achieve net photosynthetic C gains under thin snowpack in spring (Körner, 2003). It is the case of *Soldanella alpina*, species in genera *Geum* and *Potentilla*, and grasses such as *Nardus stricta*, whose leaves remain green over winter. Nevertheless, due to small radiation penetrating the snowpack, sub-snow photosynthesis seems to be limited and to only slightly contribute to the annual C balance (Körner, 2003). Rather, the overwinter green leaves have to be considered as an adaptation to short growing seasons, as they allow plants to rapidly develop following snowmelt.

Snowbed plant species, spending around nine months below the snowpack in relatively warm temperatures, do not need to invest resources in cryoprotective measures (Larcher, 1980 in Körner, 2003). Indeed, these species were shown to share some traits with plants from shady environments, such as soft leaves and a high chlorophyll content on a dry leaf mass basis (Körner, 2003). These characteristics may enhance the litter decomposition process in the snowbeds, compared to other more stressful environments, such as windy ridges, where discontinuous snow cover, and therefore possible soil freezing events, hamper the microbial activity.

1.1.4.2 On microbes

Similarly to photosynthetic activity, microbial activity also persists in snow covered alpine soils (Edwards *et al.*, 2007; Salisbury, 1985). The thermal insulation allows microscopic films of free water to form between soil particles and this supports the proliferation of many cold-adapted (psychrophylic) microbial communities (Gavazov, 2010).

More specifically, the subnivial heterotrophic activity highly depends on the duration of thawed soil and on the severity of frost events occurring before snowfall or during winter if the snow cover is discontinuous (Brooks and Williams, 1999). At sites where snow cover occurs late in fall, early soil freezing is frequent and most biotic activities decline. Some alpine microbial communities are however resistant to freeze-thaw cycles (Lipson and Monson, 1998), as well as springtail and mite communities in sub-Arctic soils (Sjursen *et al.*, 2005). Moreover, freeze-thaw events are particularly effective in physically disintegrating organic matter (OM) and releasing labile organic C, that then can stimulate the microbial activity once soils thaw under the winter snowpack (Schimel and Clein, 1996).

Microbial activity and the nitrogen (N) immobilization in the microbial biomass, especially fungi (Schmidt and Lipson, 2004), gradually increase during winter (Brooks and Williams, 1999). The result is an accumulation of NO_3^- (Heuer et al., 1999) and NH_4^+ (Bowman, 1992) under the snowpack and a very limited N leaching (Brooks and Williams, 1999). At snowmelt, soil becomes water saturated, temperature increases and microbial biomass and activity decline sharply (Bardgett et al., 2005). According to Schmidt and Lipson (2004), the winter fungi community dies-off at snowmelt and is replaced by a summer bacteria-dominated community that can tolerate higher temperatures and mostly feed on root exudates.

Moreover, snow itself acts as a nutrient reservoir by accumulating significant amounts of atmospheric depositions (aeolian dust) over winter, depending upon the provenance and direction of air fluxes (Edwards *et al.*, 2007). These nutrients, together with those resulting from the microbial community shift, are released as a pulse during the spring snowmelt and could significantly participate to the annual N-uptake of alpine plants (Bilbrough *et al.*, 2000). Hence, soil fertility in long snow covered areas seems to be relatively high (Körner, 2003), compared to other alpine and subalpine ecosystems with low snow cover. Moreover, the subnivial fluctuations in microbial activity may have important consequences on the C and N biogeochemical cycles of alpine ecosystems (Freppaz *et al.*, 2008).

1.1.4.3 On soils

The snowmelt season is crucial also for soil pedogenesis. The related intense hydrological activity may result in considerable loss of organic acids from the soil system through leaching (Brooks et al., 1996). The large meltwater availability combined with the presence of organic complexing/chelating agents are considered to be responsible of intense podzolisation on well-drained parent material (Hiller *et al.*, 2005). On the contrary, moisture levels close to field capacity on less-permeable parent material may lead to reductive conditions (Hiller et al., 2005) and the oxygen limitation may reduce OM decay (Gavazov, 2010).

1.1.5 Organic matter stability

Soil OM provides essential ecosystem services as it contributes to soil fertility, water quality and retention, biodiversity, resistance to soil erosion, and could play a fundamental role in the mitigation of climate change (Adhikari and Hartemink, 2016). Therefore, it is necessary to understand the mechanisms governing its stability, namely its preservation from mineralisation (Plante *et al.*, 2011; Sollins *et al.*, 1996; von Lutzow *et al.*, 2006) in order to maintain soil OM stocks and their associated functions.

1.1.5.1 Controlling factors

It was previously widely held that mineralisation rates of soil OM reflected the kinetics of enzymatic reactions and were consequently largely dependent on the intrinsic molecular composition of plant litter entering the soil system (Davidson and Janssens, 2006). This concept had been formalised under the term "selective preservation" (Sollins *et al.*, 1996), and assumed that soil microorganisms preferentially decomposed the inherently labile components of OM, causing the accrual of recalcitrant components (Aber *et al.*, 1990; Melillo *et al.*, 1982).

Recent studies have however questioned the idea that organic molecules could be inherently "stable" or "recalcitrant" (Lehmann and Kleber, 2015; Marschner *et al.*, 2008) by showing that potentially persistent organic molecules, such as lignin, could be mineralised relatively quickly in some soil conditions (Gleixner *et al.*, 1999; Gleixner *et al.*, 2002; Heim and Schmidt, 2007). Contrarily, supposedly labile compounds, such as polysaccharides and proteins, can persist in soil for several decades, centuries or even millennia before being mineralised (Derrien *et al.*, 2006; Gleixner *et al.*, 1999; Gleixner *et al.*, 2002). These long residence times can be in large part attributed to protection or stabilisation by soil minerals (Gleixner *et al.*, 2002; Spielvogel *et al.*, 2008).

These recent findings have led to the proposal of a new paradigm, most fully expressed by Schmidt *et al.* (2011). It suggests that selective preservation only plays an essential role in the initial stages of litter decomposition on the soil surface, while its importance becomes marginal when organic material is incorporated into the mineral soil. In the mineral soil, OM decomposition rates are instead mainly driven by its spatial accessibility to microorganisms and enzymes and by the type and number of interactions established with mineral surfaces (Figure 1.5; Lehmann and Kleber, 2015; Schmidt *et al.*, 2011; Sollins *et al.*, 1996; von Lutzow *et al.*, 2006). OM stability in the mineral soil is thus mainly governed by ecosystem properties such as climate, soil texture, mineralogy and geochemistry (Schmidt *et al.*, 2011).

Even though considerably high proportions (between 30 and 63%) of C are stored in the subsoil, between 30 and 100 cm deep (Batjes, 1996), most of the studies on soil OM stabilisation mechanisms have focused on the topsoil (Rumpel and Kogel-Knabner, 2011). This may have resulted in a significant bias in our understanding of drivers of OM stability. Indeed, manipulative laboratory experiments suggest that factors controlling C dynamics in topsoil and subsoil may be substantially different. Fierer *et al.* (2003) and Salomé *et al.* (2010) incubated topsoil and subsoil material and found that water potential and supply of fresh organic material were important for surface horizons, while nutrient input, temperature and the physical accessibility of organic substrates appeared as the main regulatory mechanisms of C mineralisation in the subsurface soil layers. Whether this divergence of controls on soil OM stability is operative under field conditions remains however difficult to evaluate.

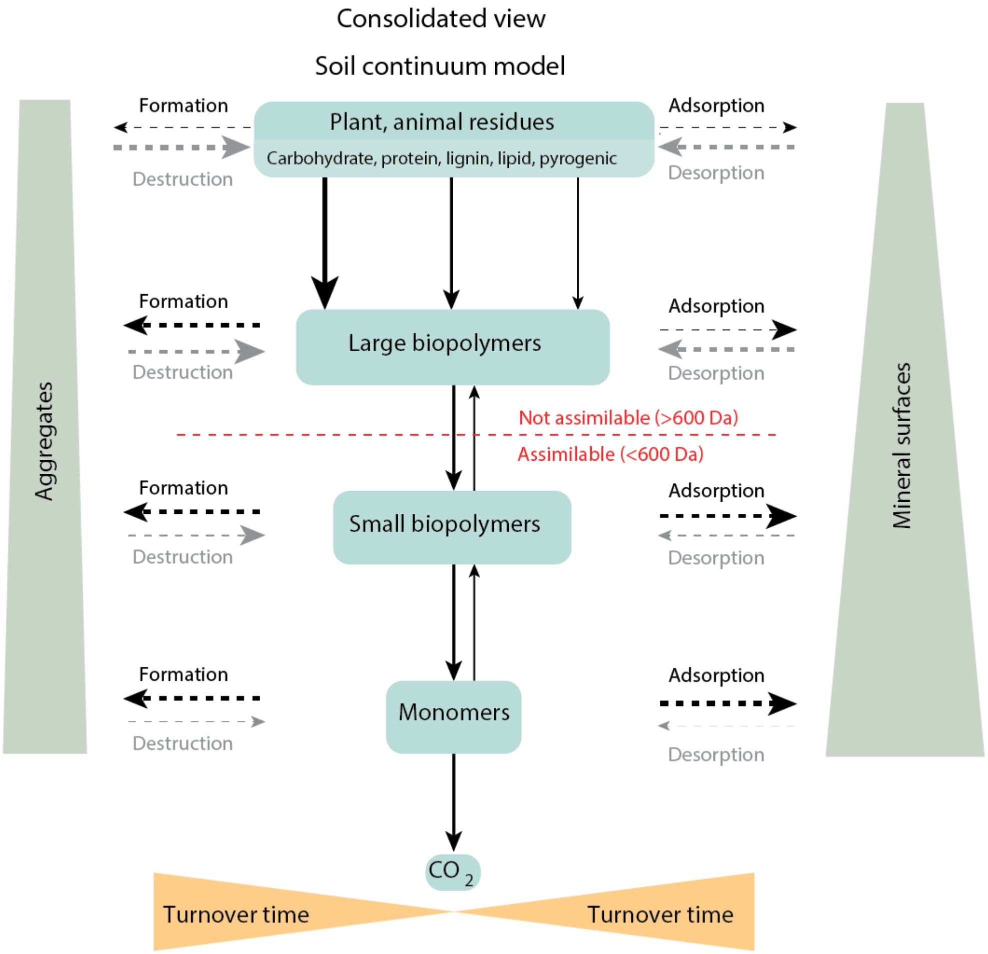

Figure 1.5 - Soil continuum model (SCM)recently proposed by Lehmann and Kleber (2015). Plant and animal residues are progressively decomposed by biotic agents, from intact fresh material to CO_2. But stabilizing factors, such as organo-mineral interactions and occlusion by aggregates, may intervene at each step of the decomposition process. Dashed arrow lines represent mainly abiotic transfers, solid lines represent mainly biotic transfers; thicker lines indicate more rapid rates; larger boxes and ends of wedges illustrate greater pool sizes; all differences are illustrative. All arrows represent processes that are a function of temperature, moisture and the biota present (Lehmann and Kleber, 2015).

1.1.5.2 Methods for the assessment of organic matter stability

Soil OM stability can be assessed with different fractionation techniques based on physical, chemical, or biological properties of OM (see Kögel-Knabner *et al.*, 2008 for a review).

Physical and chemical fractionation techniques separate soil OM into operationally-defined pools whose relevance to field-scale OM dynamics may be difficult to assess (Popleau et al., *in review*). Investigations that consider the bulk sample without pre-treatment may allow for a more integrative assessment of OM stability. In this respect, biological mineralisation during long-term incubation experiments is generally favoured (Plante *et al.*, 2011), but the long durations of incubation required to be fully informative (up to several decades) represent an impediment for processing large numbers of samples efficiently.

Thermal decomposition techniques offer a promising alternative to study soil OM stability. Results from thermal decomposition studies are consistent with those of incubation experiments (Plante *et al.*, 2011) and some physical fractionation schemes (Saenger *et al.*, 2015). The pertinence of thermal techniques is based on the assumption, validated by Plante *et al.* (2011), that thermal stability of OM is related to its biological or chemical stability, as the activation energy required for thermal bond cleavage correlates to the chemical energy required for enzymatic cleavage (Kögel-Knabner *et al.*, 2008). Schiedung *et al.* (2017) recently showed that thermal oxidation between 200 and 400°C was a poor predictor of old (17 years or older) versus recent vegetation inputs.

Pyrolysis techniques appear better suited to assess biological stability, with higher temperatures reported for break-down of persistent versus labile OM (Barré *et al.*, 2016). The Rock-Eval pyrolysis technique is now widely employed for routine analysis of OM in soil samples (see Sebag *et al.*, 2016 for a review). The method quantifies total organic and inorganic C contents of a sample (either soil or litter) and provides a wide range of parameters that can be used to evaluate OM quality and its thermal stability. When compared to other methods used to quantify pools of recent C (as assessed using ^{14}C dating), Rock-Eval analysis performed most effectively (Vinduskova *et al.*, 2015).

1.1.5.3 Specificities of the alpine environment

Alpine soils are known to contain higher organic C concentrations than at lower elevations (Leifeld *et al.*, 2009; Sjogersten *et al.*, 2011). Many studies using fractionation techniques observed that the alpine OM is mainly composed of light particulate organic matter (POM) and less of heavier mineral associated organic matter (MaOM; Budge *et al.* 2011; Leifeld *et al.*, 2009; Saenger *et al.*, 2015; Zimmermann *et al.*, 2007) compared to temperate soils. However, this held especially true for the topsoil layers (0-5 cm), while the contribution of POM becomes very limited to the deep bulk OM (Leifeld *et al.*, 2009). Apparently, plant roots are the major contributors to the POM fraction (Leifeld *et al.*, 2009). The POM fraction is considered more labile and chemically more similar to the original plant input than the MaOM is (Six *et al.*, 2001). The lability of the POM fraction is reflected in its shorter mean residence times (MRT), calculated using radiocarbon (^{14}C) dating, compared to the MaOM, being around 500 years (Budge *et al.*, 2011; Leifeld *et al.*, 2009). However, the MRT of POM is longer in high elevations soils (about 100 years) than in the lowlands (few years to few decades; Leifeld *et al.*, 2009), thus indicating decreasing rates of plant litter decomposition with elevation. By contrast the MRT of the MaOM seems to be independent from elevation, but rather to correlate with the proportion of silt and clay fraction (Leifeld *et al.*, 2009).

The MRT of POM variate along the soil profile as well. According to Budge *et al.* (2011), POM in deep soil layers of several alpine Dystric Cambisols present longer residence times and lower transformation degrees (deduced from high C/N ratio) than in the topsoil. These results were interpreted by the same authors as a result of decreasing macronutrient content and increasing physical protection with soil depth, both hampering the biological OM decomposition. The reason why POM preferentially accumulates at high elevation soils and displays long MRT is not clear yet. Besides of the limiting effects of low temperatures on OM decomposition, Budge *et al.* (2011) argue that also plant productivity, functional type of aboveground vegetation, and nutrient limitations due to low soil pH may be important controlling factors of alpine OM dynamics.

The Rock-Eval pyrolysis has been applied to alpine soils only in the studies of Saenger *et al.* (2013; 2015). These authors compared the topsoil (0-10 cm) OM thermal stability among eleven different eco-units (i.e. plant communities) from 1300 to 2340 m. Among the alpine eco-units, mountain ridges (1980-2341 m) showed high OM thermal lability and up to 69% of POM fraction. However, alpine meadows associated to Cambisols, even if located at the same elevations as mountain ridges, displayed among the highest thermal stabilities (Saenger *et al.*, 2013). Greater mineral associations and aggregation in the alpine meadows than in mountain ridges were suggested by the authors to explain the observed differences.

To date, the study of Saenger *et al.* (2013) is the first having addressed soil OM vulnerability at the landscape scale in mountain regions. However, the small panel of plant communities considered in the alpine belt (only two eco-units), as well as the lack of subsoil sampling, did not allow the authors to detect the major drivers of OM stability in the alpine ecosystem.

1.1.6 Impacts of global changes on the alpine environment

During the end of the 20th century (1975–2004), the mean annual temperature in Switzerland increased by 0.57°C per decade with a stronger trend in spring and summer seasons (Rebetez and Reinhard, 2008). After a gradual increase until the early 80's, snow precipitation in Switzerland significantly decreased (Laternser and Schneebeli, 2003) with a particularly pronounced trend at lower elevations (501-800 m a.s.l., Serquet *et al.*, 2013). Snowfall decreased above 1700 m as well, but only at the beginning and at the end of the winter season (Serquet *et al.*, 2013). At such elevations, winter temperatures are generally much lower than the melting point and, even with warmer conditions, there is little potential for a decrease in snowfall days (Serquet *et al.*, 2011). By contrast, the combination of higher temperatures and lower snowfalls during the spring season result in a thinner snow cover (IPCC, 2014), earlier melt-out dates and longer growing seasons for plants (Dye, 2002).

Future scenarios predict the continuation of this trend through the 21st century and indicate that vegetation of high latitudes and elevations are the most threatened (ACIA, 2005; IPCC, 2014).

1.1.6.1 Impacts on vegetation

Impacts of the recent climate change on alpine vegetation have been largely recorded by many long-term studies on European upper alpine and nival summits. Authors observed an increase in species richness during the last century (see Stöckli *et al.*, 2011 for a review), already noticeable on a short time scale (2001-2008; Pauli *et al.*, 2012). The newly arrived species are subalpine and lower alpine species (Matteodo *et al.*, 2013; Vittoz *et al.*, 2008a) and now, because of longer growing seasons, they are able to grow at higher elevations. Space on the summits is not a constraint to colonisation as it is widely available. However, the upward shift of plant species led, not only to higher species number, but also to a homogenisation of plant composition across Alpine Swiss summits (Jurasinski and Kreyling, 2007). Similarly, vegetation of the high northern latitudes has been changing over the past few decades and a general increase of biomass and proliferation of shrub species are responsible for the tundra "greening" (see Epstein *et al.*, 2013 for a review).

Many more uncertainties exist about the effects of climate warming at lower elevations. A shift of treeline northwards and to higher elevations is the most often observed change on European mountain ranges (see Garamvoelgyi and Hufnagel, 2013 for a review). In the Swiss Alps, the forest limit moved upward with a mean decadal increment of 28 m between 1985 and 1997 (Gehrig-Fasel *et al.*, 2007). However, between treeline and the upper alpine-nival belt, there is a wide range of plant communities whose responses to altered temperatures and precipitations have been poorly investigated so far. This is unfortunate, as identifying the most threatened plant communities is very important to establish proper conservation measures. Some previous long-term surveys focused on changes of specific plant community, such as alpine siliceous grasslands (Dupré *et al.*, 2010; Windmaißer and Reisch, 2013), calcareous grasslands (Kudernatsch *et al.*, 2005; Vittoz *et al.*, 2009), or snowbed communities (Carbognani *et al.*, 2014; Pickering *et al.*, 2014; Sandvik and Odland, 2014). However, only a couple of studies located in the Scottish highlands (Britton *et al.*, 2009; Ross *et al.*, 2012), one in the Austrian (Gritsch *et al.*, 2016), and one in the Italian Alps (Cannone and Pignatti, 2014), looked at long-term vegetation changes in a variety of alpine plant communities.

At these elevations, the effects of climate and land-use changes are difficult to disentangle. Indeed, seasonal grazing has been decreasing and many pastures have been abandoned since the end of the nineteenth century (Bätzing, 1991). This highly contributed to the forest expansion toward higher elevations (Gehrig-Fasel *et al.*, 2007; Vittoz *et al.*, 2008b) and favoured the arrival of plants from fallow and wood edge communities in the subalpine grasslands (Vittoz *et al.*, 2009). Moreover, as a result of industrial, traffic, and agronomic emissions, tropospheric concentrations of nitrogen compounds have increased remarkably, reaching levels that are likely to affect the aboveground productivity of alpine plants (Bassin *et al.*, 2007).

It has been demonstrated that nitrogen deposition causes a decrease of species richness in the Swiss montane grasslands, with oligotrophic, and usually rare, species being particularly disfavoured (Roth *et al.*, 2013). Subalpine and alpine grasslands are likely more vulnerable to negative effects of N deposition, as they have shorter growing seasons and generally thinner and nutrient poorer soils (Bowman *et al.*, 2012). However, increased N depositions may have different consequences between habitats: using a plant trait analysis, Maskell *et al.* (2010) showed that eutrophication and acidification occurred, both of which can be responsible for species loss. Indeed, in a moss-dominated alpine heath of Northern Europe, N deposition seems to trigger a decline of plant diversity and shrub, bryophyte and lichen covers, but an increase in the graminoid cover (Armitage *et al.*, 2014).

1.1.6.2 Impacts on soils

The time scale for soil development and evolution is considered to be ten times longer than that of vegetation (Theurillat *et al.*, 1998). Even if some processes operate quite fast in subalpine and alpine climates, such as formation of podzolic soil layers (few centuries, Lundstrom *et al.*, 2000), several thousand years is the time needed to form soils. Therefore, one can expect that the effects of recent climate changes are hardly detectable in terms of pedogenic processes. However, climate variables do exert both a direct and indirect influence on the amplitude of soil weathering that, in turn, controls the availability of reactive sites for OM stabilization (Doetterl et al., 2015).

Directly, temperature and precipitations are supposed to have an effect on the kinetic rate of mineral dissolution (Egli et al., 2003). Furthermore, climate warming accelerates the glacier retreat and new deglaciated areas are becoming increasingly available. The contact between large amounts of meltwaters and fine-grained sediment, which are typical of the proglacial areas, allow for high weathering rates and rapid soil development (Mavris et al., 2011). Indirectly, climate may influence the soil weathering by controlling the microbial activity and the release of organic acids, which are major agents of mineral alteration, both in siliceous (Egli et al., 2008b; Egli et al., 2010) and calcareous soils (Egli et al., 2008a). The quality and amount of these organic acids is also dependent on the vegetation type, which is as well subject to change following climate variations.

The soil OM component, with respect to the mineral one, is expected to track recent climate changes at a more comparable time scale (Theurillat *et al.*, 1998), because of the temperature-sensitivity characterizing the decomposition process. Moreover, since the soil C stock is more than twice higher than the atmosphere one (Trumbore, 2009), its response to warming may have important consequences on the ecosystem C balance and, for this reason, it is raising increasing concerns among the scientific community (see von Lutzow and Kogel-Knabner, 2009 for a review).

The understanding of climate-driven changes in the soil OM stock is particularly pertinent in mountain ecosystems. Alpine soils cover about $4 \cdot 10^6$ km^2 worldwide (Körner, 2003) and, together with northern latitude soils, they represent the largest OM stock (Leifeld et al., 2009; Sjogersten et al., 2011). These ecosystems are expected to experience a more severe warming than temperate regions (Rebetez and Reinhard, 2008), and to display higher temperature sensitivities in the OM decomposition process (Hobbie *et al.*, 2002; Leifeld *et al.*, 2009).

Global warming could have multiple and contrasting effects on OM permanence in soils (von Lutzow and Kogel-Knabner, 2009). Higher temperatures can potentially accelerate microbial respiration and therefore soil OM mineralisation, with a consequent increase of the potential CO_2 source represented by the soils and a positive feedback on the atmospheric CO_2 concentration (Bond-Lamberty and Thomson, 2010). Conversely, higher temperatures and CO_2 concentrations may increase plant net primary production and plant-derived C inputs to soil and, if this process dominates over OM mineralisation, a soil C sink potential has to be expected (Davidson and Janssens, 2006). In a short term, warming experiment (+4°C over one season), Hagedorn *et al.* (2010a) demonstrated that OM decomposition in alpine treeline soils increased much more than plant growth. However, it remains unclear if such trends would be confirmed on the long term. The increase in OM mineralisation might also induce larger nutrient availability, which would enhance plant growth (Hagedorn *et al.*, 2010b). Increasing temperatures, together with land-use changes, are also responsible of elevation shift of vegetation belts. This process is supposed to change the quality and amount of soil OM, with uncertain consequences on the decomposition rates (Hagedorn *et al.*, 2010b).

The decrease of snow precipitation, later snowfall and earlier snowmelts, may expose alpine soils to freezing temperature with higher frequency. This was shown in a Norwegian manipulative experiment (Kaste *et al.*, 2008), in which the snow removal caused soil frost; however no systematic effects on N dynamics were observed. Changes in snow cover are more likely to affect OM decomposition rates by influencing the soil moisture content and duration of waterlogging conditions. Indeed, higher temperatures alone do not increase litter decomposition rates (Aerts, 2006). A certain soil water content is necessary for microbial activity, as extracellular enzymes and soluble organic C substrates need water films to encounter. The scarcity of water (summertime drought), or its occurrence in a frozen state (e.g. permafrost), may reduce the thickness of such water films and thus lead to spatial inaccessibility of the substrate (Davidson and Janssens, 2006; Thomsen *et al.*, 2003).

Permafrost soils are intensively studied in light of the recent warming, as their thawing could release large quantities of greenhouse gases, methane being of high concern (Anthony *et al.*, 2012). Moreover, permafrost soils represent a large organic C reservoir potentially available for decomposition once frozen soil layers thaw (Schuur *et al.*, 2008). It has been estimated that 15-30% of the permafrost area worldwide could thaw by 2050 (Anisimov and Reneva, 2006) and release about 100 Pg C by the end of the twenty first century (Gruber, 2004).

Flooded soils are also vulnerable, as increasing drying trends may allow for aerobic decomposition and enhance C losses, as Bellamy *et al.* (2005) demonstrated in peat soils and bogs of England and Wales. Peatlands are generally a source of methane (CH_4), which has a greenhouse warming potential on a per molecule basis 23 times higher than CO_2 on a 100-year timescale (Ramaswamy *et al.*, 2001 in Davidson and Janssens, 2006). Hence, the warming-induced CO_2 losses from peatlands could be compensated by a reduction in CH_4 emissions, and they will not necessarily enhance global warming (Whalen and Reeburgh, 1990).

Besides the soil water content, also adsorption on mineral surfaces and occlusion in soil aggregates may reduce the access of the microbial community to OM (Sollins *et al.*, 1996; von Lutzow *et al.*, 2006). These processes are not directly related to temperature, but are rather proper of the pedogenic environment (Schmidt *et al.*, 2011). Thus, the higher their influence in the OM dynamics, the lower the temperature sensitivity of OM as it would be expected from its molecular structure and the ambient temperature ("intrinsic temperature-sensitivity"; Davidson and Janssens, 2006). Contrasting results in global warming effects on decomposition rates may therefore stem from the intervention of such environmental constrains that dampen or obscure the response of OM decomposition rate to warming.

In conclusion, many ecosystem properties controlling OM dynamics, such as vegetation, soil moisture, microbial activity and reactive sites for OM stabilization, are all expected to respond to climate changes. The understanding of the extent, and the time scale, at which these ecosystem properties are affected by recent and future climate changes would be very informative about warming effects on soil OM dynamics.

1.2 Motivation and aims of the study

The present study fundamentally aims at improving our knowledge of the subalpine-alpine ecosystem and its vulnerability to recent climate changes. Two main components of the alpine ecosystem and their interactions are investigated in detail, vegetation and soil. Within the soil compartment, a special attention is delivered to the organic component that is supposed to be the center of plant-soil interactions.

This study develops in the subalpine-alpine ecosystem for many reasons:

- it is among the most exposed and vulnerable to recent climate changes;
- many vegetation changes have been already observed in response to warming at high alpine and nival belts, but poor knowledge is available on how different subalpine and lower alpine plant communities reacted to the same changes;
- soils, humus forms, organic matter dynamics, and their determinants have been scarcely investigated at these elevations;
- the Alps provide a unique natural experimental framework because climatic conditions, plant species, productivity and soil properties change dramatically within short distances.

Therefore, the following questions are targeted in separate chapters:

- **Chapter 4**: (1) are there observable changes in the subalpine-alpine vegetation over the last 25-50 years in species richness and community composition in the Alps? (2) Do the magnitude and direction of changes vary across different plant communities and how? (3) What environmental factors best explain the observed changes?
- **Chapter 5**: (4) which soils and humus forms are associated to the main subalpine-alpine plant communities? (5) What are the determinants of their distribution in the alpine environment? (6) Are the existing classification criteria adapted to the alpine humus forms?
- **Chapter 6**: (7) what are the major determinants of OM thermal stability? (8) How does their significance vary with soil depth?

The answers to these questions will allow evaluating how future climate changes may affect vegetation, soil properties, humus forms, and OM persistence in the subalpine-alpine belt. A better anticipation of such changes is needed to implement proper conservation measures. Moreover, the identification of OM stability determinants (Chapter 6) is essential for the preservation of soil organic C stock, also beyond alpine ecosystem boundaries.

Hereafter, for practicality's sake, I will refer to the above-mentioned three study sections as:
Chapter 4: "the vegetation study"
Chapter 5: "the soil study"
Chapter 6: "the OM study".

A synthesis of the main results of the three studies and their relationships is furnished in the Chapter 7.

2 Study sites

2.1 Location

Three study sites were selected in the Northern Alps and Western Central Alps of Switzerland (Figure 2.1 and Appendix A): the Morteys area, the Réchy area and the Grimsel area. The study sites were selected because of the availability of historical vegetation records (see Chapter 3 for detailed methods).

All study sites are located above the present treeline, between 1698 and 2697 m (Table 2.1). However, because of extensive grazing and deforestations in the Middle Age, the present treeline elevation is lower than the potential one (Favilli *et al.*, 2010; Gehrig-Fasel *et al.*, 2007). The Morteys study site is located around the potential treeline (upper subalpine and lower alpine belt) and the Grimsel and Réchy sites are slightly above it (lower alpine and alpine belt; Table 2.1).

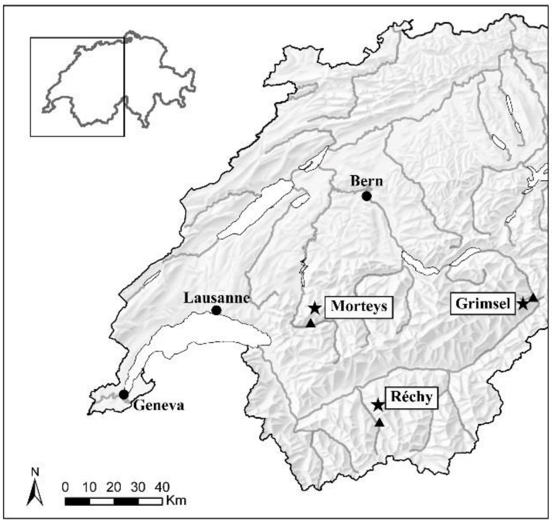

Figure 2.1 - Location of the study sites in Switzerland. Stars represent the three study sites and triangles the corresponding meteorological stations (Château-d'Oex for Morteys, Grimsel Hospiz for Grimsel, Evolène for Réchy).

Table 2.1 - Characteristics of the study sites. Coordinates, mean annual temperatures (MAT), mean annual precipitations (MAP), elevation ranges (with median between brackets), elevational belt, lithology, and number of vegetation records performed and soil profiles excavated at each study site. MAT and MAP are from www.MeteoSwiss.ch and extrapolated according to Zimmermann and Kienast (1999) with a 25 m grid cell size.

	Morteys	**Grimsel**	**Réchy**
Coordinate North	46°32'N	46°32'N	46°10'N
Coordinate East	7°09'E	8°16'E	7°30'E
MAT [°C]	2.1	-0.44	-0.53
MAP [mm]	1650	2071	1480
Elevation [m]	1698–2232 (1884)	2310–2650 (2329)	2328–2697 (2567)
Vegetation belt	Upper subalpine - Lower alpine	Alpine	Alpine
Lithology	Limestone	Granite, gneiss, granodiorite	Gneiss, micaschists, quartzite, calcshists, marble, cornieule
No. of vegetation records	12	25	26
No. of soil profiles	18	11	17

2.2 Climate

The climatic conditions slightly differ between the three study sites in relationship to their biogeographic region and elevational belt. Due to its internal position in the Alps, the climate of the Réchy area tends towards continental conditions, while Morteys and Grimsel have a more oceanic climate.

In the Morteys site, the mean annual temperature is about 2.1 °C and the annual precipitations are 1650 mm (Zimmermann and Kienast, 1999). The annual sum of fresh snow thickness decreased by 34.1 cm per decade between 1964 to 2011, while the mean summer temperature (from June to September) increased by 0.47 °C per decade during the same period at the closest meteorological station (Château-d'Oex, 1029 m; Figure 2.2 and Figure 2.3).

The plots of the Grimsel site are characterized by mean annual temperature and precipitations of -0.44°C and 2071 mm, respectively (Zimmermann and Kienast, 1999). The annual sum of fresh snow thickness decreased by 71.2 cm per decade in average, and the mean summer temperature rose by 0.41°C per decade between 1964 and 2011 (Grimsel Hospiz, 1980 m; Figure 2.2 and Figure 2.3).

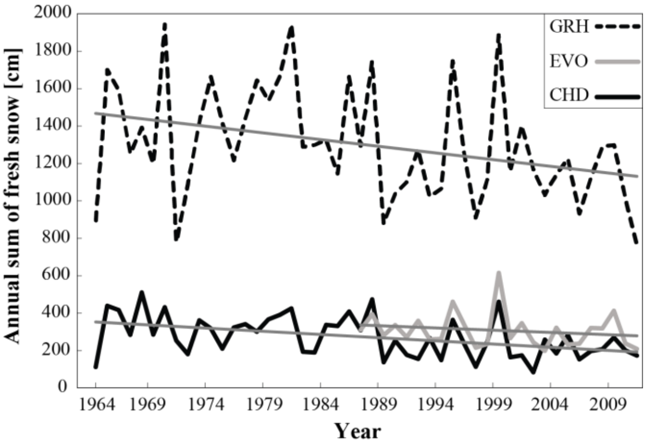

Figure 2.2 – Variation of the annual sum of the fresh snow thicknesses in the study sites. Measured daily at 5:40 a.m. from 1964 to 2011 at weather stations of Château-d'Oex - CHD (Morteys site) and Grimsel Hospiz - GRH (Grimsel site) ; and from 1987 to 2011 at Evolène (EVO, Réchy site) weather station (MeteoSwiss network, Begert et al., 2005). The overall decrease of the snow amount amongst the three stations is significant (ANCOVA test, p-value < 0.001).

The Réchy area is as cold as the Grimsel, but is the driest amongst the three study sites, with a mean annual temperature of -0.53°C and 1480 mm of annual precipitations (Zimmermann and Kienast, 1999). The annual sum of fresh snow thickness decreased by 24.1 cm, whereas the mean summer temperatures increased by +0.25 °C per decade (Evolène, 1825 m; Figure 2.2 and Figure 2.3) during the 1987-2013 timespan (no data available before).

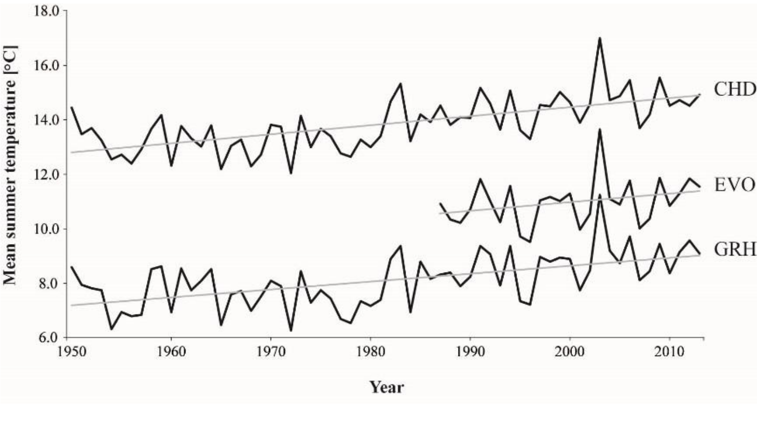

Figure 2.3 – Variation of the mean summer temperatures in the study sites. Mean temperatures recorded from June to September during the 1950-2013 period at Château-d'Oex - CHD (Morteys site) and Grimsel Hospiz - GRH (Grimsel site) weather stations and from 1987 to 2013 at Evolène (EVO, Réchy site). All the stations belong to the MeteoSwiss network (Begert et al., 2005)

2.3 Geology and geomorphology

The Morteys valley belongs to the Median Plastiques Prealps Nappe (Appendix B), originated in the Pennic zone and thrust towards NNW during the setting of alpine orogeny. This nappe is formed of limestone and marls, deposited from the Dogger (Middle Jurassic period) 170 Ma ago up to the Valanginian (Lower Cretaceous) 100 Ma (Bonzanigo, 1996; Lehmann, 2006). The Morteys valley is a synclinal basin, therefore the oldest Jurassic rocks form the external valley slopes, while the younger Cretaceous rocks form the valley axis.

The Grimsel area belongs to the Aar massif, which is part of the Helvetic zone thrusted towards the northwest during late Alpine tectonics (Appendix B; Stampfli, 2001). The Aar massif is part of the Variscan basement and more precisely of the external crystalline massifs (such as Argentera, Pelvoux, Bellondonne, Mont Blanc, Aiguilles Rouges and Gothard massifs). It consists of granodiorite and granite rocks, intruded during the late Variscan orogeny in a pre-Variscan gneiss and Palaeozoic migmatite and amphibolite (Abrecht, 1994).

The Réchy area consists of three different zones, having distinct geology (Stampfli, 2001; WWF Valais, 1986). The Houillère zone is formed of rocks metamorphized during the alpine orogeny (e.g. quartzite).The Siviez-Michabel nappe (Middle Penninic or Briançonnais s.l.) is a Paleozoic basement covered by a Permo-Carboniferous to tertiary sedimentary sequence. This nappe contains Permian granitic intrusions. The Tsaté nappe (Upper penninic zone) represents the ophiolite sequence of the Alpine oceanic crust metamorphized during the alpine orogeny (serpentinites, metagabbros, metabasalts, and prasinites). The associated sediments are represented by calcschists, some from the Upper Cretaceous (Série Grise, grey flysch type series and the Série Rousse). Some “cornieule” (a dolomite-gypsum greywacke) and gypse are also present, especially around the Roc d’Orzival summit.

The three study sites were covered with glaciers during the late Pleistocene glaciation (Würm). The onset of the melting of the Rhone glacier in Switzerland is dated circa 21'000 years BP and continued to the oldest Dryas, around 16’000 years BP (Ivy-Ochs et al., 2004). This must be considered as the maximum soil age in the study sites. However, many morphodynamic processes triggered the removal, transport, and accumulation of material during the Quaternary, leading to a complex mosaic of sediments of different ages (Baruck et al., 2016; Theurillat et al., 1998). Loess deposits are also very likely in each study area.

Beside this general framework, each study area presents some geomorphologic peculiarities, listed hereafter.

The Morteys valley is characterized by a karstic system that drains soils and produces an underground hydrological network. Grykes and dolines are the surficial traces of such a karstic system.

In the Grimsel area, the Oberaar glacier deposited various moraines between 1860 and 1920, at the end of the Little Ice Age (Ammann, 1979). The 1860 moraine is the parent material of two soil profiles in this study (G350 and G421; Table 5.1). Other moraine deposits of the Grimsel area are most probably older (post Last Glacial Maximum).

The Rechy area offers a wide variety of geomorphological processes related to glaciers (two rock glaciers - Lona and Becs-de-Bossons), gravity movements (gelifluction and solifluction), and cryoturbation (soil polygons, stone stripes). The ensemble of these periglacial features led the Réchy and Lona areas to be nominated “Swiss geotope” by the Swiss Academy of Sciences (Reynard *et al.*, 2012). Some dolines formed by the dissolution of gypsum are also encountered.

2.4 Soils and humus forms

To date, no information on the diversity of soil types and humus forms exists for the three study sites. According to Bonzanigo (1996), soils in the Morteys area might be homogeneous because of the uniform climate and lithology existing in the valley. However, Richard *et al.* (1977) suggested the presence of accumulations of aeolian acidic sands in the Morteys valley that would favour the development of siliceous snowbeds. In this case, soils would be less uniform than expected. From the geological and geomorphological descriptions of the two other sites, acidic soils are expected in the Grimsel area and a mosaic of acidic and alkaline soils in the Réchy area. If the lithology is known to play a fundamental role in pedogenic processes, determinants of the distribution of humus forms are still poorly known, especially at the alpine belt. Therefore, any proposal relating to the humus forms occurring at the study sites would be uncertain in light of current knowledge.

2.5 Vegetation

The Morteys area has an extremely rich flora, counting more than five hundred plant species (http://www.pronatura-fr.ch/vanil-noir) and more than 20 plant communities were recorded by Richard *et al.* (1977) in its vegetation survey. Vegetation types occurring above the present treeline show substantial differences according to the slope exposure. On the south-exposed slopes, thermophilous grasslands dominated by *Laserpitium latifolium* (*Caricion ferrugineae*) are found at lower elevations, while mesophilous and xerophilous facies of calcicolous alpine grasslands (*Seslerion caeruleae*) are distributed in mosaic at higher elevations. On the north-exposed slopes, calcicolous meso-hygrophilous sedge grasslands (*Caricion ferrugineae*), ridges dominated by graminoid tundra (*Elynion*) and subalpine tall-herb vegetation (*Adenostylion*) are observable in mosaic (Richard *et al.*, 1977). Heathland belonging to the *Rhododendro-Vaccinion* are found at lower elevations. In the piedmont, at Morteys-Dessus and Morteys-Dessous localities, subalpine pastures (*Poion alpinae*) are present because of cattle grazing. The present treeline (around 1800 m) is formed by maple forests (*Lunario-Acerion*) and Norway spruce forests (*Vaccinio-Piceion*).

The left-hand side of the Grimsel Oberaar lake has been studied by Ammann (1974), whereas no data exist (to my knowledge) about the eastern part of the study area (between the Oberaar lake and the

Triebtenseelicken Pass, and beyond the pass). Ammann (1974) reported 20 vegetation types (associations or species groups), which distribution is highly influenced by the last glacier advance. Youngest moraines are covered by the pioneer alliance *Epilobion fleischeri*, whereas older ones are characterized by siliceous subalpine grasslands (*Nardion strictae*) mixed with the siliceous alpine grasslands (*Caricion curvulae*), mostly located on convex topography. On flat terrains, probably more fertile, the *Nardion strictae* grasslands are dominated by the grass *Agrostis schraderiana*. Wet depressions and wetlands are characterized by the alliance *Caricion fuscae*, and snowbeds by the *Salicion herbaceae*. Subalpine shrublands (*Juniperion nanae*) and some willow species belonging to the *Salicenion waldsteinianae* are found in patches between the subalpine grasslands. The present treeline (around 2000 m) is formed by larch and Norway spruce (*Vaccinio-Piceion*).

The higher part of the Réchy valley, even if less than 15 km^2, contains the majority of alpine ecosystems (WWF Valais, 1986) and around 25 plant communities (Richard *et al.*, 1993). Among them, some alluvial wetlands, situated between the Réchy river meanders, are of particular interest because of their fragility and rarity. Such ecosystems harbour a variety of vegetation types, such as *Caricion lasiocarpae*, *Caricion fuscae* and *Caricion davallianae*, respectively distributed along a gradient of decreasing humidity. One of the six Swiss stations of the rare plant grass *Hierochloë odorata* is also located in the same area. On sandy-gravelly alluvions, reworked during the river floodings in spring, a rare vegetation type is encountered: the *Caricion bicolori-atrofuscae*. Rare arctic species, sheltered in the alpine nunataks during the Riss and Würm glaciations, are harboured in this vegetation type. Snowbed vegetation is found above 2300 m, and it is typically represented by the *Salicion herbaceae*. Some calcareous snowbeds (*Arabidion caeruleae*) are also present on alkaline parent material. Among grasslands, the alliances *Nardion* and *Caricion curvulae* dominate on quartz, gneiss and micaschists, whereas the *Elynion myosuroidis* is found on calcschists, cornieule and dolomie. The present treeline (around 2200 m) is constituted by larches and Swiss stone pines (*Larici-Pinetum cembrae*).

2.6 Management

The three study sites have been partially included in natural reserves for several decades. Except for Grimsel, where there has been no cattle grazing since 1953 (year of the Oberaar dam construction), the two other sites are currently pastured in some parts. Thanks to the natural reserve management in Morteys, the land-use (cow and sheep grazing) has barely changed during the last 40 years. In Réchy, the type and amount of cattle fluctuated since the 1970s, with alternating cow and sheep grazing, the proportions depending on both elevation and location.

The total nitrogen deposition in Morteys and Grimsel areas for the year 2007 amounted to 10.4 and 6.8 kg N ha^{-1} yr^{-1} on average, respectively (according to Roth et al., 2013; data from FOEN Federal Office for the Environment). Data for the Réchy area were not calculated, but are probably comparable to those of Grimsel area because of the similar elevations and distance to main towns.

3 General methods and sampling strategy

3.1 Vegetation data

3.1.1 The vegetation study

The first scope of this study was to investigate the reactions of different subalpine-lower alpine vegetation to recent climate changes (i.e. “the vegetation study”, Chapter 4).

To target this aim, historical vegetation records covering a variety of vegetation types were necessary to be compared with recent ones. Therefore, the first step of this study consisted of identifying the historical plant inventories available in the Swiss Prealps and Western Central Alps (easily accessible from Lausanne University). Moreover, these plant inventories had to be representative of the main vegetation types encountered in the subalpine-alpine ecosystem. Amongst the available data, a selection of the most promising historical records was performed according to criteria of reliability and possibility to relocate them. The historical records were achieved by several botanists from 1965 to 1990, with most data being collected during the 1970s (1980s in the case of wet snowbeds). The inventories were only partly published (Ammann, 1974; Richard et al., 1977; Richard et al., 1993), but field books were available for most of them and they represented the main information source. Because of their localization on topographic or vegetation maps (1:25'000 or more precise), the plot areas were approximately localized in the field, with a precision of ± 10-50 m.

Each area was extensively visited in the field and, on the basis of information contained in the historical field books (site description, elevation, surface, slope and exposure), the possible plot sites were defined. The exact plot location was selected in order to have a species composition as close as possible to the historical one. When no area corresponded to the historical description, or when vegetation was markedly different, other factors than climate (for example: landslides, major human interventions, erroneous plot localisation by the historical botanist) were likely responsible of the observed discrepancies. Such sites were thus discarded in order to not overestimate the climate change impacts on vegetation. A new exhaustive record of all vascular plants was performed during summers 2013 or 2014 at the phenological optimum, within the same area as the historical one. The nomenclature of species is according to Aeschimann et al. (1996). Species cover was visually estimated, as in historical inventories, according to cover classes of Braun-Blanquet (1964; see Table 4.1 for details).

The plots were permanently marked with metal plates in soil (Figure 3.1) and the four corners measured with a high precision GPS (GeoXT, Trimble, Sunnyvale, CA, USA) in order to enable their future use as permanent plots.

Figure 3.1 – Plot marker. Example of a metal plate used to mark diametric opposite corners of the vegetation survey surface. Picture: S. Messerli.

For very small plots (<4 m^2), or when the GPS precision was lowered down by cloudy weather or mountain features, only the GPS coordinate of the plot centre was taken. Two metal plates per plot were used and, looking towards the mountaintop, they were placed on the bottom left and upper right corners, respectively. Eleven plots stand out as exceptions to this rule and metal plates are located on the two other corners or on the ridge top.

In total, 89 vegetation records, including five replicates, were performed. However, not all of them were retained for the vegetation study. The replicates were done when several plot locations were possible according to available information. Finally, the most reliable plot in each replicate pair (i.e. the one whose species composition was the closest to the historical record) was retained. Only records separated by a distance > 10 m were retained in order to avoid spatial autocorrelation, and other records were dropped out because their re-localisation was considered not reliable enough. Finally, 67 plots were localised with a high confidence level (Appendices C1, C3, C4, C5). Details of the 22 discarded vegetation records, and their plant species lists, are given in Appendix C2 and C6, respectively.

A clustering analysis (using the Hellinger distance and the Ward aggregation algorithm) of cover-weighted historical and recent inventories together (i.e. 67 x 2 =134 records) allowed to group vegetation records with similar species composition and cover. Then, an indicator value was assigned to each species representing its specificity and fidelity for a certain group of records. The function *Indval* of the

R package *labdsv* was used. Large mean abundance of a species within a group compared to the other groups, and high frequency of that species among records of that group, produced high indicator values for that species (Borcard *et al.*, 2011; p. 97). Then, a permutation test provided the statistical significance of the species indicator values. Species, whose indicator value was significant for a certain group of records, were considered as characteristic of that group. Finally, each group of records was associated to a specific plant community type of the Swiss vegetation classification system (Delarze *et al.*, 2015), based on its characteristic species (Appendix C3, C4 and C5).

In total, seven vegetation types were identified, each corresponding to a phytosociological alliance given between brackets: calcareous grasslands (*Seslerion*); subalpine pastures (*Poion alpinae*); windy ridges (*Elynion*); siliceous subalpine grasslands (*Nardion*); siliceous alpine grasslands (*Caricion curvulae*); typical snowbeds (*Salicion herbaceae*) and wet snowbeds (*Caricion bicolori-atrofuscae*). The description of these vegetation types is given further. The subalpine pasture group was discarded from the vegetation study (Chapter 4), because it contained an insufficient number of records (n=4) to draw solid conclusion. Therefore, 63 pairs of inventories, distributed among 6 vegetation types, were retained in the vegetation study (Table 3.1).

3.1.2 The soil and OM studies

Among the 89 vegetation records performed, 46 were accompanied by a soil description (Table 5.2 and Appendix D). These 46 vegetation records, and their associated soil profiles, were all considered in the soil (Chapter 5) and OM (Chapter 6) studies. With some exceptions, the vegetation records were associated to the same plant community types as determined in the vegetation study, without repeating the cluster analysis. Among the 46 vegetation records, 7 were discarded from the vegetation study because of their not-reliable re-location (see above), and were thus considered in the soil and OM studies only. As these records were not included in the cluster analysis, their attribution to a plant community type was performed by considering their species composition and cover, on the basis of personal knowledge, and without the support of statistical methods.

Among these seven vegetation records, two could not be attributed to any plant community type defined in the vegetation study. Their species composition and cover were typical of an additional vegetation type: the calcareous snowbeds (*Arabidion caeruleae*). Other two records, considered among the windy ridges (*Elynion*) in the vegetation study but with a species composition closer to the calcareous snowbeds than to windy ridges, were associated to this vegetation type for the soil and OM studies.

The four vegetation records belonging to the subalpine pastures (*Poion alpinae*), firstly discarded in the vegetation study, were considered at this step. In total, 46 plant inventories, distributed among 8 vegetation types, were retained for the studies of soils and OM stability (**Table 3.1**).

3.1.3 The vegetation types

Hereafter, the eight vegetation types, object of this study, are briefly described according to the Swiss vegetation classification (Delarze *et al.*, 2015) and are associated to the corresponding phytosociological alliance name (Table 3.1, Delarze *et al.*, 2015). Moreover, the characteristic species identified by this study within each vegetation type are mentioned.

Table 3.1 – List of vegetation types object of this research, correspondence with the phytosociological alliances, and number of plots retained in each study. (*): among the four vegetation records composing the calcareous snowbeds in the soil and OM studies, two were considered as windy ridges in the vegetation study.

Vegetation type	**Phytosociological alliance**	**No. of plots in the Vegetation study**	**No. of plots in the Soil and OM studies**
Calcareous grasslands	*Seslerion caeruleae*	10	10
Subalpine pastures	*Poion alpinae*	-	4
Windy ridges	*Elynion myosuroidis*	13	4
Calcareous snowbeds	*Arabidion caeruleae*	-	4*
Siliceous subalpine grasslands	*Nardion strictae*	12	4
Siliceous alpine grasslands	*Caricion curvulae*	11	9
Typical snowbeds	*Salicion herbaceae*	8	7
Wet snowbeds	*Caricion bicolori-atrofuscae*	9	4

3.1.3.1 Calcareous grasslands (*Seslerion caeruleae* Br.-Bl. 26)

This vegetation type is characterized by a high species richness and large abundance of Leguminosae family (Figure 3.2). Tussock species, as *Sesleria caerulea* and *Carex sempervirens*, dominate and often form rungs parallel to contour lines as a consequence of solifluction. It is generally located on very steep, south exposed slopes, with shallow, stony soils on calcareous parent material. This alliance in Switzerland has its optimum at the alpine belt (2000-2500 m), but it often reaches lower elevations, replacing forests under grazing. Among the characteristic species of the alliance (Delarze *et al.*, 2015), *Bupleurum ranunculoides* and *Hieracium villosum* were found in this study. Moreover, *Laserpitium siler*, *L. latifolium*, *Carex sempervirens* and *Helianthemum nummularium* ssp. *grandiflorum* were very frequent and covered large surfaces.

Figure 3.2 - *Seslerion caeruleae*, plot M3128, 1843 m.

3.1.3.2 Subalpine pastures (*Poion alpinae* Oberdorfer 50)

This vegetation type is often situated on flat terrains, in a concave topography leading to the accumulation of snow and percolating water (Figure 3.3). Pasture occurs, and therefore, several nitrophilous species, such as *Poa alpina* and *Phleum rhaeticum*, dominate. The permanence of this alliance at the subalpine belt is linked to the pasturing, which avoids the colonisation by trees. The soils are relatively wet and deep. In this study, the alliance was characterized by *Cerastium fontanum* ssp. *vulgare*, *Crepis aurea*, *Phleum alpinum* aggr., *Alchemilla vulgaris* aggr. and *Plantago alpina*.

Figure 3.3 - *Poion alpinae*, plot M2980, 1945 m.

3.1.3.3 Windy ridges (*Elynion myosuroidis* Gams 36)

The dense tussocks of *Elyna myosuroides* (Cyperaceae family), interposed by low-stature plants and many terricolous fruticose lichens, dominate this plant community type (Figure 3.4). This vegetation type is situated at the alpine belt, between 2200 and 2800 m, on ridges exposed to wind. Besides erosion and physical damages, strong winds determine also irregular snow cover thereby exposing soils to freezing temperatures (-30 °C according to Ozenda, 1985). *E. myosuroides* is able to survive such harsh conditions by means of leaf and root resistance techniques (Ozenda, 1985). Soils can be either acidic or alkaline, corresponding to different plant associations within the same alliance. In addition to *E. myosuroides*, other characteristic species encountered in this study were *Antennaria carpatica*, *Draba aizoides*, *Gentiana tenella* and *Agrostis alpina*.

Figure 3.4 - *Elynion myosuroidis*, plot R3901, 2697 m.

3.1.3.4 Calcareous snowbeds (*Arabidion caeruleae* Br.-Bl. 26)

This vegetation type is generally found on north-exposed slopes and calcareous parent material (Figure 3.5) at the alpine belt. As snowbeds in general, the snow cover is long and the growing seasons short (3-4 months). Soils are rich in scree deposits and quite unstable and permeable. In the most humid part of the snowbed, there is a discontinuous carpet of small-stature plants, mostly rosette hemicryptophytes, whereas dwarf shrubs as *Salix retusa* and *Salix reticulata* dominate in the periphery. The four plots belonging to this vegetation type were characterized by the presence of *Salix retusa*, *Ranunculus alpestris*, *Soldanella alpina* and *Dryas octopetala*. *Adenostyles alliariae* was also covering large surfaces in two plots.

Figure 3.5 - *Arabidion caeruleae*, plot M2716, (left) under snow on 24.7.2013 and (right) on 3.09.2013, 1966 m.

3.1.3.5 Siliceous subalpine grasslands (*Nardion strictae* Br.-Bl. 26)

These grasslands, dominated by the grass *Nardus stricta*, are widespread at the subalpine-lower alpine belt on acidic and nutrient-poor soils (Figure 3.6). The absence of manuring, a regular pasture, or mowing, favor this vegetation type. The development of *N. stricta is* especially enhanced by the pasture, since the stiff, silica-rich leaves of this grass are avoided by cattle (Massey *et al.*, 2007). At the alpine belt, several intergrades between the *Nardion* and the *Caricion curvulae* (see below) are frequent. The species richness of *Nardion* is generally lower than subalpine calcareous grasslands. In this study, the following plant species were significantly associated to *Nardion*: *Ajuga pyramidalis, Arnica montana, Campanula barbata, Gentiana acaulis, Geum montanum* and *Hypochaeris uniflora*. Poaceae species, such as *N. stricta* and *Festuca rubra* aggr., were dominant in cover.

Figure 3.6 - *Nardion strictae*, plot G295bis, 2329 m.

3.1.3.6 Siliceous alpine grasslands (*Caricion curvulae* Br.-Bl. 26)

This plant community type grows in the same conditions as the *Nardion* (acidic and poor soils), but at the alpine belt where it corresponds to the climax (Figure 3.7). The long-lived clonal sedge *Carex curvula* dominates this vegetation type. This species forms dense tussocks, among which lichens are very frequent. Transitions stages with the siliceous snowbed (*Salicion herbaceae*, see below) or alpine heaths (*Loiseleurio-Vaccinion*) are possible in places of long snow cover and on windy ridges, respectively. Besides *C. curvula*, characteristic species of this alliance were: *Festuca halleri*, *Hieracium piliferum* aggr., *Senecio incanus* s.str. and *Trifolium alpinum*. Some individuals of the rare *Gentiana alpina* were found in one plot (R4209).

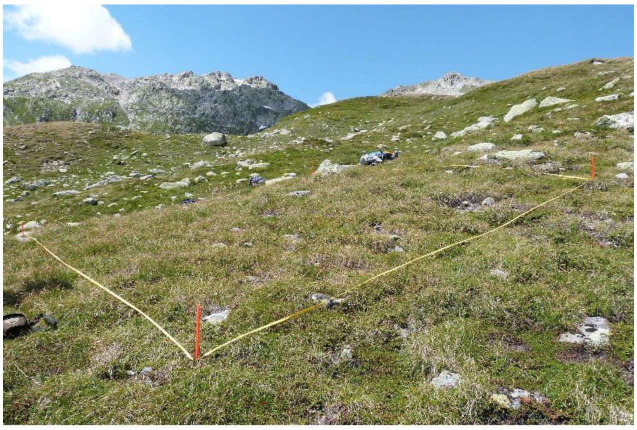

Figure 3.7 - *Caricion curvulae*, plot G335, 2410 m.

3.1.3.7 Typical snowbeds (*Salicion herbaceae* Br.-Bl. 26)

This vegetation type is found from the subalpine to the subnival belt where the snow cover lasts for 9-11 months per year and soils are wet also during summer (Figure 3.8). That long snow cover is the result of slow melting because of north exposure or concave topography, with accumulation by wind. Generally associated to siliceous parent materials, this vegetation type can grow on calcareous substrates when the accumulation of decalcified fine earth and/or OM is important enough to acidify the surface soil layer (Ellenberg, 1988). The dwarf willow *Salix herbacea*, other small stature plants generally reproducing by stolons and mosses dominate such plant community type. Species as *Alchemilla pentaphyllea, Carex foetida and Sibbaldia procumbens* were almost exclusively found in this alliance.

Figure 3.8 - *Salicion herbaceae*, Réchy valley, below “Col de Cou”, 2440 m ca.

3.1.3.8 Wet snowbeds (*Caricion bicolori-atrofuscae* Nordhagen 37)

This vegetation unit is associated to alluvial deposits bordering lakes and alpine streams, or located downstream of firns (Figure 3.9). In comparison with the typical snowbeds, this plant community type is linked to the presence of running water, which does not directly result from the duration of snow cover, but rather on its amount and melting patterns. The plant cover is never dense and mosses are dominant. Soils are water saturated all year long and water is often alkaline (pH 7 to 8), although poor in carbonates. Even if its elevation range is wide (from 1600 to 2800 m), this alliance is rare in the Alps as it was frequently destroyed by the hydroelectric dam constructions. Most of the characteristic plant species of this vegetation type are pioneer post-glacial relicts and are considered vulnerable or near threatened by the IUCN criteria. In this study, characteristic species of this vegetation unit were *Carex bicolor*, *Juncus triglumis* and *Equisetum variegatum*. The more vulnerable species, such as *Carex atrofusca* and *Carex microglochin*, were absent in the studied plots but they were observed in the Réchy valley (WWF Valais, 1986).

Figure 3.9 - *Caricion bicolori-atrofuscae*, plot R5061, 2650 m.

3.2 Soil data

3.2.1 Soil description and characterization

Soil description was performed following the guidelines provided by the Food and Agriculture Organization of the United Nations (FAO, 2006). Depth, colour (according to the Munsell soil colour chart), relative abundance of calcium carbonate (established by 10% HCl test), structure, percentage of skeleton (> 2 mm), and fine roots (< 2 mm in diameter) of each soil horizon were estimated in the field. Organic (Oi, Oe and Oa), mineral topsoil (A), and mineral subsoil horizons (E, B, and C) have been named in the field according to Baize and Girard (2009) and then converted to the international FAO nomenclature (FAO, 2006). The nomenclature of soil references is according to IUSS Working Group (2015) and that of humus form follows Jabiol et al. (2013).

3.2.2 Sampling

Samples were collected almost in each described horizon, including the organic ones, for a total of 231 samples. They were collected in summer, within the three months following snow melt, irrespective of the vegetation type. A part of the plant species composing the aboveground biomass were totally decomposed during fall and winter, and their litter could not be collected. Therefore, the plants composing the litter samples were the most resistant to decomposition, and not the ensemble of plant species. Most of the times, dead leaves composing the litter were from Cyperaceae and Poaceae, and were still fixed at the base of living plants. This was typical for plant species growing in turfs, such as *Carex sempervirens* and *Nardus stricta*. In some calcareous grasslands, different layers of such leaves were observed on the basis of colour variations. This probably indicates different litter ages and thus its accumulation through time.

Among the plant species whose litter could not be sampled, there were mainly forbs. This may indicate their higher degradability compared to graminoids, or their removal by external agents, such as wind and snow.

3.2.3 Routine analyses

Samples were dried at 45°C. The mineral soil samples were then sieved at 2 mm (fine earth fraction) and a part of the sieved sample was crushed to powder in an agate mortar. The organic samples were ground to 0.12 mm mesh size with a pulveriser (14 Fritsch Tracomme AG).

The pH H_2O was measured with a lab pH meter (Metrohm SA) fitted with a double-junction combined glass electrode. The measurement was conducted in a suspension of fine earth in deionized water (1:2.5 soil water ratio) after 2 h of agitation.

The texture of the fine earth fraction was assessed by laser diffraction (Malvern™ Mastersizer 2000) operated in manual mode. Prior to analysis, calcium carbonate was removed by reaction with 10% HCl and rinsed several times until a pH > 6 was reached. The OM was then removed with 10-35% hydrogen peroxide (H_2O_2). During and after the OM digestion, the pH was neutralized with sodium hydroxide (NaOH) 0.1 - 0.5 M. Finally, soil mineral particles suspended in dilute Na-hexametaphosphate (40 g/L) were processed by a Hydro2000S module.

The C/N ratio was calculated on the oven-dried crushed samples of organic (Oi, Oe and Oa) and topsoil mineral layers (A) only, with a CHNS Elemental Analyser FlashEA 1112. Calcium carbonate in the A horizons was removed prior to analysis by addition of 10% HCl and subsequent rinsing. Analytical precision and accuracy were determined by replicate analyses and by comparison with Organic Analytical Standard composed of purified DL-Methionine. They were better than 0.1% (1σ) and 0.01% (1σ) for carbon and nitrogen determinations, respectively.

3.2.4 The Rock-Eval method

The organic carbon content and the organic matter properties of the 231 samples were obtained by thermal analysis performed with a Rock-Eval 6 Pyrolyser (Vinci Technologies). Twenty samples had TOC (Total Organic Carbon) concentrations that were too low for reliable analysis (TOC < 0.2%) and/or abnormal pyrolysis curves and were deleted from the dataset; therefore 211 samples were retained for the analyses. Between 40 and 70 mg of dried crushed sample were pyrolised in an inert N_2 atmosphere with increasing temperatures from 200 up to 650°C with a heating rate of 25°C/min. The residual sample was then oxidised under oxygenated atmosphere starting at a temperature of 400 increasing until 850°C with the same heating rate. The two phases of thermal decomposition released hydrocarbon compounds (HC), CO_2, and CO which are measured continuously. The sum of these carbon fractions (excluding the CO_2 released above 400°C during N_2-pyrolysis and above 650°C during oxidation, which corresponds to the mineral C), represents the TOC concentration (Lafargue *et al.*, 1998).

The amount of HC released relative to TOC is called the Hydrogen Index (HI) and it is considered as proportional to the atomic H:C ratio in the sample. Similarly, the amount of CO_2 and CO released relative to TOC is called the Oxygen Index (OI) and it is considered as proportional to the atomic O:C ratio. The HI and OI indices are considered as proxies of the organic matter quality (Carrie et al., 2012).

The amount of hydrocarbons released during pyrolysis between 200 and 650°C forms a compositional bell curve called the S2 pyrogram. The shape of this pyrogram is sample-specific and is indicative of the thermal stability of organic molecules composing the sample. The area under the S2 pyrogram was subdivided into four sections (A1, A2, A3 and A4) using temperature cut-offs frequently used in the literature (Sebag et al., 2016): 200-340°C for A1, 340-400°C for A2, 400-460°C for A3 and 460-650°C for A4. Thermally labile organic molecules are supposed to release high quantities of HC during the early stage of the pyrolysis process (i.e. large A1 and A2 areas), while thermally stable organic molecules crack later (i.e. large A3 and A4 areas). On this basis, thermal stability of each sample was represented by two indices previously suggested by Sebag et al. (2016): the R-Index, as the proportion of the refractory OM fraction [$R=(A3+A4)/(A1+A2+A3+A4)$], and the I-Index as an indicator of preservation of thermally labile immature OM [$I=\log10(A1+A2)/(A3)$]. These two indices are inversely proportional and only the R-Index was used as an indicator of OM thermal stability in the present study.

The TOC was corrected for hygroscopic moisture by oven drying dried crushed samples of organic and mineral soil layers. In order to minimize mass losses by oxidation and decomposition, temperature and duration of heating were adapted to the type of sample: 65°C during 30 h for organic layers and 105°C during 24 h for the other layers

4 Vegetation changes in the subalpine-alpine belt

4.1 Abstract

While the upward shift of plant species has been observed on many alpine and nival summits, the reaction of the subalpine and lower alpine plant communities to the current warming and lower snow precipitation has been little investigated so far. To this aim, 63 old, exhaustive plant inventories, distributed along a subalpine–alpine elevation gradient of the Swiss Alps and covering different plant community types (acidic and calcareous grasslands; windy ridges; snowbeds), were revisited after 25 to 50-years. Old and recent inventories were compared in terms of species diversity with Simpson diversity and Bray-Curtis dissimilarity indices, and in terms of community composition with Principal Component Analysis. Changes in ecological conditions were inferred from the ecological indicator values.

The alpha-diversity increased in every plant community, likely because of the arrival of new species. As observed on mountain summits, the new species led to a homogenisation of community compositions. The grasslands were quite stable in terms of species composition, whatever the bedrock type. Indeed, the newly arrived species were part of the typical species pool of the colonized community. In contrast, snowbed communities showed pronounced vegetation changes and a clear shift towards dryer conditions and shorter snow cover, evidenced by their colonisation by species from surrounding grasslands. Longer growing seasons allow alpine grassland species, which are taller and hence more competitive, to colonize the snowbeds.

This study showed that subalpine-alpine plant communities reacted differently to the on-going climate changes. Lower snow/rain ratio and longer growing seasons seem to have a higher impact than warming, at least on plant communities dependent on long snow cover. Consequently, they are the most vulnerable to climate change and their persistence in the near future is seriously threatened. Subalpine and alpine grasslands are more stable and, until now, they do not seem to be affected by a warmer climate.

This chapter is an excerpt from the publication:
Matteodo M, Ammann K, Verrecchia EP, Vittoz P (2016) Snowbeds are more affected than other subalpine-alpine plant communities by climate change in the Swiss Alps. Ecology and Evolution 6, 6969-6982. (Appendix H).

The Introduction and part of the Material and Methods have been removed from the published paper and they were included in Chapter 1, 2, and 3.

4.2 Aims

In this study the following questions are targeted:

1. Are there observable changes in the subalpine-alpine vegetation over the last 25-50 years in species richness and community composition in the Alps?
2. Do the magnitude and direction of changes vary across different plant communities and how?
3. What environmental factors explain the observed changes?

4.3 Materials and methods

For the purpose of this study, 63 exhaustive plant inventories performed on six plant community types during the period 1964-1990 and located between the subalpine and alpine belts of the Swiss Alps have been revisited. A time-comparison of species frequencies and cover was performed, and with the help of indicator values, the main environmental drivers of the observed changes were identified.
Study sites are extensively described in Chapter 2, and methods in Chapter 3.

4.3.1 Data analyses

The potential mistakes in species identifications, or changes in nomenclature and aggregation level between the historical and recent inventories, were corrected by a scrupulous check of possible synonymies and by aggregating the pairs of species with frequent confusions into the same taxon. One frequent problem in plant monitoring studies is the overlooked species in one of the surveys (Burg *et al.*, 2015; Vittoz and Guisan, 2007). This bias is particularly likely to cause artefact in this study, as recent inventories involved generally two botanists instead of one in the historical records, and because the historical inventories, especially those of Richard *et al.* (1977), were not performed for monitoring purposes, but for the classification of plant communities.

Changes in diversity between pairs of records were not expressed in terms of species richness but using the Simpson diversity index, which is less sensitive to the species with low cover. This is justified in order to minimize the influence of a possible bias related to the fact that species with very low cover are mainly those overlooked (Vittoz and Guisan, 2007).

Two conversions of Braun-Blanquet's scale were used for subsequent analyses. The Braun-Blanquet's scale was converted into the median of the cover class (Table 4.1), in order to test the changes in the species cover between the different periods. By contrast, for all other analyses (Simpson diversity, Bray-Curtis dissimilarity, PCA, mean ecological values), numerical codes (Gillet, 2000) were used because they preserve the importance of the less abundant species, a crucial point in such analyses, by reducing the weight given to dominant ones (high cover).

Table 4.1 – Braun-Blanquet's scale used in both historical and recent inventories to estimate plant cover, the corresponding cover range and medians, used in analyses of cover changes. Numerical codes used in all other analyses are also listed.

Braun-Blanquet's code	Cover range	Median of the cover range [%]	Numerical code (Gillet, 2000)
r	1 or 2 individuals	0.05	0.1
+	<1%	0.5	0.5
1	1-5%	3	1
2	6-25%	15	2
3	26-50%	37.5	3
4	51-75%	62.5	4
5	76-100%	87.5	5

The difference between recent and historical species frequencies were calculated and tested with a restricted permutation test following Kapfer *et al.* (2011) within each plant community. Treating historical and recent inventories separately, the occurrences of each plant species amongst plots were shuffled randomly 999 times and new frequencies were calculated for each repetition. Significance levels were assessed by counting the number of times the changes in frequency between random historical and recent data was larger or equal to the observed changes in frequency between observed historical and recent data. For the species present simultaneously in at least 25% of the historical and recent inventories, a mean cover was calculated considering only the plots where the species was observed.

Changes in mean cover were tested with the same restricted permutation test used for species frequency but using the mean cover values instead (Kapfer *et al.*, 2012).

The floristic shifts between historical and recent records were visualized using two Principal Component Analyses (PCA, R *vegan* library): one based on species composition and cover, and the other based on presence-absence data. The cover values were previously submitted to Hellinger transformation, which is recommended when performing PCA with species cover data (Borcard *et al.*, 2011). In order to test the significance of the temporal shifts in species composition and cover along the first three axes of PCA, a multivariate analysis of variance (MANOVA) was applied on the differences of axis scores against the intercept for each vegetation type individually (Vittoz *et al.*, 2009b).

Landolt ecological indicator values (Landolt *et al.*, 2010) were used to investigate which of the environmental factors were related to the changes. Based on the same principle of Ellenberg indicator values for flora of Central Europe (Ellenberg *et al.*, 1991), the Landolt species indicator values have been developed for the Alpine flora. These semi-quantitative parameters, although inferred from field experience and not from direct measurements, have been shown to give pertinent indications about the species ecological optima within small spatial areas in Alpine landscapes (Scherrer and Körner, 2011). Specifically, the temperature indicator value is significantly correlated with the average soil temperature, which is far more representative of actual conditions experienced by low-stature alpine plants than the air temperature interpolated from meteorological stations (Scherrer and Körner, 2011). Landolt indicator values are species-specific, vary between 1 and 5 and express increasing species requirements in terms of air temperature (T), light (L), soil humidity (F), soil pH (R) and nutrient content (N). Mean indicator values per plot were calculated with the cover as a weight. Temporal changes of mean indicator values were checked using Pairwise Wilcoxon-Mann-Whitney tests.
All data processing and analyses were performed with R software, version 3.1.1 (R Core Team, 2014).

4.4 Results

4.4.1 Distribution amongst vegetation types

63 pairs of reliable records have been retained (Table 4.2 and Appendix C1): 10 in the calcareous grasslands, 13 in the windy ridges, 12 in the siliceous subalpine grasslands, 11 in the siliceous alpine grasslands, 8 in the typical snowbeds and 9 in the wet snowbeds. A clustering analysis (using the Hellinger distance and the Ward aggregation algorithm) of cover-weighted historical and recent inventories together showed that all old and recent records were placed by pairs in the same group corresponding to their respective plant community, except for one snowbed plot (R3935), which shifted from the wet to the typical snowbeds. For subsequent analyses, this record was retained at its original group.

Table 4.2 – Distribution of historical surveys amongst study sites and vegetation types. Number of plots, time spans, authors, and elevation ranges of historical and recent surveys ordered by study site (upper part) and vegetation types (lower part). The names of the historical botanists are abbreviated as follows: Jean-Louis Richard (JLR), Klaus Ammann (KA), Benoît Bressoud (BB), Olivier Duckert (OD). Numbers in brackets refer to medians.

Site	No. of plots	Historical survey	Author(s) of historical data	Elevation [m]
Morteys	12	1972-1979 (1973)	JLR	1698-2232 (1884)
Grimsel	25	1964-1973 (1970)	KA	2310-2650 (2329)
Réchy	26	1977-1990 (1981)	BB, JLR, OD	2328-2697 (2567)
Vegetation type				
Calcareous grasslands	10	1972-1973 (1973)	JLR	1698-2099 (1807)
Windy ridges	13	1975-1990 (1979)	BB, JLR, OD	2180-2697 (2430)
Siliceous subalpine grasslands	12	1964-1973 (1967)	KA	2312-2370 (2320)
Siliceous alpine grasslands	11	1965-1989 (1970)	JLR, KA	2300-2682 (2528)
Typical snowbeds	8	1970-1981 (1973)	BB, JLR, KA	2313-2685 (2460)
Wet snowbeds	9	1977-1990 (1988)	JLR	2468-2677 (2585)

4.4.2 Diversity changes

Between the historical and the recent surveys, 47 out of 63 plots show an increase in alpha-diversity and 16 show a decrease. The magnitude of the increase varies between vegetation types (Figure 4.1). The windy ridges show the highest increase in the mean Simpson diversity index (+6.3 ± 6.0, difference between medians being significant with a p-value = 0.004), followed by the siliceous subalpine grasslands (+4.8 ± 6.7, p-value = 0.017) and the wet snowbeds (+4.1 ± 3.5, p-value = 0.004). The increase of alpha-diversity in the other plant communities is not significant.

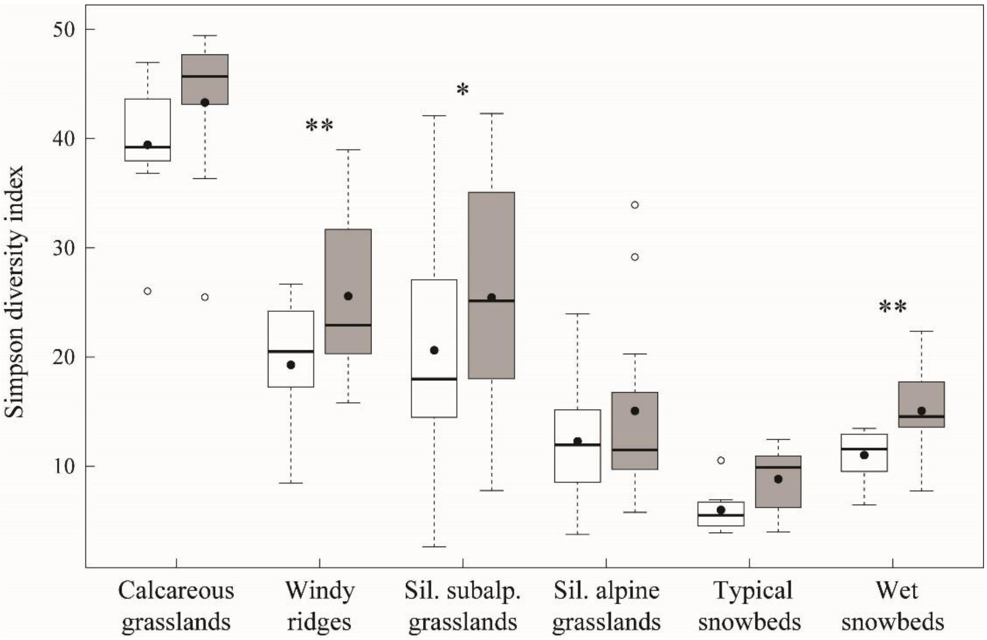

Figure 4.1 - Simpson diversity index for historical (white boxes) and recent (grey boxes) inventories in six plant communities. "Sil.": Siliceous; "subalp.": subalpine. Black dots represent the mean values, the black line is the median and boxes are limited by 1st and 3rd quartiles. Stars above the boxes indicate a significant change between historical and recent inventories, according to a pairwise Wilcoxon-Mann-Whitney test: * $p<0.05$; ** $p<0.01$.

Beta-diversity shows an opposite trend with a slight decrease of the mean Bray-Curtis dissimilarity index between historical and recent records in each plant community, except for the calcareous grasslands (Figure 4.2), whose inventories always show the same low dissimilarity level. The highest homogenisation is observed in the siliceous alpine grasslands, where the mean dissimilarity index decreased by 0.05 ± 0.03 (p-value = 0.002), followed by the windy ridges (-0.04 ± 0.04, p-value = 0.002) and the siliceous subalpine grasslands (- 0.04 ±0.04, p-value = 0.010). The two snowbeds also show a dissimilarity decrease, but not significantly.

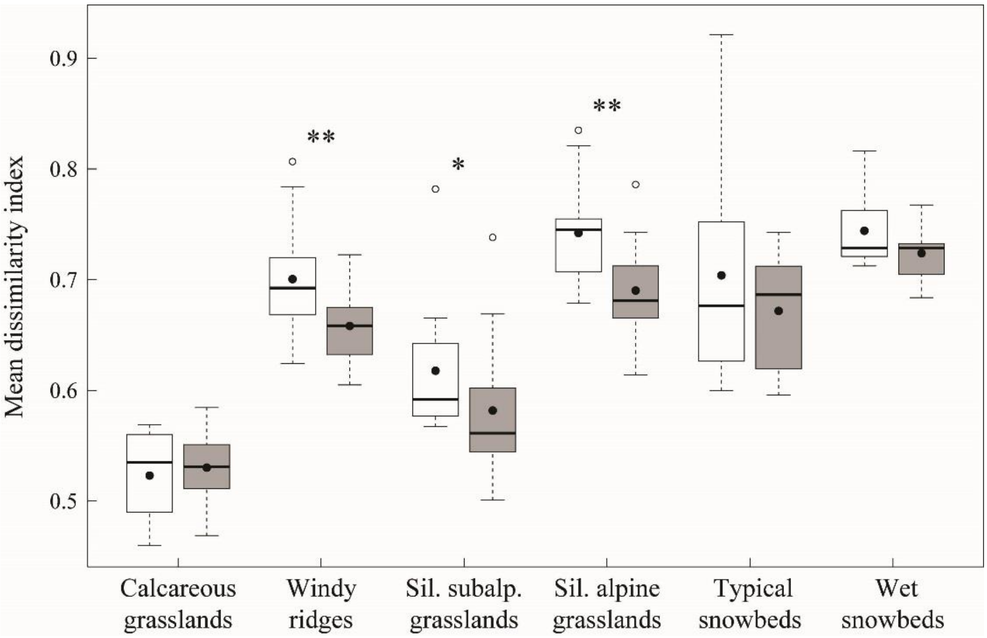

Figure 4.2 - Averages of Bray-Curtis dissimilarity indices amongst historical (white boxes) and recent (grey boxes) inventories in six plant communities. Same symbols as in Figure 4.1.

4.4.3 Shifts of plant communities

The six plant communities display different directions and amplitudes in their temporal shifts in the cover-weighted PCA (Figure 4.3). The first two axes of PCA explain 23.3% of the total variance (PC1: 13.0%; PC2: 10.3%). The most evident shifts are those of snowbeds: the typical ones show a significant (p-value = 0.012) unidirectional trend towards the siliceous alpine grasslands, while the recent species composition of the wet snowbeds is significantly closer (p-value = 0.006) to the typical snowbeds than the historical composition. The windy ridges plots shift in two main directions (p-value = 0.047), either towards calcareous grasslands or the siliceous ones. The three grassland communities have no significant shift in species composition. In particular, the calcareous grasslands display a high stability in terms of species composition.

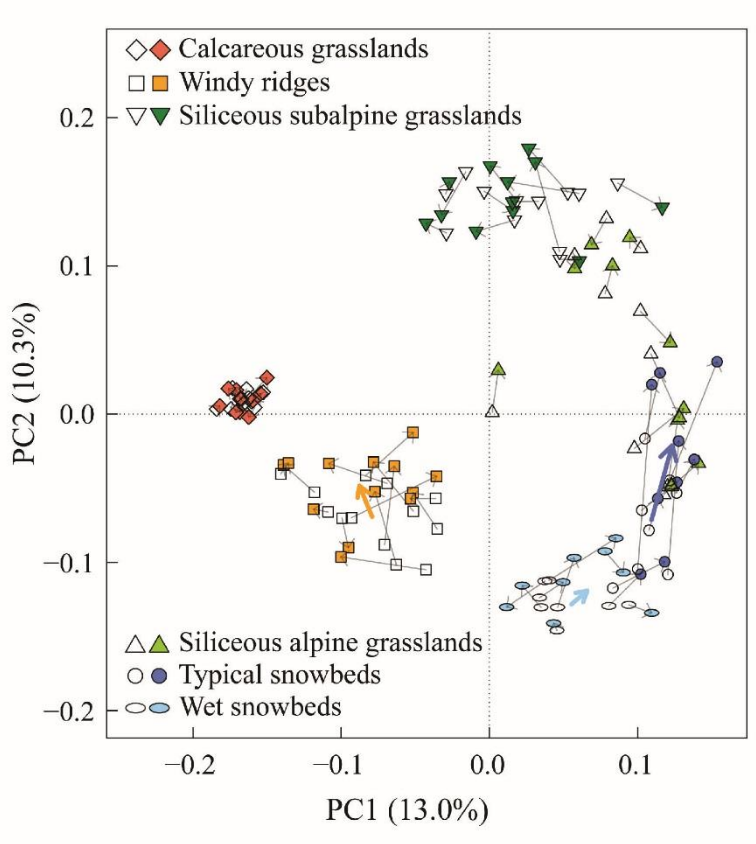

Figure 4.3 - Principal Component Analysis (PCA) based on species composition and cover. The first axis represents 13.0 % of the variance and the second 10.3%. Couples of historical (empty symbols) and recent (full symbols) records are connected with thin arrows. Thick arrows represent a significant shift of the plant community centroids.

Similar trends, in direction and magnitude, are displayed when presence-absence data are considered (Figure 4.4). However, four couples of records originally attributed to the siliceous alpine grasslands are here assimilated to the typical snowbed group, sharing with it the same unidirectional trend towards siliceous grasslands. These records have a species composition similar to those of typical snowbeds but, because of the dominance of some grassland species, they are assimilated to the alpine grassland group when cover is taken into account. Hence, they can be considered as transition between snowbeds and siliceous alpine grasslands.

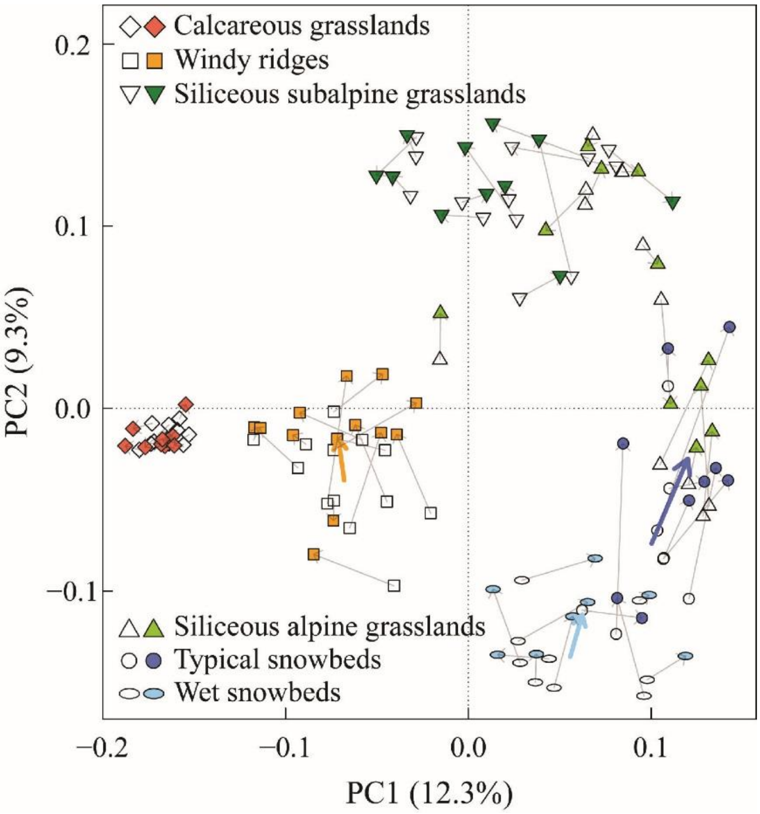

Figure 4.4 - Principal Component Analysis (PCA) based on species composition (presence-absence). The first axis represents 12.3 % of the variance and the second 9.3%. Same symbols as in Figure 4.3.

4.4.4 Changes in species frequency and cover

In all the vegetation types but the calcareous grasslands, the number of species, whose frequency increased since the historical survey, exceed species whose frequency decreased (Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.q82j0), and only increasing frequencies are significant. Regarding changes in species cover, most of the species in the calcareous grasslands, the siliceous subalpine and alpine grasslands show a decrease in the mean cover, whereas most of the species in the windy ridges, the typical and wet snowbeds increase in cover. But very few cover changes are significant.

In the calcareous grasslands, five species with their optimum mostly at the subalpine belt, increase significantly: *Festuca ovina aggr.*, *Globularia cordifolia*, *Cirsium acaule*, *Plantago atrata s.str.*, and *Polygala alpestris*. Interestingly, *Globularia cordifolia*, a typical species of upper montane-lower subalpine belt according to the temperature indicator value (Landolt *et al.* 2010), was absent in the historical survey, but is present in 50% of the recent plots. *Carex sempervirens* shows a strong decrease in mean cover (-15%, p-value = 0.001). In windy ridges, species from both calcareous (*Anthyllis vulneraria subsp. alpestris* and *Selaginella selaginoides*) and siliceous grasslands (*Hieracium *angustifolium*), or from the ridge community itself (*Agrostis alpina*) and generalist species (*Campanula scheuchzeri*), display a significant frequency increase.

The occurrence of three subalpine species (*Solidago virgaurea ssp. minuta*, *Trifolium pratense ssp. nivale* and *Arnica montana*) is significantly higher in recent siliceous subalpine grasslands surveys than in the historical ones. *Nardus stricta* markedly decreases in mean cover (-11.5%, p-value = 0.029). In the siliceous alpine grasslands, four species typical of this community (*Euphrasia minima*, *Agrostis rupestris*, *Homogyne alpina* and *Hieracium alpinum*) are distributed more widely amongst recent surveys than in the historical ones.

The species, whose frequency and cover greatly increased in typical snowbeds, are mostly from siliceous alpine grasslands as well: *Leontodon helveticus* increases by 62.5% in frequency (p-value = 0.019) and 3.3% in cover (not significant), while *Helictotrichon versicolor* was absent in the historical survey, but is present in half of the recent plots (marginally significant, p-value = 0.057). Between the other species increasing both in frequency and cover (defined as "winners", Appendix E1), most of them are typical of grasslands and are generalists (*Ligusticum mutellina, Nardus stricta).* In contrast, the species with the most important, but not significant, cover decrease (*Carex foetida*) is typical of snowbeds.
In the wet snowbeds, some species mostly associated to typical snowbeds, such as *Sibbaldia procumbens*, increase in frequency (+55.6%, p-value = 0.019), while *Juncus triglumis*, *Saxifraga androsacea* and *Gentiana bavarica,* three species growing in wet snowbeds, decrease in terms of mean cover (-26.3%, p-value = 0.008; -18.4%, p-value = 0.026; -15%, p-value = 0.047; respectively).

4.4.5 Ecological indicator values

The six vegetation types display mean temperature indicator values (Landolt *et al.*, 2010) that reflect their distribution in elevation, with highest values for the calcareous grasslands (Figure 4.5a). The calcareous grasslands and the typical snowbeds are the only plant communities showing a significant increase in their mean temperature values between inventories (p-value = 0.010 and p-value = 0.004, respectively). Similarly, the value for soil humidity (F) reflects the moisture conditions of the plant communities, with the four types of grasslands having lower values than the two snowbed communities (Figure 4.5b). Species present in the recent records of the typical and wet snowbeds have, on average, lower values than the composition of historical surveys, indicating their preference for drier conditions. However, only the decrease in the latter one is significant (p-value = 0.004).

None of the studied plant communities show significant variations between historical and recent surveys in terms of soil nutrient requirements (Figure 4.5c), light and soil pH (Appendices E2 and E3), according to the corresponding mean ecological indicator values.

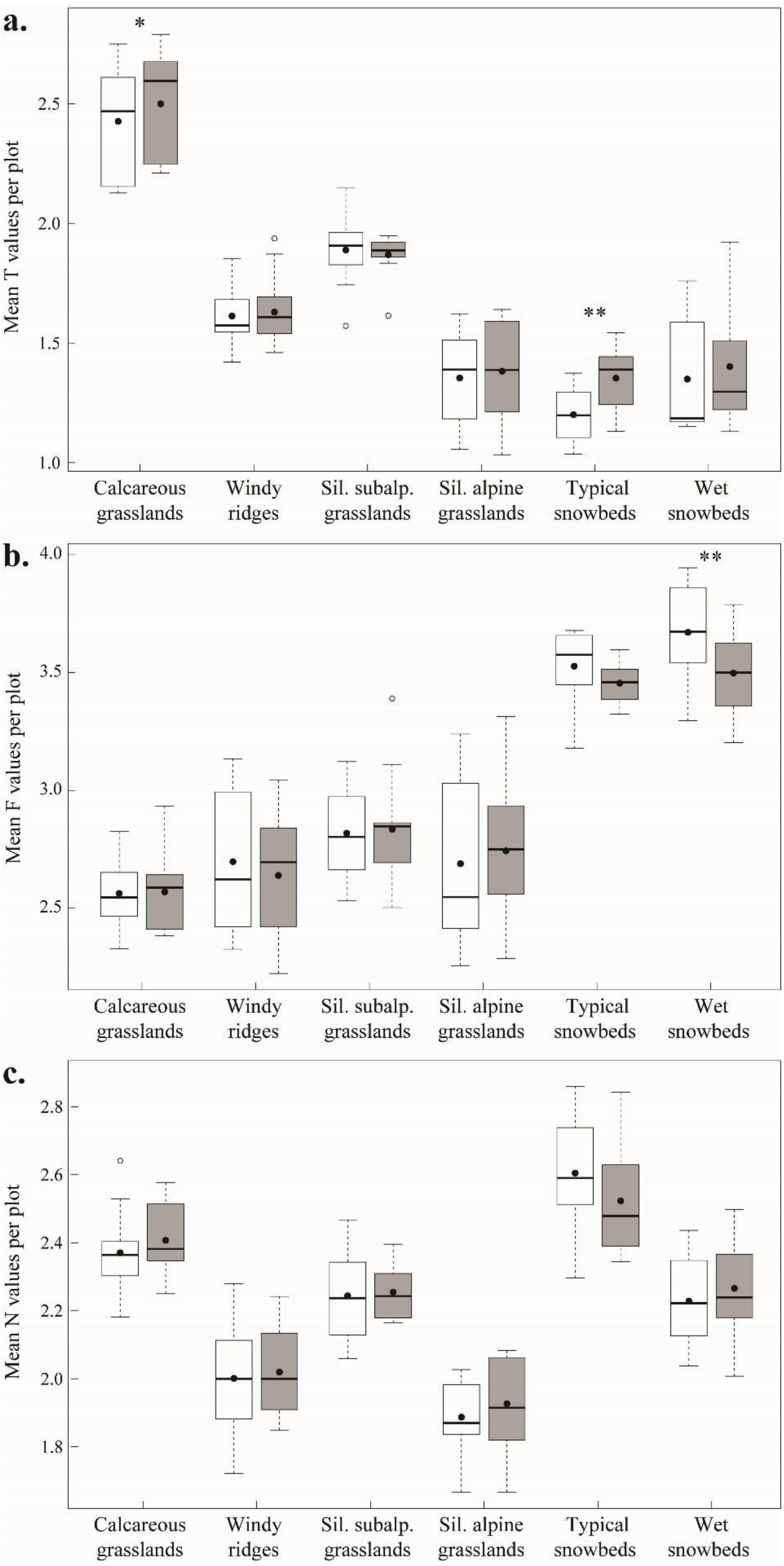

Figure 4.5 - Cover-weighted means of indicator values (Landolt et al., 2010) for temperature **(a)**, soil humidity **(b)** and soil nutrient content **(c)** in historical (white boxes) and recent (grey boxes) inventories. Same symbols as in Figure 4.1.

4.5 Discussion

The results of this study clearly indicate that vegetation changed over a 25-50 years timespan at the subalpine-alpine level in the Swiss Alps. The six plant communities displayed similar alpha and beta-diversity changes, but also various reactions to past environmental changes in terms of species composition.

4.5.1 Alpha and beta-diversity

The increase in species richness, expressed as Simpson diversity index at the plot-scale, is observed in each plant community. There are three possible explanations: (1) new species arrived since the historical time; (2) the recent inventories were more exhaustive than the historical ones, or (3) the new species are the result of inaccurate location of the plots. The last option can be excluded because it cannot result in a systematic increase for all the vegetation types. The second option could be meaningful only for the least frequent species (i.e. occurring in one or two new plots), but not for those with a considerable increase (for example *Globularia cordifolia* in the calcareous grasslands). Moreover, many of these species are easily visible in terms of size and/or difficult to confuse with other species. Therefore, the colonisation of plots by new species is at least partly responsible for the observed increase in alpha-diversity. Many previous studies observed the same trend over the last three decades on alpine plant communities (Britton *et al.*, 2009; Kudernatsch *et al.*, 2005; Sandvik and Odland, 2014; Vittoz *et al.*, 2009b), or even just over six years in snowbeds (Carbognani *et al.*, 2014; Pickering *et al.*, 2014). Olsen and Klanderud (2014) observed that species poor communities were more susceptible to species invasion than highly diverse species communities. Our results do not confirm such a trend, as the highest species increase was observed on the windy ridges community, which are more diverse than typical snowbeds.

The increase in species richness is related to an increase in the floristic similarity inside the plant community, except in the calcareous grasslands. Similar homogenisation was first highlighted on seven European Alpine summits by Jurasinski and Kreyling (2007), and on a variety of alpine plant communities since then (Britton *et al.*, 2009; Carbognani *et al.*, 2014; Ross *et al.*, 2012). According to their observations, the biotic homogenisation results from two processes: the invasion of widespread and generalist species, and a decline of rare and specialized species. Generalist species may be able to spread in new areas previously unsuitable, thanks to less constraining conditions for their establishment and survival, such as longer growing seasons through climate warming, or increased nutrient availability (Britton *et al.*, 2009). Indeed, such a pattern is apparent in this study, where snowbed specialists decrease in cover while grassland generalist species increase in frequency and cover (see Appendix E1). An increasing alpha-diversity coupled with a homogenisation can be explained by the arrival of previously missing species in the community, completing the typical species ensemble for a given vegetation type (e.g., *Agrostis alpina* in the windy ridges, *Arnica montana* in the siliceous subalpine grasslands).

4.5.2 Snowbeds

The main changes in plant composition are observed in the typical snowbeds, which show a marked shift of species composition and cover towards the siliceous alpine grasslands, and in the wet snowbeds, whose composition tends towards the typical snowbeds (Figure 4.3 and Figure 4.4). Therefore, the snowbeds are now more similar to the siliceous alpine grasslands than they were in the 1970s. This is confirmed by the observed colonisation by species from siliceous alpine grasslands (*Helictotrichon versicolor*) in the typical snowbeds or their increase in both frequency (*Leontodon helveticus)* and cover (*Nardus stricta*). This expansion of grassland species is reflected in the increase of the temperature indicator value and in the decrease of the humidity one (Figure 4.5a and Figure 4.5b). These conclusions are consistent with results from previous long-term monitoring across alpine areas of the Scandes (Kapfer *et al.*, 2012; Sandvik and Odland, 2014; Virtanen *et al.*, 2003), Scotland (Britton *et al.*, 2009), Caucasus (Elumeeva *et al.*, 2013), Japan (Kudo *et al.*, 2011), and Greenland (Daniëls *et al.*, 2011).

Similar changes have been observed even on shorter time-scales, as in 6-year surveys from Italy (Carbognani *et al.*, 2014) and Australia (Pickering *et al.*, 2014). All these studies agree that the arrival and expansion of grassland species in the snowbed communities is likely a consequence of longer growing seasons induced by earlier snow-melt dates.

The melt out date, which is an important driver of arctic and alpine plant growth (Jonas *et al.*, 2008), shifted earlier by 1-4 days per decade between 1998 and 2015 at 2110-2630 m a.s.l. next to our three study sites (Appendix E4). This shift, although not significant and covering a short time period, is corroborated by satellite observations in the high latitude and high elevation areas of the Northern Hemisphere (Dye, 2002).

This is probably the consequence of two associated factors: firstly, the increase of mean annual temperature, which has been calculated as 1.82 K between 1961 and 2008 in Switzerland (Serquet *et al.*, 2013), which is equivalent to the double of the mean change for the Northern Hemisphere (Rebetez and Reinhard, 2008), and secondly the decrease of the snowfall/precipitation ratio estimated to be around 0.25% per year at the beginning and the end of the snow season from 1961 to 2008 (Serquet *et al.*, 2013). The spring decreasing trend of snowfall/precipitation day ratio has been observed even at 2,500 m a.s.l. by Marty and Meister (2012) but is generally more pronounced at lower elevations (Scherrer *et al.*, 2004; Serquet *et al.*, 2013).

In the three present study sites, despite a high inter-annual variability, the annual sum of fresh snow thickness decreased by 0.49 to 0.96% per year between 1964 and 2011 (Figure 2.2). The autumn and spring months seem to be crucial for snow duration, because at that period of the year, air temperatures are closer to the melting point than during the winter (Serquet *et al.*, 2011), and a slight increase is sufficient to reduce the snowfall part of precipitations. The lower snow amount and earlier melting dates observed in the study sites were accompanied by lagged snow falls in autumn (Appendix E4).

The resulting longer growing season (+5 to 14 days per decade between 1998 and 2015, not significant, Appendix E4) allows the invasion of generally more competitive species, such as graminoids (Dullinger *et al.*, 2007). These species now have enough time to accomplish their life cycle in a snowbed. The establishment of species from adjacent communities could have been enhanced by (i) the proximity of grasslands to snowbeds (mostly <20 m from the study sites), (ii) the snowbed potential of trapping seeds (Larsson and Molau, 2001), and (iii) the high dispersal capacity of certain grassland species. Indeed, the increase in frequency of *Leontodon helveticus* could be associated to its pappus appendage, which was shown to give an advantage to plant species in colonising new Alpine summits (Matteodo *et al.*, 2013).

Moreover, snow is an efficient scavenger of atmospheric pollutants, which are leached through the snowpack, mainly at the beginning of the melt period (Johannessen and Henriksen, 1978). The consequent high load of nitrogen into the snowbed soils can damage certain species (as the moss *Kiaeria starkei*; Woolgrove and Woodin, 1996b) and favour the establishment of acquisitive (nutrient-rich) plants. For example, graminoid cover has been shown to be directly related to nitrogen deposition in acidic grasslands (Dupré *et al.*, 2010). However, an increase of the mean nutrient indicator value (Landolt *et al.*, 2010) that could support this hypothesis has not been observed in the study sites (Figure 4.5c). But, we cannot exclude that higher temperatures, combined with relatively high nutrient level in the soil, allow more thermophilous species (grassland species) to establish in the snowbeds, independently from the length of the growing season.

The snowbed species are able to respond positively to experimental warming (Arft *et al.*, 1999; Sandvik and Totland, 2000) and can theoretically profit for earlier snow-free habitats. But they are restricted to snowbed habitats because of lower competition from co-occurring plants (Heegaard and Vandvik, 2004). The arrival of taller species from the surrounding grasslands, might increase the competition and induce a decrease of typical snowbed species. Hulber *et al.* (2011) suggested that the presence of neighbours in snowbed systems leads to competitive effects rather than facilitative ones, which can be expected in such harsh environmental conditions (Choler *et al.*, 2001). Moreover, the role of competition might increase with warming, as experimentally observed by Olsen and Klanderud (2014). In the study sites, no significant decrease is observed, but the strong decrease in cover of *Carex foetida* could be a first sign of such an evolution.

Similarly to the typical snowbeds, but over a shorter time period (median of historical records years = 1988, Table 4.2), the wet snowbeds show increasingly dry conditions. The reduction of snow precipitation, combined with higher temperatures, likely shorten the amount and duration of water supply (Beniston *et al.*, 2003) to these communities, mostly located under melting firn. The cover decrease of typical alliance species and the diffusion of snowbed species, in parallel with the reduction of the mean humidity indicator value (Figure 4.5b), indicate that these sites are rapidly shifting toward typical snowbed communities. The same drying trend was observed with the expansion of some graminoids and shrub species in Norwegian wet snowbeds (Sandvik and Odland, 2014), on soligenous and ombrogenous mires (Ross *et al.*, 2012; Virtanen *et al.*, 2003), and springs (Britton *et al.*, 2009). These last vegetation types do not belong to snowbeds, but they are subject to the same water-logged conditions, which limit the growth of taller plants. Diverse alpine plant communities, directly related to high water supply, seem to respond similarly to climate changes.

4.5.3 Grasslands

In contrast to plant communities related to long snow cover, calcareous and siliceous grasslands demonstrate a high stability of species composition and cover, whatever the bedrock type (Figure 4.3 and Figure 4.4).
Similar results were obtained by warming experiments on subalpine meadows in the Rocky Mountains (Price and Waser, 2000), on calcareous grasslands in northern England after a 13-yr exposure to climate changes (Grime *et al.*, 2008), and observed too by long-term surveys in the Alps (Vittoz *et al.*, 2009b; Windmaißer and Reisch, 2013). These authors identified many possible explanatory factors. Firstly, the high plant density and belowground phytomass of subalpine grasslands, compared to the sparse vegetation of alpine and nival summits or to the low species abundance in snowbeds, lead to high competition levels for light and soil resources, which restricts the establishment of new species (Choler *et al.*, 2001). Secondly, the extreme longevity of some grass species (*C. curvula* can reach a maximum of 5000 years; de Witte *et al.*, 2012), the persistence of their shoot and root systems and their clonal growth, that allows the continuous recolonisation of vegetation gaps, result in a high resilience to interannual variations (Hillier *et al.*, 1990) with a consequent long-term persistence. For example, *Laserpitium siler*, which was a dominant species in half of the plots in calcareous grasslands, is highly competitive in terms of light and water resources and occupies a wide elevation range, thus likely preventing colonisation by new species. Thirdly, the steep slopes where the calcareous grasslands are established could also explain their stability. According to Theurillat and Guisan (2001), slopes steeper than 40° (which is often the case in this study) may act as barriers to upward dispersal of species.

Nevertheless, this general stability is also accompanied by new species or increase in frequency. Some of these species (*Globularia cordifolia*, *Cirsium acaule*), although frequently associated to calcareous grasslands, have their optimum at lower elevations. Conversely, the only significantly declining species, *Carex sempervirens,* has its optimum at the lower alpine rather than the subalpine belt. These changes in composition are reflected by a significant increase of the mean indicator value for temperature observed across the calcareous grasslands (Figure 4.5a). In conclusion, although displaying a high stability, these grasslands seem to experience the arrival of species from lower elevations, as repeatedly observed on alpine and nival summits (see Stöckli *et al.*, 2011 for a review). Interestingly, in long-term studies focused on lower elevation grasslands (Britton *et al.*, 2009; Elumeeva *et al.*, 2013; Ross *et al.*, 2012; Vittoz *et al.*, 2009b; Windmaißer and Reisch, 2013), most of the species decreasing in frequency and/or cover have an alpine to arctic distribution, while those increasing have broader or lower elevation ranges.

Siliceous subalpine and alpine grasslands show a different trend with supplementary species either having very widespread distribution (*Euphrasia minima*, *Homogyne alpina*) or arriving from the same species pool (*Arnica montana, Hieracium alpinum*). This process, known as range filling, was already observed in the Italian Alps by Cannone and Pignatti (2014) and seems to be predominant compared to the upward shift. Indeed, neither did montane species colonize the siliceous subalpine grasslands, nor did subalpine species move upward and colonize the siliceous alpine grasslands. The abovementioned stabilizing factors appear to be important in these siliceous grasslands.

According to Dullinger *et al.* (2012), the elevational shift of plant species observed on alpine summits may display faster cool edge expansion than warm edge retreat because of the potentially long persistence of declining populations under unsuitable conditions. The stability of the subalpine and alpine grasslands, while snowbeds are changing, seems to confirm this prediction and indicates that, during the last few decades, subalpine and lower alpine species expanded upwards from their elevational range rather than shifting it.

4.5.4 Windy ridges

The community on windy ridges shows a significant change in species composition according to the PCA (Figure 4.3 and Figure 4.4). Indeed, the centroid shifts towards the calcareous grasslands, although some of the recent inventories are closer to the siliceous grasslands instead. The species increasing in frequency confirm this pattern, with some related to the calcareous grasslands and others to the siliceous ones. The different shifts seem to be related to soil pH, as shown by soil analyses, but a higher number of plots would be necessary for a better understanding of these divergences.

Research on comparable habitats (such as alpine heaths on windy ridges) show diversified reactions to past climatic changes, from very limited changes (Elumeeva *et al.*, 2013), to an increase in dwarf shrubs (Virtanen *et al.*, 2003) or graminoid increase related to a dwarf-shrub and forb decrease (Ross *et al.*, 2012). The only common feature is the lichen decrease, attributed either to summer reindeer grazing (Virtanen *et al.*, 2003), or to nitrogen deposition (Armitage *et al.*, 2014), trampling, and climate warming (see Ross *et al.*, 2012 and references therein). Unfortunately, the majority of our historical inventories do not give any indication of lichen covers (Appendix C1). Consequently this study cannot confirm such a trend.

4.5.5 Long-term implications

This study is the first of its kind to assess the way different plant communities in the subalpine and lower alpine belts of the European Alps reacted to climate changes over the last two to four decades. It demonstrates that reactions differ considerably between vegetation types, with the most important changes in those linked to long snow cover.

The vulnerability of *Salicion herbaceae* (typical snowbeds) was already suspected by Braun-Blanquet (1975). Indeed, monitoring Eastern Switzerland vegetation of a very late snowmelt patch dominated by the moss *Polytrichum sexangulare* from 1921 to 1947, Braun-Blanquet (1975) observed an increasing cover of snowbed plant species in response to shorter snow cover and warmer temperatures. Moreover, he hypothesized that snowbeds will be progressively invaded by species from the surrounding siliceous grasslands. Therefore, it is likely that, during the last few decades, some snowbed communities took refuge in *Polytrichum sexangulare* communities, altering their species composition. Simultaneously, snowbed species colonized many summits and slopes, where, as a result of glacier and snow cover reductions, new snowbed areas were available for colonisation (Grytnes *et al.*, 2014). Therefore, snowbed species can still find suitable areas in the coldest micro-habitats, but with potential detrimental consequences for the communities currently present. This corroborates the theory of Scherrer and Körner (2011), who sustained that alpine terrain offers a variety of thermal micro-habitats over very short distances, which will be suitable for the majority of species.

Beniston *et al.* (2003) predicted that, with a temperature rise of 4°C in 2071-2100 (Christensen *et al.*, 2002), the snow volume in the Alps at 2000 m may reduce by 50% and the melting season advanced by 50-60 days. As this study clearly demonstrates, changes in snow precipitations may have a stronger impact on the subalpine-alpine plant communities than warmer temperatures, at least for communities directly dependent on snow cover as a limit to the growing season. However, very probably, the grasslands will not be able to stand such a temperature increase without important changes as well. But, with the available data, it is not possible to conclude if changes will still be very slow, like those observed until now, which will induce a large local extinction debt (Dullinger et al., 2012), or if strong and sudden changes are expected after forest colonisation, successive years of drought, development of diseases (Ayres and Lombardero, 2000), or the arrival of new herbivores (Pellissier *et al.*, 2014). Future monitoring of alpine grasslands will be particularly important to address these questions.

Acknowledgements

We thank Marie-José Petétot, Loïc Liberati and Swanee Messerli for their help in the field; Beat Rihm (Meteotest) for providing calculation of nitrogen deposition on our study sites, François Gillet, Stéphanie Grand and Vanessa Rion for their suggestions and contributions in the statistical analyses, Benoît Bressoud for his contribution to the record data, Karin Verrecchia for checking the English version and two anonymous reviewers for their useful comments on an earlier version of the manuscript.

5 Soils and humus forms in the subalpine-alpine belt

5.1 Abstract

When studying plant community dynamics, helpful elements may come from the study of soil and, in particular, its humus layers. Humus forms play a central role in the functioning of terrestrial ecosystems, being at the interface between vegetation, soil organisms, parent material, and under the control of climatic variables. Humus forms of the alpine environment, and their relationships with ecosystem properties, have been hardly investigated so far. The aim of this study was to fill this gap, taking advantage of the large ecosystem diversity on short space-scale that the alpine environment offers.

Eight subalpine-alpine vegetation types, spanning a gradient of soil acidity and snow cover, were visited and their soil profiles and humus forms described. Physical and chemical properties of each soil horizon were recorded in 46 soil profiles. By means of redundancy analyses, the most important correlations between humus forms and environmental descriptors were identified. Finally, the specifics of alpine humus forms, with regards to lower elevation ones, were highlighted.

Ten main groups of soil type and the same number of humus forms were identified. The soil types and its solution pH reflected the lithology of the parent material. By contrast, C/N ratios of the organic layers were mostly influenced by the vegetation type. Lithology of soil's parent material and climate importantly shaped the humus form distribution: Mulls were mostly found on calcareous parent materials, at lower elevations and therefore warmer sites. On the contrary, Moders and Mors were associated to siliceous materials and colder sites. Topography was important as well: roots were abundant in humus forms located on slopes, while humus forms presenting waterlogging conditions were exclusively found in depressions. Vegetation played a secondary role.

This study provided an exhaustive inventory of soils and humus forms occurring among the most representative vegetation types of the alpine environment. Moreover, the ecosystem properties driving the alpine humus form development were for the first time identified.

5.2 Aims

In this study the following goals are targeted:

1) identification of soils associated to the eight plant communities under study;
2) description of their main physical and chemical properties;
3) investigation of the diversity of alpine humus forms and description of their characteristics;
4) investigation of the principal environmental factors driving the distribution of humus forms;
5) emphasizing of specifics of the alpine environment within humus forms classification criteria.

5.3 Materials and methods

For the purpose of this study, eight subalpine-alpine vegetation types (Table 3.1), spanning a gradient of soil acidity and snow cover, were visited and their soil profiles and humus forms described. A total of 46 profiles and 232 soil samples were studied. Morphological descriptions were completed by laboratory analyses of pH H_2O (here after referred as "pH"), grain-size distributions, and CHN concentrations. Study sites are extensively described in Chapter 2, and methods in Chapter 3.

5.3.1 Data analyses

The relationship between the humus forms and the main parameters employed for their identification (Table 5.1) were visualized using a Principal Component Analyses (PCA, R *vegan* library). A circle of equilibrium contribution (Borcard *et al.*, 2011) allowed to identify the most important parameters for the humus form distribution. All variables were scaled and reduced (mean = 0, variance = 1) prior to analysis.

The influence of selected environmental factors (Table 5.1) on the humus form distribution and the parameters employed for their identification was assessed by total RDA (Redundancy Analysis). The parameters employed for the humus form identification were used as response variables and environmental variables as explanatory variables. Quantitative variables were scaled and reduced prior to analysis. Two different RDA were performed: the first considered all environmental factors (Table 5.1), while in the second the "Vegetation" factor was omitted in order to assess its importance by comparison with the first RDA. The relationship between the response data and the explanatory variables was tested by permutation test with 1000 repetitions.

5.4 Results

5.4.1 Diversity of soil types among vegetation types

The 46 soil profiles have been classified into ten main groups of soil references (Table 5.2 and Figure 5.1), unevenly distributed among the eight plant community types under study. Calcareous vegetation types were characterized by Calcaric, Eutric, and Dystric Cambisols. All soils of subalpine pastures were classified as Dystric Cambisols. The siliceous grasslands were associated to Umbric, Entic, and Albic Podzols. The siliceous snowbeds were associated to soils showing waterlogging conditions as Gleysols and Stagnosols, but two Podzols and one Regosol were also observed in the typical snowbeds. Among the two Podzol profiles, one showed a high degree of evolution, with an E horizon particularly well developed (Albic Podzol, profile G336, Table 5.2 and Appendix D). Leptosols were equally distributed among calcareous and siliceous vegetation types.

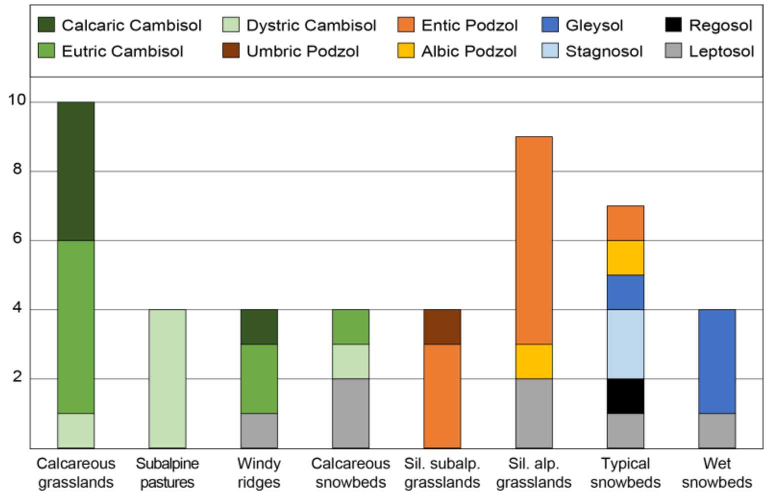

Figure 5.1 - Number and type of soil profiles described in each vegetation type (Chapter 3). Soils are grouped into ten principal soil references (IUSS Working Group, 2015). "Sil.": siliceous; "subalp.": subalpine; "alp.": alpine.

Table 5.1 – Parameters employed for the identification of humus forms and potential environmental drivers. The parameters employed for the humus form identification were used in the PCA and RDA, and the environmental factors were used in the RDA as explanatory variables. Annual precipitations and summer temperatures are extrapolated for each soil location from the Swiss meteorological stations (www.meteoswiss.ch) according to Zimmermann and Kienast (1999). For lithologies, the 'Calcareous' category refers to limestones, calcareous sandstones, marbles and surficial deposits (screes and moraines) derived almost exclusively from these materials. The 'Mixed' category contains surficial deposits of mixed origin (sedimentary, metamorphic, crystalline components). The 'Si-rich' (Silicium rich) category contains granites, gneisses, quartzites and surficial deposits derived almost exclusively from these materials. The eight vegetation types are described in Chapter 3. Ranges and medians are given for quantitative variables only.

Parameters employed for humus form identification

Variable	**Remarks**	**Range (median)**
Rhizic	Humus forms having more than 25% of dead or living roots in the total volume (Jabiol *et al.*, 2013)	0-1
Water	Presence of waterlogging conditions	0-1
Oe	Presence of an Oe horizon, continous or discontinuous	0-1
Oa	Presence of an Oa horizon, continous or discontinuous	0-1
A	Presence of an A horizon	0-1
pH_A	pH of the A horizon or, if this was missing, pH of the first horizon under the O	3 - 7.4 (5.4)
A_massive	Presence of an A horizon with massive structure	0-1
A_sg	Presence of an A horizon with single-grain structure	0-1
A_micro	Presence of an A horizon with micro-granular structure (aggregates < 1 mm)	0-1
A_meso	Presence of an A horizon with meso-granular structure (aggregates 1-4 mm)	0-1

Environmental factors

Variable	**Remarks**	**Range (median)**
NS gradient	North-South gradient; equals to 0 - cosinus [radian (Aspect)]	From -1 (North) to 1 (South) (-0.03)
Slope	Steepness	0°- 50 ° (20°)
Topography	Topography, estimated visually	Three categories: depression, slope and ridge
Precipitations	Average of annual precipitation sum for the period 1961-1990	1396 - 2218 mm (1650 mm)
Summer temp.	Monthly average temperature for the period 1961-1990, from June to September, included	4.8 - 10 °C (6.7 °C)
Lithology	Lithology of the soil's parent material	Three categories: Calcareous, Mixed and Si-rich
Vegetation	Vegetation type	Eight categories: Calcareous grasslands; Subalpine pastures; Windy ridges; Calcareous snowbeds; Silic. Subalp. Grasslands; Silic. Alp. Grasslands; Typical snowbeds; Wet snowbeds.

The soil types substantially reflected the lithology of their parent material (Figure 5.2). All Cambisols were found on calcareous lithology, and most of the Podzols on Si-rich (Silicium-rich) ones (granite, gneiss, quartzite). Hydromorphic soils, such as Gleysols and Stagnosols, were found only on surficial deposits with a potentially mixed lithology. Leptosols were equally distributed among lithologies of soil parent material.

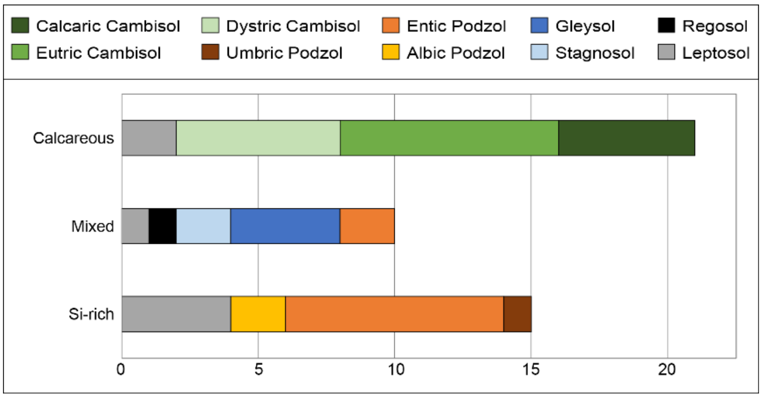

Figure 5.2 - Relation between the soil type and the lithology of its parent material. For lithologies, the 'Calcareous' category refers to limestones, calcareous sandstones, marbles and surficial deposits (screes and moraines) derived almost exclusively from these materials. The 'Mixed' category contains surficial deposits of mixed origin (sedimentary, metamorphic, crystalline components). The 'Si-rich' category contains granites, gneisses, quartzites and surficial deposits derived almost exclusively from these materials.

The elevation distribution of soil profiles depended upon the location of the vegetation records, and therefore it was skewed with respect to a random sampling. Cambisols were present on the whole elevational gradient, from 1698 m (subalpine belt) to 2697 m (alpine belt). Podzols (Umbric, Entic, and Albic) were located from the forest line to the alpine belt, between 2310 and 2685 m. Similarly, Stagnosols, Gleysols, and Regosols were situated in the alpine belt, from 2440 m to 2650 m. Elevation gradient of Leptosols was wide, from 1979 (subalpine belt) to 2650 m (alpine belt).

Table 5.2 – Characteristics of the soil profiles: name of the soil profile; study site; elevation; aspect of the slope; steepness of the slope; depth of soil pit (the soil was not always dug until the parent material was reached); lithology of the soil's parent material (cf. Table 5.1); vegetation type (cf. Chapter 3); soil type according to Baize and Girard (2009) and IUSS Working Group (2015) and humus forms according to Jabiol et al. (2013).

Profile	Site	Elevation [m asl]	Aspect [°]	Slope [°]	Soil pit depth [cm]	Parent material	Lithology of parent material	Vegetation type	Soil type (Baize & Girard 2009)	Soil type (IUSS Working Group 2015)	Humus form (Jabiol et al. 2013)
M2716	Morteys	1966	320	30	41	Limestone colluvium	Calcareous	Calcareous snowbeds	BRUNISOL DYSTRIQUE hemiorganique, sur colluvionnement calcaire	Dystric Cambisol	MESOMULL
M2844	Morteys	1698	122	28	33	Clayey limestone and marl	Calcareous	Calcareous grasslands	CALCOSOL décarbonaté en surface, hémiorganique	Calcaric Cambisol	OLIGOMULL (Rhizic)
M2965-6	Morteys	1932	180	45	34	Limestone colluvium	Calcareous	Calcareous grasslands	CALCOSOL leptique, hémiorganique, issu de colluvionnement calcaire	Calcaric Cambisol	OLIGOMULL (Rhizic)
M2976	Morteys	1981	0	0	43	Compact limestone	Calcareous	Subalpine pastures	BRUNISOL DYSTRIQUE, leptique, humique	Dystric Cambisol	EUMESOAMPHI
M2980	Morteys	1945	340	10	50	Compact limestone	Calcareous	Subalpine pastures	BRUNISOL DYSTRIQUE rédoxique	Dystric Cambisol	OLIGOMULL
M3109	Morteys	1900	146	39	39	Limestone-rich moraine	Calcareous	Subalpine pastures	BRUNISOL DYSTRIQUE, leptique, colluvionné en surface, à charge calcaire	Dystric Cambisol	OLIGOMULL
M3126	Morteys	1716	108	48	25	Compact limestone	Calcareous	Calcareous grasslands	CALCISOL leptique bathycarbonaté, hémiorganique	Eutric Cambisol	OLIGOMULL (Rhizic)
M3127	Morteys	1747	120	35	30	Compact limestone	Calcareous	Calcareous grasslands	CALCISOL leptique hémiorganique	Eutric Cambisol	OLIGOMULL (Hyperhumic, Rhizic)
M3128	Morteys	1855	142	38	44	Compact limestone	Calcareous	Calcareous grasslands	CALCISOL haplique hémiorganique	Eutric Cambisol	OLIGOMULL (Hyperhumic, Rhizic)
M3132	Morteys	1972	165	11	68	Limestone-rich moraine	Calcareous	Subalpine pastures	BRUNISOL DYSTRIQUE rédoxique, hémiorganique	Dystric Cambisol	MESOMULL
M3138	Morteys	1711	142	33	26	Detritic limestone	Calcareous	Calcareous grasslands	CALCISOL bathycarbonaté leptique	Calcaric Cambisol	DYSMULL (Hyperhumic, Rhizic)
M3139	Morteys	1774	158	27	27	Detritic limestone	Calcareous	Calcareous grasslands	CALCISOL leptique	Eutric Cambisol	OLIGOMULL (Hyperhumic, Rhizic)
M3140	Morteys	1997	136	35	32	Detritic limestone	Calcareous	Calcareous grasslands	CALCOSOL leptique, hémiorganique, issu de colluvionnement calcaire, à charge calcaire	Calcaric Cambisol	OLIGOMULL (Rhizic, Skeletic)
M3141	Morteys	2099	135	27	23	Detritic limestone	Calcareous	Calcareous grasslands	BRUNISOL EUTRIQUE OU DYSTRIQUE, sur colluvionnement calcaire	Dystric Cambisol	OLIGOMULL (Rhizic)
M3150	Morteys	1951	210	31	20	Limestone colluvium	Calcareous	Calcareous grasslands	CALCISOL leptique, hémiorganique	Eutric Cambisol	DYSMULL (Hyperhumic, Rhizic)
M3167	Morteys	1979	50	28	11	Compact limestone	Calcareous	Calcareous snowbeds	LITHOSOL-CALCISOL bathycarbonaté	Rendzic Cambic Leptosol	MESOMULL (Lithic)
M3592	Morteys	2232	20	18	35	Compact limestone	Calcareous	Calcareous snowbeds	CALCISOL caillouteux, colluvial, hémiorganique	Eutric Cambisol	DYSMULL (Hyperhumic, Skeletic)
M4121	Morteys	2180	330	50	2	Compact limestone	Calcareous	Calcareous snowbeds	LITHOSOL holorganique	Rendzic Leptosol Hyperhumic	Hyperlithic PARAHUMUS (Rhizic)
G47	Grimsel	2317	180	30	42	Gneiss and micaschist-rich moraine	Si-rich	Silic. subalp. grasslands	PODZOSOL OCRIQUE colluvial, juvénile, leptique, pierreux	Hyperskeletic Entic Podzol Colluvic	HEMIMODER (Rhizic)
G90	Grimsel	2441	156	10	42	Granite, granodiorite, diorite	Si-rich	Silic. alp. grasslands	PODZOSOL OCRIQUE	Entic Podzol	HUMIMOR (Rhizic)
G92	Grimsel	2511	0	0	28.5	Granite, granodiorite, diorite	Si-rich	Silic. alp. grasslands	PODZOSOL OCRIQUE leptique	Leptic Entic Podzol	HEMIMODER
G291	Grimsel	2348	140	5	51	Gneiss and micaschist-rich moraine	Si-rich	Silic. subalp. grasslands	PODZOSOL HUMIQUE leptique SUR PODZOSOL tronqué	Umbric Podzol	HUMIMOR (Hyperhumic, Rhizic)
G334	Grimsel	2310	145	20	52	Gneiss and micaschist	Si-rich	Silic. alp. grasslands	PODZOSOL MEUBLE caillouteux	Skeletic Albic Podzol	HUMIMOR (Rhizic)
G336	Grimsel	2497	0	0	46	Granite, granodiorite, diorite	Si-rich	Typical snowbeds	PODZOSOL MEUBLE leptique, développé dans un paléo Podzosol Meuble	Albic Podzol	HEMIMODER (Bryoic)
G339	Grimsel	2650	45	5	23	Granite, granodiorite, diorite	Si-rich	Silic. alp. grasslands	RANKOSOL alpin, graveleux, leptique	Umbric Leptosol	HEMIMODER
G340	Grimsel	2560	320	20	27	Granite, granodiorite, diorite	Si-rich	Silic. alp. grasslands	RANKOSOL alpin, à horizon A humifère, graveleux, podzolisé	Umbric Leptosol	HEMIMODER
G350	Grimsel	2326	160	18	32	Gneiss and micaschist-rich moraine	Si-rich	Silic. subalp. grasslands	PODZOSOL OCRIQUE leptique	Leptic Entic Podzol	DYSMODER (Rhizic)
G403	Grimsel	2313	0	20	15.5	Gneiss and micaschist	Si-rich	Typical snowbeds	RANKOSOL alpin, graveleux, leptique, podzolisé, hémiorganique	Umbric Leptosol	HEMIMODER
G421	Grimsel	2312	167	20	52	Gneiss and micaschist-rich moraine	Si-rich	Silic. subalp. grasslands	PODZOSOL OCRIQUE pierreux, issu de cordon morainique	Hyperskeletic Entic Podzol	HEMIMODER (Rhizic)

Profile	**Site**	**Elevation [m asl]**	**Aspect [°]**	**Slope [°]**	**Soil pit depth [cm]**	**Parent material**	**Lithology of parent material**	**Vegetation type**	**Soil type (Baize & Girard 2009)**	**Soil type (IUSS Working Group 2015)**	**Humus form (Jabiol et al. 2013)**
R264R	Réchy	2489	0	0	45	Mixed moraine	Mixed	Typical snowbeds	REDOXISOL à horizon réduit de surface	Gleyic Stagnosol	EUANMOOR
R267R	Réchy	2685	272	5	30	Quartzite	Si-rich	Typical snowbeds	PODZOSOL OCRIQUE leptique	Entic Podzol	HEMIMODER (Rhizic)
R3901	Réchy	2697	251	6	50	Marble and phyllitic calcschist	Calcareous	Windy ridges	BRUNISOL EUTRIQUE hémiorganique, leptique, juvénile, développé dans un Régosol cryoturbé issu de loess et de quartzites, sur calschistes et quartzites	Endocalcaric Eutric Cambisol (Humic)	DYSMULL
R3913	Réchy	2599	3	20	41	Mixed moraine	Mixed	Typical snowbeds	REGOSOL polygénétique, colluvial	Skeletic Regosol (Colluvic, Humic)	MESOMULL
R3934	Réchy	2468	116	5	8	Mixed moraine	Mixed	Wet snowbeds	REDUCTISOL TYPIQUE	Gleysol	EUANMOOR (Bryoic)
R3935	Réchy	2468	1	10	36	Mixed moraine	Mixed	Typical snowbeds	REDUCTISOL TYPIQUE	Gleysol	EUANMOOR-MESOMULL
R4003	Réchy	2595	240	35	40	Calcareous colluvium	Calcareous	Windy ridges	CALCOSOL décarbonaté en surface, leptique, issu de colluvionnement calcaire, hémiorganique, bilithique	Calcaric Cambisol	OLIGOMULL
R4209	Réchy	2581	207	14	31.5	Gneiss	Si-rich	Silic. alp. grasslands	PODZOSOL OCRIQUE	Leptic Entic Podzol	HEMIMODER (Rhizic)
R4217	Réchy	2568	0	0	36	Quartzite-rich alluvial deposits	Mixed	Wet snowbeds	REDUCTISOL TYPIQUE graveleux, leptique	Gleysol	EUANMOOR
R4468	Réchy	2440	342	3	34.5	Mixed moraine	Mixed	Typical snowbeds	REDOXISOL sur REDUCTISOL STAGNIQUE	Stagnosol on Gleysol	HEMIMODER
R4469	Réchy	2578	182	18	43	Mixed moraine	Mixed	Silic. alp. grasslands	PODZOSOL OCRIQUE hémiorganique	Entic Podzol	HEMIMODER
R4471	Réchy	2682	64	22	52	Quartzite, metaconglomerate	Si-rich	Silic. alp. grasslands	PODZOSOL OCRIQUE leptique, pierreux	Leptic Entic Podzol	HEMIMODER
R4482	Réchy	2450	225	30	52	Phyllitic marble, calcschist	Calcareous	Windy ridges	CALCISOL leptique, pierreux	Eutric Cambisol	OLIGOMULL
R5061	Réchy	2650	299	18	32	Mixed moraine	Mixed	Wet snowbeds	REDUCTISOL TYPIQUE colluvionné en surface	Gleysol Epicolluvic	EUANMOOR
R5067	Réchy	2528	20	8	20.5	Mixed moraine	Mixed	Silic. alp. grasslands	PODZOSOL OCRIQUE leptique	Leptic Entic Podzol	DYSMODER (Rhizic)
R5141	Réchy	2567	340	32	21	Gneiss and micaschist	Si-rich	Wet snowbeds	REGOSOL humique, issu de colluvionnement	Skeletic Leptosol (Colluvic)	HEMIMOR (Rhizic)
R5145	Réchy	2430	275	36	30	Quartzite, metaconglomerate	Mixed	Windy ridges	REGOSOL hémiorganique, colluvial, à charge calcaire de profondeur	Skeletic Leptosol (Colluvic, Humic)	OLIGOMULL (Rhizic)

5.4.2 Physical and chemical soil properties

Grain-size distribution was mainly related to the study sites (Figure 5.3): samples from the Morteys site, characterized by a limestone lithology, displayed higher clay concentrations than the two other sites, where the clay percentage never exceeded 10%. Among the Morteys plant community types, the texture of soil samples from the subalpine pastures (Dystric Cambisols) was homogenously silty clay loam and silty clay, whereas those from calcareous grasslands and snowbeds were more variable, and some samples were attributed to loamy and silty loam texture classes.

The Grimsel and Réchy study sites were differentiated according to their relative proportions of silt and sand: the Réchy site was dominated by the silt fraction and presented mainly silty loam textures; the Grimsel site showed instead variable proportions of silt and the textures were sandy loam to silty loam. The relationship between the grain-size distributions and the plant community or soil type appeared to be weaker than with the study site. It has to be noted that the texture of Eutric and Calcaric Cambisols observed on windy ridges (Réchy site) was similar to that of other soil types from the same site and substantially different from the other Cambisols present in the Morteys site (Figure 5.3).

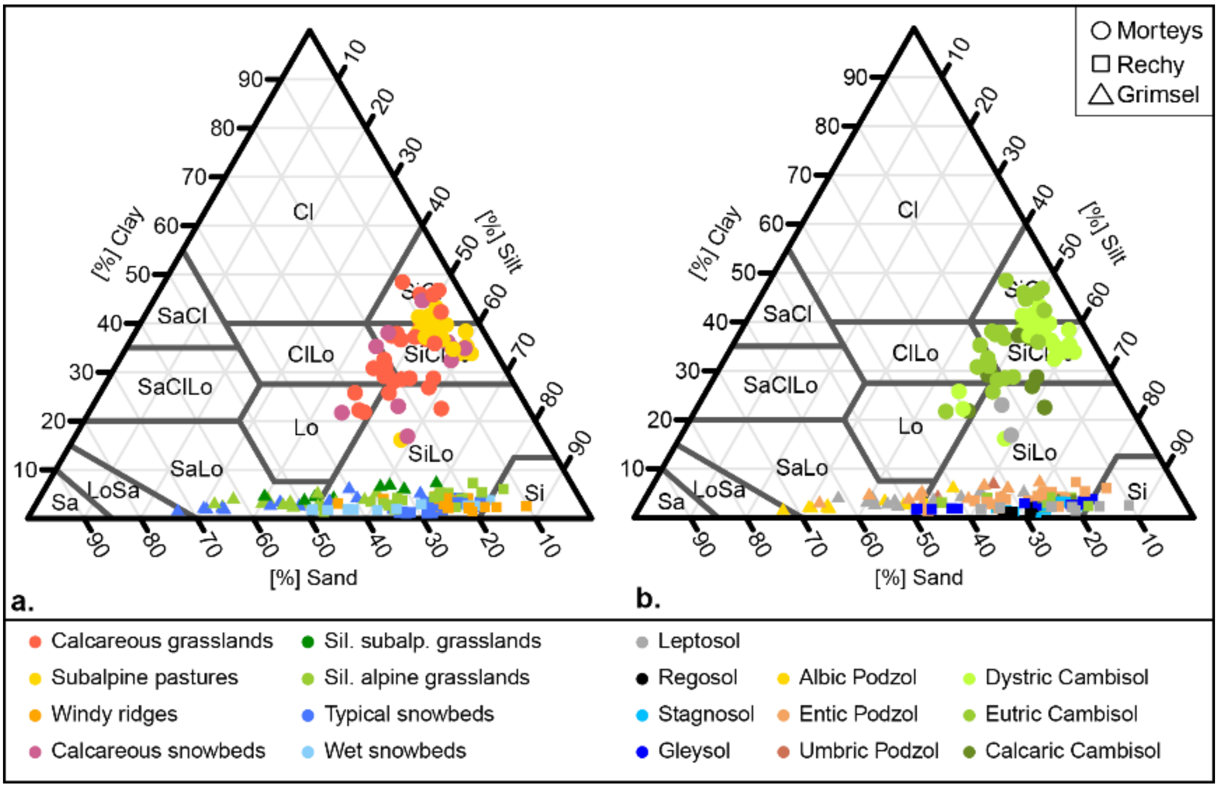

Figure 5.3 - Textural ternary diagrams of the fine earth (< 2 mm) of A, E, B and C horizons. Symbols represent the three study sites (Chapter 3), colors represent **(a)** the eight plant communities and **(b)** the ten soil types. Same abbreviations as in Figure 5.1. Textural classes follow IUSS Working Group (2015). “Clay”: 0-2 µm; “Silt”: 2-63 µm; “Sand”: 0.063-2 mm.

The gradient in soil pH was broadly consistent with the type of plant community (Figure 5.4). Calcareous grasslands, windy ridges, and calcareous snowbeds showed higher soil pH (from 5.3 to 8.2) than in siliceous grasslands and snowbeds (from 3 to 6.2). The wet snowbeds, even if developed on siliceous parent material or mixed moraine (Table 5.2), presented higher pH values than the other siliceous vegetation types. Contrarily, the subalpine pastures, even if located in a limestone-dominated site (Morteys site), presented relatively lower soil pH ranges. Organo-mineral horizons (A) had generally lower soil pH values than mineral horizons. This was particularly obvious in the soils of windy ridges, where the difference of average pH between mineral and A horizons reached 1.4 units (< 1 unit for the other plant communities). Wet snowbeds presented same pH ranges for A and mineral horizons.

The eluvial (E) horizons were not merged neither with A nor mineral horizons because of their peculiar characteristics showed in the OM stability study (Chapter 6). Because of their small number (four samples in total), these horizons were not considered in the following boxplots of pH and C/N distribution (Figure 5.4 and Figure 5.5).

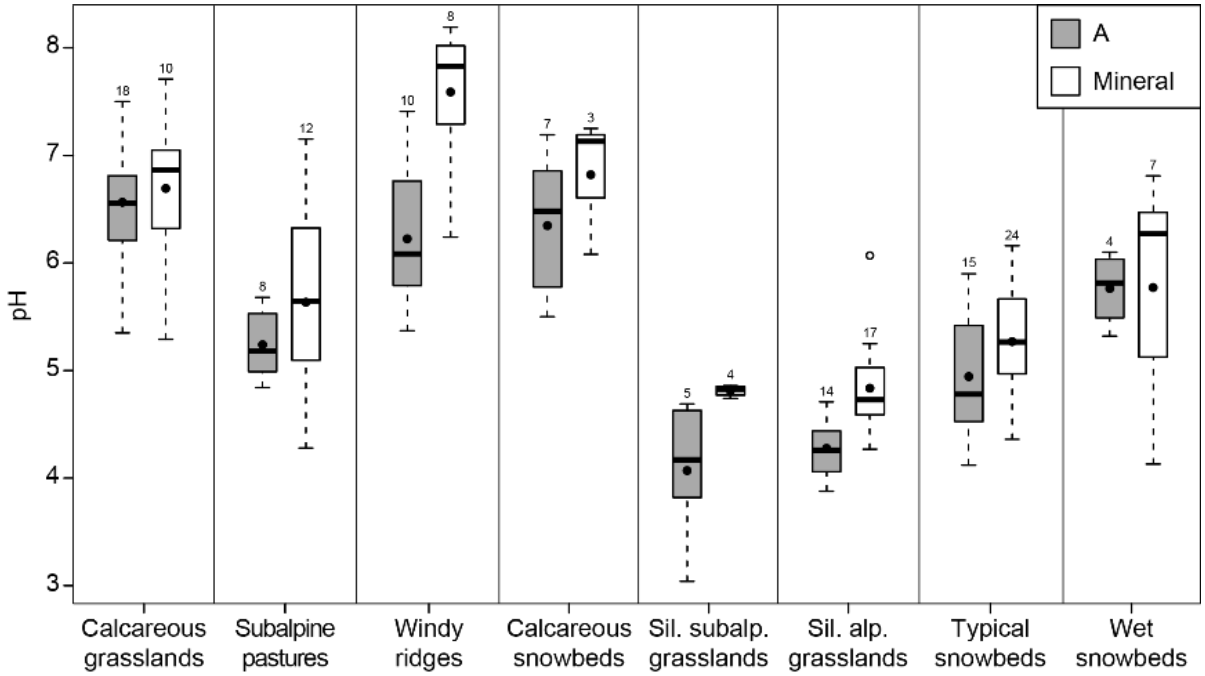

Figure 5.4 - pH distribution among A and mineral layers (B and C horizons) in the eight plant communities. Same abbreviations as in Figure 5.1. Black dots represent the mean values, the black line is the median, and boxes are limited by 1st and 3rd quartiles. Numbers of observations are indicated above boxplots.

The organic C concentration decreased from litter to mineral horizons consistently in all the plant community types (Figure 5.5a). This decrease was particularly pronounced between O and A horizons. Litter layers showed variable percentages of organic C, reaching maximum values in a moss-rich sample of typical snowbeds (59%) and minimum ones in calcareous grasslands (29%). The A horizons were in general C-rich (9.3% in average, Appendix F1), especially those from calcareous grasslands (13% of C in average). The same trend is maintained in mineral horizons, where the highest values (7.2% in average) were found in calcareous grasslands.

Total Nitrogen (N) concentrations decreased from organic to mineral horizons but not linearly in each vegetation type (Figure 5.5b). N concentrations in litter samples (organic N in this case) were highly variable: snowbeds, either calcareous or siliceous, reached the highest values (1.5% in average), while grasslands were the lowest (0.9% in average). In calcareous and siliceous grasslands (both subalpine and alpine), a relative increase in N concentrations was observed in Oe and Oa samples. The same trend appeared in the subalpine pastures but the only Oe sample available cannot allow further conjectures. N concentrations of A horizons presented a high variability among and within vegetation types. Higher concentrations were found in subalpine pastures and in calcareous grasslands and snowbeds, the three plant community types investigated in the Morteys site. N concentrations in the mineral layers were very low and followed the same trend as A horizons.

The C/N ratio (organic C / total N) linearly decreased from litter to A horizons (Figure 5.5c). The C/N ratio was not computed in mineral layers because of their concentrations being too close to the detection limit of the machine. A small error of such N concentrations would have notably skewed the results. The litter C/N variability was relatively high among and within each vegetation type. The litter collected in calcareous and siliceous grasslands displayed higher C/N ratios (between 32 and 70) compared to all other plant communities (between 19 and 34). C/N ratios of A horizons showed high variability among vegetation types (values varying between 7 and 20).

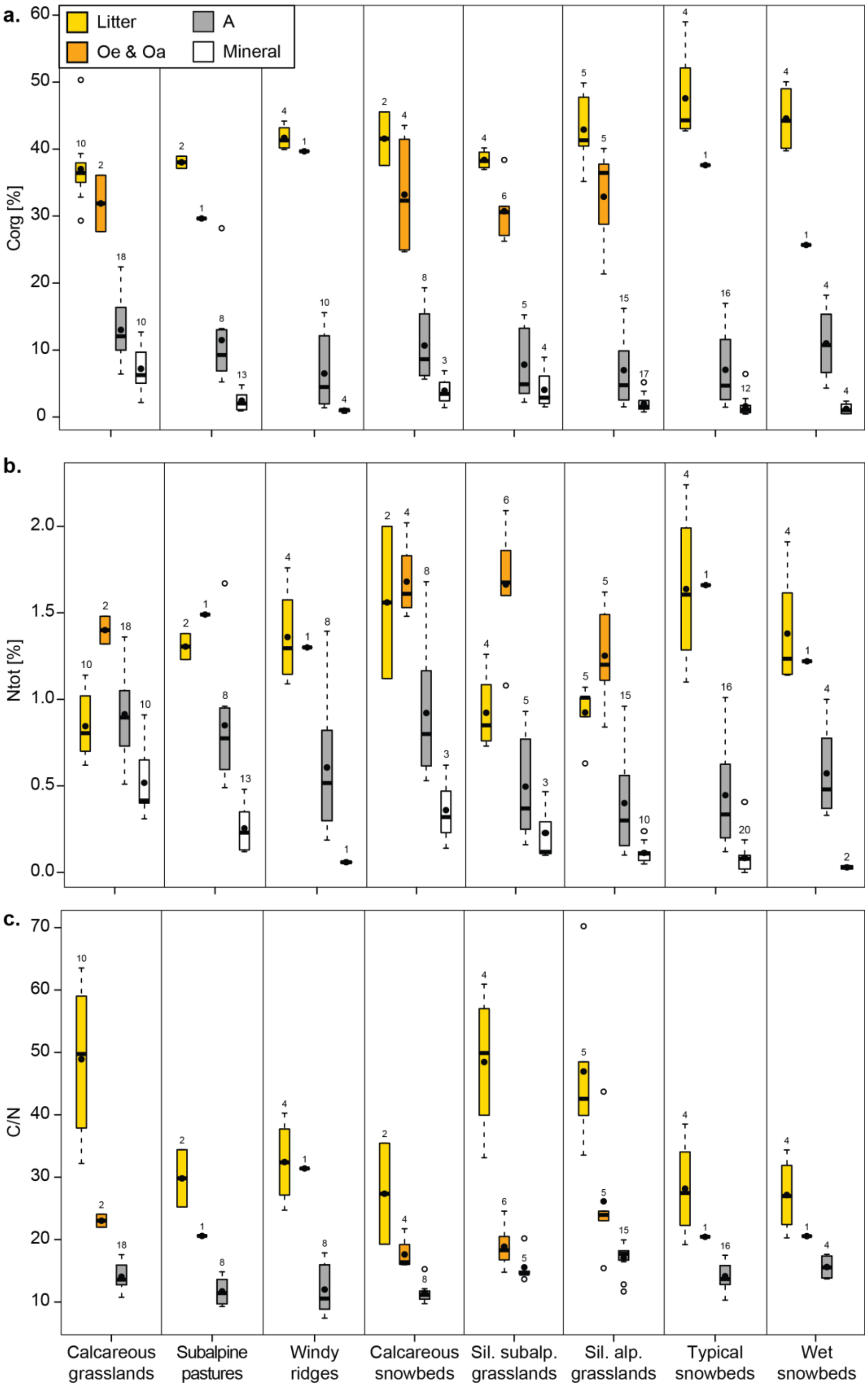

Figure 5.5 – Total Carbon and Nitrogen concentrations among horizons and vegetation types. **(a)** Organic Carbon (Corg), **(b)** total Nitrogen (Ntot) concentration and **(c)** C/N ratio among litter, Oe and Oa, A and mineral (B and C) horizons in the eight plant communities. Same abbreviations as in Figure 5.1 and symbols as in Figure 5.4.

5.4.3 The diversity of humus forms and their characteristics

Ten main groups of humus forms, from Mull to Mor, were identified (Table 5.2). Apart from the Euanmoor, which is semi-terrestrial, all other forms are terrestrial humus forms.

Among parameters employed for the humus form identification (Table 5.1), the pH of the A horizon and its structure resulted as the most important according to PCA (Figure 5.6). Mull forms were associated to meso-granular structures and high pH of the A horizon, compared to Moders and Mors that were associated to lower pH and micro-granular or single-grain structures. Dysmoder and Mor forms distinguished from other Moders because of the occurrence of an Oa horizon. The Euanmoors showed intermediate pH values and were clearly separated from all other terrestrial forms because of the waterlogging conditions. Their A structure was massive in all cases except in one profile (R264R), where a meso-granular structure was found instead.

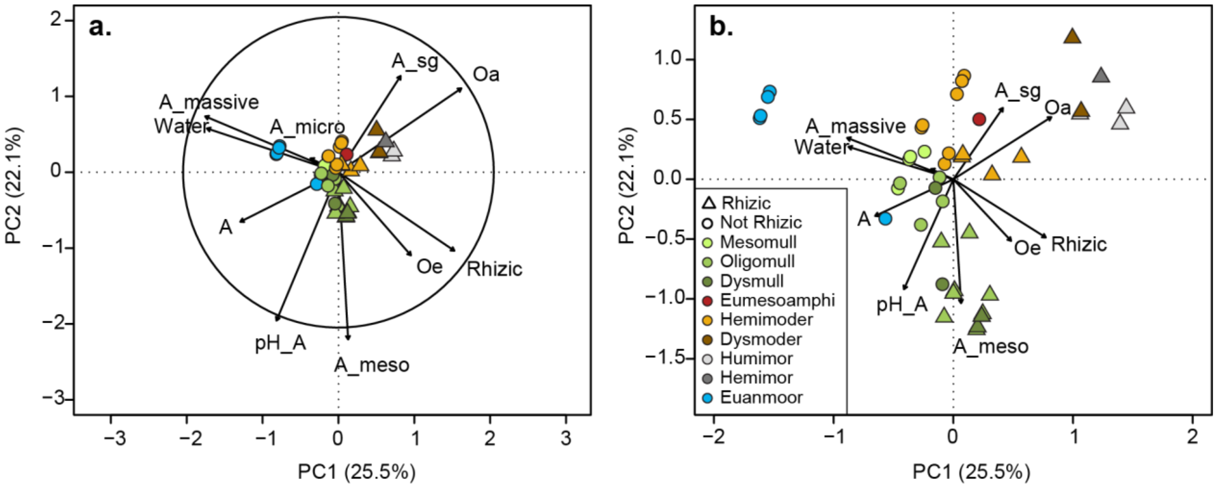

Figure 5.6 - Principal Component Analysis (PCA) based on parameters for identification of humus forms. The first axis represents 25.5% of the variance and the second 22.1%. Colors represent the groups of humus forms, and symbols whether these are Rhizic (Jabiol et al., 2013) or not. The Hyperlithic Parahumus form (1 observation) was omitted for lack of pH data. Abbreviations: “Oe”, “Oa”, “A”: presence of Oe, Oa, A horizons respectively; “A_massive”,“A_sg”, “A_micro”, “A_meso”: different A structures, respectively massive (Anmoor A; Jabiol et al., 2013), single grain, micro-granular (aggregates < 1 mm), meso-granular (aggregates 1-4 mm); “Water”: presence of waterlogging conditions, “pH_A”: pH of the A horizon or, if this was missing, pH of the first horizon under the O; “Rhizic”: humus forms having a rhizic horizon between 25 and 75% of the thickness of combined diagnostic horizons or having > 25% of dead or living roots in the total humus form volume (Jabiol et al., 2013). **(a)** Distance biplot (scaling 1): distance among objects are approximations of their Euclidean distances in multidimensional space; the angles among descriptor vectors are meaningless. The circle of equilibrium contribution defines variables which contribution is higher than average. **(b)** Correlation biplot (scaling 2): distances among objects are not approximations of their Euclidean distances, the angles between descriptors reflect their correlation (Borcard et al., 2011). “A-micro” was omitted to facilitate easy reading.

5.4.4 Main environmental factors driving the distribution of humus forms

5.4.4.1 Vegetation type

The calcareous plant communities were associated to Mull forms (Meso-, Oligo- and Dysmull; Figure 5.7). Eumull, the humus form having the most efficient nutrient recycling among mulls (Jabiol *et al.*, 2013), was not observed. A Eumesoamphi was detected in a subalpine pasture and a Hyperlithic Parahumus (having continuous rock under litter and within 2 cm from the soil surface; Jabiol *et al.*, 2013) in a calcareous snowbed. Moder and Mor forms were associated to siliceous grasslands (both subalpine and alpine) and to typical snowbeds. An Hemimor was recorded in the wet snowbeds and a Mesomull in a typical snowbed. Euanmoor forms were only observed in snowbeds plant communities.

Roots were abundant (Appendix F1), leading to the use of the suffix “Rhizic” in 22 humus form names (having a rhizic horizon between 25 and 75% of the thickness of combined diagnostic horizons or having > 25% of dead or living roots in the total humus form volume; Jabiol *et al.*, 2013). Most of them were observed on grassland soils, and particularly under calcareous and siliceous subalpine grasslands, where all humus forms were described as Rhizic.

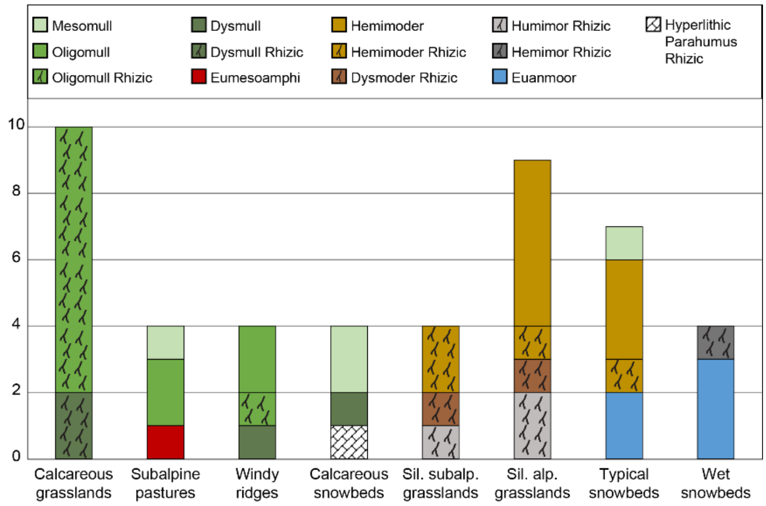

Figure 5.7 - Number and type of humus forms described in each vegetation type (Chapter 3). Humus forms are grouped into ten principal humus form references (IUSS Working Group, 2015). The Rhizic form (Jabiol et al., 2013) of some humus forms is indicated by a specific symbol. Same abbreviations as in Figure 5.1.

5.4.4.2 Soil type and soil parent material

The type of soil, notably its acidity and the waterlogging conditions, shaped the distribution of humus forms (Figure 5.8). Mull forms were prevalently found in association with Cambisols; Moder and Mor forms with Podzols, and Anmoor forms with Stagnosols and Gleysols. Leptosols had no specific humus forms except the Hyperlithic Parahumus. Rhizic humus forms were absent from hydromorphic soils (Gleysol and Stagnosol) and Regosols.

Consistently, the lithology of the soil's parent material clearly separated humus forms in two groups: Mulls mostly on calcareous parent material and Moder and Mor on siliceous ones (Figure 5.9). Soils developed on surficial deposits with mixed lithology (sedimentary, metamorphic and crystalline components) displayed both Mulls and Moders. All Anmoor forms were associated to the mixed lithology. The Eumesoamphi and the Hyperlithic Parahumus forms occurred on calcareous parent material.

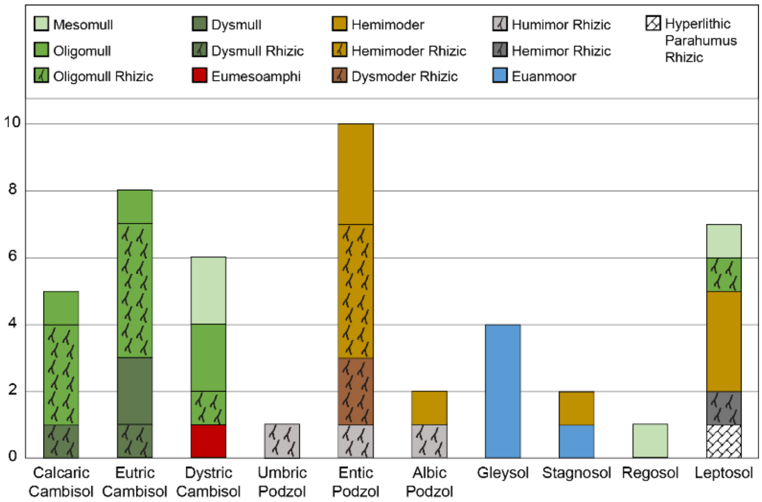

Figure 5.8 - Number and type of humus forms described in each soil reference group (IUSS Working Group, 2015).

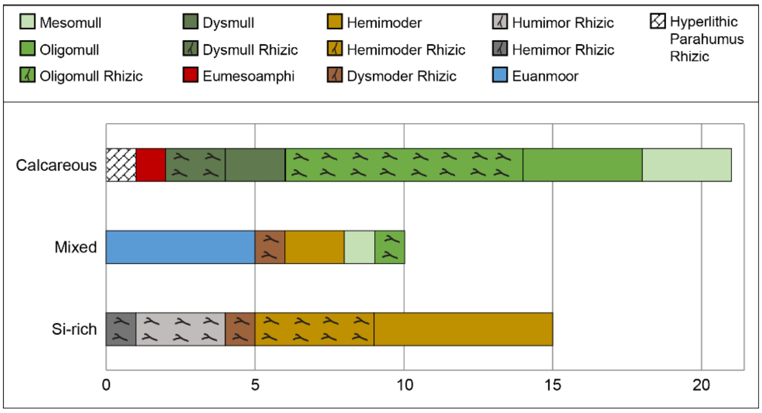

Figure 5.9 - Relationship between the lithology of soil's parent material and the humus forms (IUSS Working Group, 2015). For lithologies, refer to Table 5.1.

5.4.4.3 Temperature and precipitation ranges

The gradient of mean summer temperatures and annual precipitations of this study importantly shaped the humus form distribution (Figure 5.10). However, it has to be reminded that the three study sites (Morteys, Réchy, Grimsel) differ in terms of elevation and biogeographic regions, besides lithology (Chapter 2), showing thus differences in climate. Therefore, the humus form distribution along gradients of summer temperatures and annual precipitations could result from the variation of all parameters associated to the study sites (geology, vegetation, etc.), in addition to climatic variations.

Mull forms were mainly found at Morteys site that, being lower in elevation, is the one showing the highest summer temperatures. Nevertheless, four Mulls were found also at cooler temperatures, showing that this humus form can occur at colder site as well. Among Mulls, Rhizic forms were generally found at lower elevation (mainly below 2000 m) than their relative non-rhizic form (all above 1900 m). Moders and Mors were found only above 2300 m (Table 5.2), at both Réchy and Grimsel sites, irrespective of the precipitation regime. Humimors were found only at Grimsel and the unique Hemimor was found at Réchy. Anmoors were observed only at Réchy, above 2400 m.

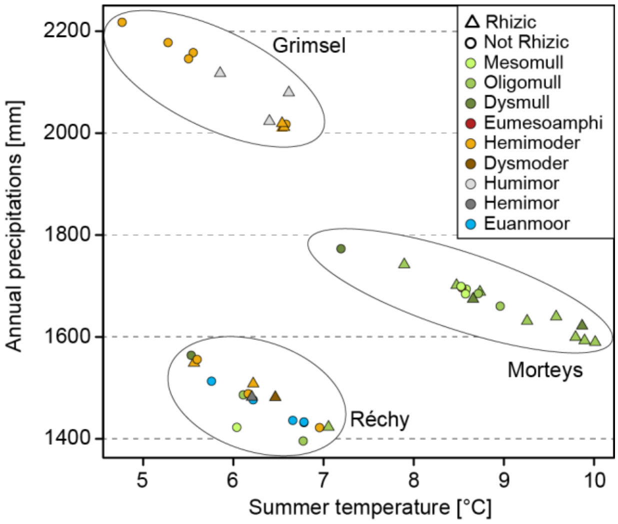

Figure 5.10 - Relationship between mean summer temperatures and annual precipitations of each humus form type. Colors represent the groups of humus forms, and symbols whether these are Rhizic (Jabiol et al., 2013) or not. Points are grouped by study sites.

5.4.4.4 Topography

The humus form distribution was influenced by topography as well (Figure 5.11). Indeed, Anmoors were found only in depressions, while Rhizic forms mostly on slopes. The distribution of Mulls, Moders and Mors appeared poorly related to topography. Nevertheless, only Mull forms were observed on ridges.

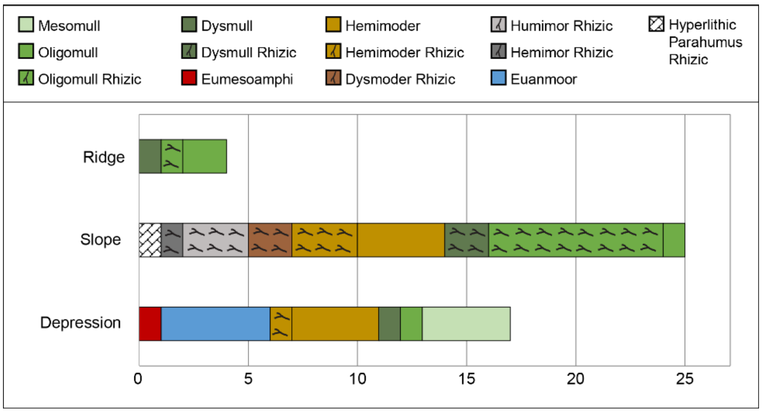

Figure 5.11 - Relationship between topography and the humus forms (IUSS Working Group, 2015). The three categories of topography (ridge, slope, depression) have been estimated visually by the author.

5.4.4.5 The combined influence of environmental factors

The respective influence of various environmental factors (Table 5.1) on the humus form distribution, the correlation among them and with the parameters of humus form identification (Figure 5.6) is summarized in the redundancy analysis of Figure 5.12a. The selected environmental factors explained a significant part (60.5%) of humus form variation (permutation test, F=3.3, P-value < 0.001).

Slope, summer temperatures and North-South gradient play an important role in the dispersion of humus forms along the first axis, which opposes Mulls to Moders and Mors. The parameters defining the Mull forms, such as abundance of roots (Rhizic), the meso-granular structure of the A horizon (A_meso) and its higher pH, are associated to higher summer temperatures, steeper and south-exposed slopes. The second axis, correlated to lithology of soil's parent material, annual precipitation and the presence of snowbed vegetation (Figure 5.12a), separates Dysmoders and Mors from Anmoors. Consistently, waterlogging conditions are associated with snowbed vegetation, while single grain structure and presence of Oa horizons are correlated with Si-rich lithology and higher precipitations.

The environmental factor "Vegetation" is influenced by climate, topography and soil parent material as much as the humus forms. This makes its presence in the canonical ordination questionable. When the vegetation type was removed from the analysis (Figure 5.12b), the dispersion of humus forms along the first and second axis did not change considerably and the remaining environmental factors explained 44,6% of the variance (F=3.6, P-value < 0.001).

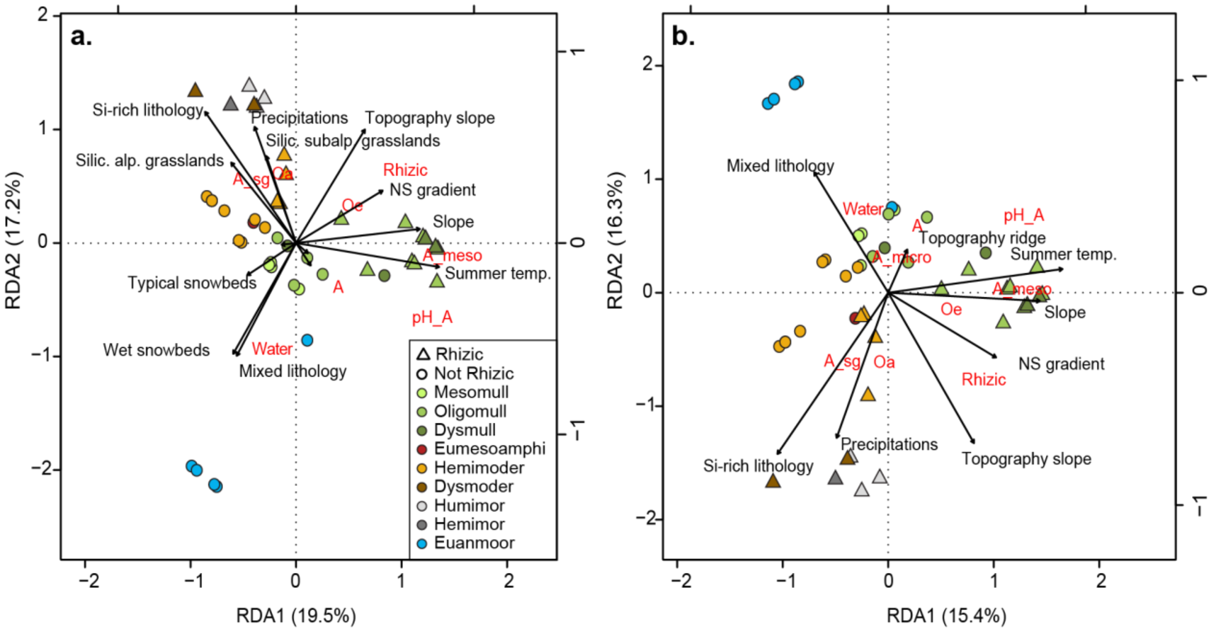

Figure 5.12 - Redundancy analysis (RDA) representing **(a)** the influence of environmental variables (black arrows and text; Table 5.1) on the distribution of humus forms (symbols), and on parameters for the identification of humus forms (red text; Figure 5.6). Colors represent the groups of humus forms, and symbols whether these are Rhizic (Jabiol et al., 2013) or not. The Hyperlithic Parahumus form (1 observation) was omitted for lack of pH data. Abbreviations in addition to those listed in Figure 5.6: "Summer temp.": mean summer temperature; "Silic.": siliceous; "alp.": alpine; "subalp.": subalpine; "NS gradient": North-South gradient (cf. Table 5.1). For easy reading, some environmental variables (Vegetation of subalpine pastures, calcareous snowbeds and windy ridges) with low explaining power were omitted. Were also omitted "A_micro" and "A_massive" among parameters for identification of humus forms for easy reading. **(b)** Same as (a) but without the "Vegetation" variables. Scaling 2 in both RDA.

5.5 Discussion

Eight plant communities, encompassing a large variety of ecosystems, were chosen as sampling units in order to investigate the diversity of soil types and humus forms in the subalpine and alpine belts. In relatively undisturbed environments as the alpine one, the plant species composition well reflects variations of environmental conditions, as the soil parent material, the topography and the climate. Such parameters, together with living organisms and time, are fundamental forming factors of soil and humus forms (Jenny, 1941). This study aimed to evaluate their respective influence on properties of humus forms.

5.5.1 The role of parent material

Mull humus forms were almost exclusively occurring within calcareous lithology (only two exceptions in a siliceous typical snowbed); while Moders and Mors were exclusively associated to Si-rich parent materials (Figure 5.9). In the present study, it was challenging to determine whether this is related to the nature of soil parent material, or to differences in litter degradability between calcareous and siliceous plant communities. By assuming that the litter degradability is negatively related to the C/N ratio (Cornwell *et al.*, 2008), then the high C/N ratio of grassland litters is an indication of their low degradability. Calcareous and siliceous grasslands showed similar C/N ratios of litters (Figure 5.5c), suggesting that the potential for degradation was lithology-independent, and rather influenced by factors linked to the graminoids (Poaceae, Cyperaceae and Juncaceae) traits. If the litter degradability is lithology-independent, then the distribution of humus forms can indeed be related to the lithology of soil's parent material. A previous study comparing humus forms of coniferous and deciduous forests in the whole France reached the same conclusion (Ponge *et al.*, 2011).

Based on its mineralogy and alterability, the soil parent material can influence the humus form by determining the percentage of base saturation and its pH environment (Duchaufour, 1977), which have a direct impact on the macroinvertebrates (Ponge, 1993) and the structure of the microbial population (Mannisto *et al.*, 2007). According to Ponge (2003), nutrient-rich soils foster the activity of earthworms and bacteria that are, respectively, the dominant faunal and microbial group in biomass in Mull forms. On the contrary, nutrient-poor, acidic soils, allow for the development of enchytraeids and fungi, especially abundant in Moders and less in Mors. In this study, macroinvertebrates observations were rare probably because of the harsh climatic conditions characterizing the alpine environment. However, some earthworms and enchytraeids (taxonomy not determined) were found in Mull forms of the Morteys site (Appendix F2), which is the lowest in elevation and entirely on limestone parent material. No macroinvertebrates were observed in the Réchy and Grimsel sites.

Besides soil pH, the parent material can influence decomposition patterns through its ability to release mostly clay, silty, or sandy material. As demonstrated by Bullinger-Weber *et al.* (2007), earthworms tend to avoid sandy soils because sand particles exert an abrasive action on their soft skin (Curry, 2004). The Morteys soils, mostly with silty clay loam texture (Figure 5.3), were in this sense also favorable to the earthworm occurrence. Differences in faunal and microbial communities among lithologies of soil's parent material were also confirmed by variations in the A horizon structure. This presented mostly meso-granular aggregates in Morteys, whereas micro to single-grain structures were observed in the Grimsel and Réchy sites (Appendix F1). Consistently, the single-grain structure of the A horizon was associated to Si-rich lithology in the RDA (Figure 5.12), while meso-granular aggregates, high pH and roots abundance, were associated to warm summer temperatures.

This points out the role of climate, and thus elevation, in the humus form distribution. Therefore, it can be suggested that the Mull presence on calcareous lithology was probably linked to an ensemble of favorable conditions, such as low acidity, silty clay loam texture and warmer temperatures, for effective decomposition. These conditions were not met on Si-rich lithology, where Moder and Mor forms dominated instead.

In addition, it must be pointed out that the nature of parent material can locally influence the litter quality, and thus its degradability. Nicolai (1988) observed that litter from European beech (*Fagus sylvatica*) growing on nutrient-rich calcareous soils was enriched in Ca, Mg, Na, and K, compared to beech trees growing on nutrient-poor acidic soils, with the observed consequence that the turnover of the nutrient-rich litter was faster than the nutrient-poor one.

Furthermore, A horizons of soils associated to calcareous grasslands were characterized by high organic C content (Figure 5.5a and Appendix F1). This could be another effect of the limestone parent material that provides an active calcium carbonate fraction (i.e. the finest part of total calcium carbonate), which seems to efficiently bind OM with mineral components (Muneer and Oades, 1989). Therefore, on one hand, calcareous parent material, by its action on soil pH, soil texture and litter nutrient content, seems to establish favorable conditions for a relatively rapid OM decomposition. However, on the other hand, the abundance of calcium hinders the decomposition and favors the OM accumulation in A horizons, probably stabilized by mineral interactions. This aspect is better examined in Chapter 6.

Finally, Anmoor forms were exclusively associated to mixed lithology (Figure 5.9). The 'Mixed' category contains rocks of mixed origin (sedimentary, metamorphic, crystalline components). This category was often attributed to colluvial deposits located in topographical depressions. There, percolating water and snow accumulate, favouring the formation of Anmoors. Moreover, most of the studied depressions were located on moraine deposits, which often are of mixed lithology. The association of Anmoors with mixed lithology was therefore indirect, and rather the result of topography.

5.5.2 The role of climate

Variations of summer temperatures and annual precipitations occurring in this study are due to differences in elevation and biogeographic region considered (Chapter 2). Progressively colder summer temperatures with increasing elevation were associated to a certain gradient of decreasing decaying activity from Mesomull to Moders and Mors; whereas differences between Moders and Mors seemed not related to temperature variations (Figure 5.10). The RDA (Figure 5.12) confirmed the importance of summer temperatures in the humus form distribution. Three Humimor forms were found where precipitations were the highest (Grimsel), and many Moders were found at the driest site (Réchy). Despite the number of Mor observations are not sufficient to draw conclusions, a possible role of annual precipitation in the respective distribution of Moders and Mors can be hypothesized and needs further studies to be confirmed.

As previously observed in forest humus forms (Ponge *et al.*, 2011), a decrease in temperature and an increase in precipitations likely explain the declining decaying activity. Higher temperatures increase OM decomposition rates (Aerts, 1997) when there is no water limitation (Aerts, 2006), as in the studied sites. Moreover, higher mean annual temperature could lead to higher weathering rates directly by enhancing chemical reactions (Egli *et al.*, 2003; Jenny, 1941; Turner *et al.*, 2010), or indirectly by fostering microbial activity with subsequent production of organic acids with weathering capacities (Egli *et al.*, 2008a). The higher litter turnover and weathering rates expected in the warmer sites release more nutrients in the soil, and these have positive feedbacks on the OM decomposition (Ponge, 2013; Zhang *et al.*, 2008). Rather, at higher elevations, the lower temperatures are supposed to decelerate both biotic and abiotic chemical processes and the higher precipitations to increase soil leaching with subsequent nutrient losses. This could explain the OM accumulation and the predominance of Moder and Mor forms above 2300 m. Nevertheless, a Dysmull was found at the uppermost soil profile, at 2697 m, in association with a windy ridge vegetation. This indicated that harsh climate per se is not a limit for the Mull occurrence if other conditions, such as vegetation and topography (see below) are favorable.

In mountain regions, thermic conditions change drastically according to the slope aspect as well. This was apparent in the RDA (Figure 5.12) where south-facing slopes (high north-south gradient) were related to Mull forms. Ascher *et al.* (2012) showed that the higher temperatures recorded on south-facing slopes affect the enchytraeids populations and increase their decomposing activity. As a consequence, soil OM accumulates in north-facing slopes (Egli *et al.*, 2009). Moreover, the high solar radiations present on south-facing slopes and ridges, provoke important contrasts of soil temperature and humidity, which can physically accelerate the litter decomposition (Duchaufour, 1977).

The Rhizic form of Oligomulls and Dysmulls occurred systematically at lower elevations than their non-rhizic forms. This could be a sort of artefact related to the sampling design, as Rhizic Mull forms were mainly associated to calcareous grasslands (for topography and vegetation-related reasons, see below) and these ecosystems were situated at lower elevations than the other mull-forming vegetation types.

In the present study, the lowest in elevation and thus warmer sites (Morteys) are all on calcareous bedrock, while higher and thus colder sites (Réchy and Grimsel) are mostly on siliceous substrates. Climate and geology are often correlated in the mountain environment, with the proportion of precipitations (Körner, 2007) and siliceous rocks (Pfiffner, 2014; Stampfli, 2001) increasing along with the elevation because of orogenic processes. This makes their specific contribution on distribution of humus forms difficult to evaluate. Moreover, climate importantly influences vegetation that is also a determinant factor for humus form development.

5.5.3 The role of topography

Topography is a major soil forming factor, especially in the alpine landscape where it is highly variable, even at micro-scale. Its role on humus forms is well illustrated by the exclusive presence of Anmoor in topographical depressions (Figure 5.11), where shallow water-tables and snow accumulation (i.e. “snowbed”) hamper the oxygen diffusion and thus the decomposition of organic matter. This leads to the formation of histic organo-mineral horizons typical of Anmoors. Moreover, rhizic forms were mainly observed on slopes. Roots are essential for plant anchorage (Körner, 2003) and therefore crucial for plant stability on steep slopes, exposed to soil erosion and solifluction.

Finally, humus forms on ridges were all Mulls, including a Dysmull found at the uppermost soil profile (2697 m). Litter production on ridges is relatively low as plant cover is sparse and many lichens occupy the surface (cf. Chapter 2). The litter amount is further lowered by the action of wind that exports part of the litter produced. These processes combined may lead to sufficiently low litter inputs into the soil for an effective degradation by soil organisms.

5.5.4 The role of vegetation

Calcareous grasslands, subalpine pastures, windy ridges and calcareous snowbeds were mainly associated to Mull forms, siliceous grasslands (both subalpine and alpine) to Moders and Mors, and snowbeds mainly to Anmoors (Figure 5.7 and Figure 5.12). The same environmental drivers that shape distribution of humus forms, namely climate, soil parent material, topography and time, importantly influence the vegetation types. When the vegetation factor was omitted in the RDA, the distribution of humus forms in the multidimensional plane (Figure 5.12) underwent weak changes. In agreement with Ponge *et al.* (2011), this finding suggested that vegetation plays a minor role on development of humus forms, compared to other environmental variables. Nevertheless, as vegetation represents the main source of soil OM inputs (Rumpel and Kogel-Knabner, 2011), its role is certainly not negligible and worth to be mentioned in the framework of this study.

Vegetation (aerial and subterranean parts) can influence the humus forms by determining the quality and the amount of the litter entering the soil system. In this study, the C/N ratio has been used as a proxy for litter quality (Cornwell *et al.*, 2008). As previously discussed, grassland litters showed higher C/N ratios than any other plant communities and this independently of the soil parent material. As mentioned in the Chapter 3, the litter was collected at the snowmelt and it was composed by species not decomposed during winter (the most resistant). Graminoids (Poaceae and Cyperaceae families) were often among those species and were therefore important components of litter samples, especially in grasslands. Some molecular components of the Graminoids tissues could be responsible of their resistance and of the high C/N values measured in grassland litters. A characterization of molecules composing the litter would allow confirming it. According to Duchaufour (1977), the C/N values measured in grassland litters would characterize Moder and Mor humus forms. Indeed, this was the case for siliceous grasslands, but not for the calcareous ones where, despite their high C/N litter ratio, only Mull forms were observed. In addition, biomass production was higher in calcareous grasslands than in any other plant community but this was not sufficient to overpass the local OM degradation rate. The warmer temperatures and less acidic soils characterizing the calcareous grasslands were probably sufficient to allow effective litter decay. These elements further confirm the preponderant role of climate and parent material on the formation of humus forms.

Furthermore, the grassland vegetation (both calcareous and siliceous) displayed an increase in N concentrations in Oe and Oa, relative to litter horizons (Figure 5.5b). This may indicate differential C and N mineralization rates among plant communities. According to Bocock *et al.* (1960) and other references cited in Duchaufour (1977), N-rich leaves, i.e. with a low C/N value, release CO_2 and mineral N at almost the same rate, maintaining a C/N relatively constant or slightly decreasing during decomposition. On the contrary, N-poor leaves, i.e. with a high C/N ratio, decay slower. In this later case, the N release is especially delayed compared to the CO_2 one, which instead, can be quite effective. This mechanism seems to occur in the studied grassland communities, providing clues about their relatively low degradability.

The influence of alpine vegetation on the humus forms is through belowground litter, more than the aboveground one. Indeed, Rhizic humus forms were frequent and mainly associated to grasslands. In the alpine environment, and especially in grass-dominated vegetation, the plant root system is particularly developed and its biomass strongly exceeds that of aboveground parts (Reisigl and Keller, 1987). Some plant species, such as *Carex sempervirens* and *Sesleria caerulea* in calcareous grasslands, *Nardus stricta* (Fitter *et al.*, 1998) and *Carex curvula* in siliceous grasslands (Grabherr, 1989), are characterized by particularly important and long-lived root systems. Their abundance in grasslands may explain the frequent association of this vegetation type to Rhizic forms.

The root turnover and the root exudate production are supposed to provide large amounts of fresh OM. This C source was shown to favor microbial activity and N-mineralization in the rhizosphere (priming effect; Kuzyakov, 2002). If the occurrence of roots stimulates the decomposition, rhizic forms would be expected mostly in association to Mull forms. This was not the case in the present study where, on the contrary, Dysmoder, Humimor, and Hemimor forms were all found in their rhizic form. This implies that when large amounts of OM are delivered by the root system in an unfavorable context for decomposition (in terms of parent material and climate), then this OM accumulates and Moder-Mor humus forms are observed. This is in agreement with Bradley and Fyles (1996) findings, according to which the priming effect was visible only in Mull forms, and not in the Mor ones.

Furthermore, plants can delay the calcium (Ca^{2+}) lixiviation in calcareous soils. As shown by Havlicek and Gobat (1996), herbaceous plants are able to extract Ca^{2+} from the soil skeleton through their roots-associated fungi, and this up to 40 cm depth. Then, by litter deposition, the calcium is released at the soil surface and hence the Ca^{2+}-stock is maintained. Hence, it can be assumed that plants in calcareous vegetation types concur with soil parent material to maintain suitable nutrient and pH conditions for the microbial activity.

5.5.5 The role of time

When climate, geology, and topography parameters are kept constant, humus forms are supposed to quickly react to vegetation changes (Bernier and Ponge, 1994; Frouz and Novakova, 2005). In the framework of this study, despite important climatic changes during the last 25-50 years, vegetation shifts were shown to be relatively weak (Chapter 4), and therefore drastic transformations in humus forms were not expected. Some changes could have been observed in the snowbed plant communities, which significantly shifted towards siliceous alpine grasslands (Chapter 4). However, traces of past vegetation were not observed in snowbed humus forms neither, suggesting that these were likely in equilibrium with present ecosystem properties. As shown by the RDA (Figure 5.12), vegetation type is not determinant for the differentiation of humus forms, and the permanence of waterlogging conditions may be sufficient to guarantee the Anmoor presence.

However, humus forms have their own spatio-temporal scale. Some changes in response to vegetation shift could occur in the future. An analysis of macrorests with the small-volume methods developed by Ponge (1984) would likely allow detecting them.

5.5.6 The classification of humus forms

The humus forms of this study were named according to Jabiol *et al.* (2013), who proposed a classification system in harmony with the World Reference Base for Soil Resources (IUSS Working Group, 2006). It seems pertinent to recap the criteria of the humus form nomenclature used in the key from Jabiol *et al.* (2013) in order to better understand this issue.

Mull forms display biomacro- or biomesostructured (meso-granular) A horizons, with an absence of Oa horizon (OH according to Jabiol *et al.*, 2013) and at least two of the following properties: 1) presence in the A horizon of living earthworms or their casts; 2) presence of a very sharp transition (<3 mm) between organic and organo-mineral horizons (A); 3) pH of the A horizon > 5. Then, according to the presence/absence and to the continuity/discontinuity of Oi (OL) and Oe (OF) horizons, the different Mull forms are defined.

Moder forms include biomicrostructured (micro-granular), massive, or single grain A horizon, the presence of Oa, the absence of non-zoogenic Oe (i.e. formed by fungal activity), and one of the following properties: 1) no sharp transition Oa/A horizon; or 2) pH of the A horizon < 5. Finally, according to the thickness and continuity/discontinuity of Oa, the different Moder forms are defined.

Mor forms may not have the A horizon, and when present it has biomicro, massive or single grain structure. Moreover, Mor forms have: 1) non-zoogenic Oe; 2) very sharp transition (< 3 mm) of O to A, AE or E horizons; 3) pH of E or AE or A horizon < 4.5. Then different Mor forms are defined according to the continuity/discontinuity of Oe and the presence/absence of Oa and biomicrostructured A.

This classification key appeared fairly inadequate for the alpine humus forms and, in many cases, no reference name corresponded to the humus forms observed in the field. Hereafter, the problematic cases and the solutions adopted are discussed.

1. In this determination key, certain structures of the A horizon are associated to specific organic horizon succession. In the present study, such associations were not always observed. For

example, many humus profiles were composed by an Oi horizon, mainly concentrated under grass turfs, a discontinuous Oe or in pockets within the A horizon, an absence of Oa, and a microstructured A horizon with pH < 5. With such a horizon succession (Oi/Oe/A), a Mull form fits, although the microstructure and pH of the A horizon would instead drive the humus towards a Moder or Eumor form. After several discussions with experts of humus forms (Jean-François Ponge, Augusto Zanella), it was chosen that the structure of the A horizon should have priority over the horizon succession. Therefore, a humus form as the one described above is named Hemimoder. The presence of an Oa horizon, required for Moder forms in the key of Jabiol *et al.* (2013), is considered as not necessary for the Hemimoder form in this study. The absence of an Oa horizon, or its discontinuity, may also indicate a regression from a previous phase with a continuous Oa horizon, formed in different environmental conditions than the present ones (J.-F. Ponge, pers. comm.).

2. According to Jabiol *et al.* (2013), the microstructured A is associated to pH < 5 (Moder). In this study, the same structure was found at pH > 5, and was then included in Mull.
3. Another common issue encountered, was the recognition of the non-zoogenic Oe. According to Jabiol *et al.* (2013), this Oe horizon is formed by the action of cellulose-lignin decomposing fungi. However, mat of fungal material were rarely observed in the present study, and doubts raised frequently about the nature of the Oe horizons (zoogenic or not). This criterion, very useful in forest ecosystems, seems thus more difficult to apply in the alpine one. In the present study, when fungal material was recognized within the Oe horizon, the humus form was attributed to Mor, provided that other conditions were fulfilled. Oe horizons, without evidences of fungal activity, were considered as zoogenic.
4. Finally, despite the limiting conditions for biological activities and decomposition of OM characterizing the Moder forms with respect to Mulls, organic horizons could be quite thin and discontinuous. The presence and thickness of Oi and Oe horizons in Moder forms were comparable to those in Mull forms. Sometimes, the Oi thickness in Mull forms was even greater than in Moder forms. This was especially true in *Carex sempervirens* turfs, where senescent leaves remained fixed at the base of the plant (Figure 5.13).

Figure 5.13 - Detail of a *Carex sempervirens* turf. Profile M3138, Dysmull (Hyperhumic, Rhizic). Elevation: 1711 m. The different colors of the litter layer may indicate different stages of decomposition. Leaves start to decompose while they are still fixed to the living plant.

According to these reflections, and in agreement with the PCA of Figure 5.6, two parameters were considered crucial for the determination of humus forms in the present study: the structure of the A horizon and its pH.

Mulls were attributed to humus forms having a pH of the A horizon > 5, with micro, meso or macro-granular structure, and Oa absent. The continuity/discontinuity of the Oe and Oi horizons allowed to define the different Mull forms, as indicated in Jabiol *et al.* (2013):

- Oe present and continuous: Dysmull
- Oe missing or discontinuous and Oi present: Oligomull
- Oe missing and Oi present but discontinuous: Mesomull

When the pH of the A horizon was < 5, the following rule was followed:

- Microstructured or single grain A, Oa absent and Oe zoogenic possible: Hemimoder
- Single grain A, Oa present and Oe zoogenic possible: Dysmoder
- Single grain A or A absent, Oa present and Oe non-zoogenic present: Humimor
- A absent, Oa present and Oe non-zoogenic absent: Hemimor

According to the classification of humus form proposed by Jabiol *et al.* (2013), the structure of the A horizons is retained as crucial for the definition of humus forms. This directly reflects the community of soil organisms and hence their efficiency in litter decay (Brethes *et al.*, 1995; Ponge, 2003). Meso- (1-4 mm) and macroaggregates (> 4 mm) are considered to be earthworm casts and they define Mull forms, while microaggregates (< 1 mm) can be related to enchytraeid or microarthropods casts, and they are common in Moder and Mors (Coleman *et al.*, 2004). Single-grain and massive structures are non-zoogenic.

There is little evidence that this correspondence between structure of the A horizon and community of decomposing soil organisms is valid also in alpine ecosystem. The study of soil macro-, meso- and micro-fauna in the alpine ecosystem is up to now very limited, and it is hard to determine the organisms responsible of the OM decay.

The soil fauna of the topsoil was not targeted by this study. Nevertheless, some earthworms and enchytraeids were found in calcareous soils at the Morteys site, and corresponded to Mull forms. This would then corroborate that soil fauna is indeed at least partly responsible of the A structure. No earthworms and enchytraeids were found at the other sites, but their presence was not searched for.
Beside the decomposer organisms, the size distribution of mineral particles has also an obvious effect on the soil structure (Bullinger-Weber *et al.*, 2007). In the present data set, microstructured and single-grain A horizons were especially associated to Si-rich parent materials (Figure 5.12), with sandy to silty texture.

Moreover, plant roots end exudates can be important engineers in alpine ecosystem. Extracellular polysaccharides produced by plant roots exert a major role as binding agent in aggregate formation (Oades, 1984). However, how they influence the aggregate size is still unknown. Aggregates of different shapes and sizes were often found in the proximity and around fine roots (shaping a sort of small grape of aggregates), while almost no structure is present in distal parts. These "rhizogenic aggregates" have irregular shapes and have a "fluffy" consistence, compared to the enchytraeid or earthworm casts, which are considered isodiametric since they passed through a digestive tract.
The remarkable abundance of roots in certain humus profiles led to the identification of three OR horizons (> 75% in volume of dead or living roots; Jabiol *et al.*, 2013), and of 22 Rhizic forms (Figure 5.14).

Figure 5.14 - Detail of a Rhizic humus form. Profile M3126, Oligomull (Rhizic). Elevation: 1716 m. The OR horizon of Jabiol et al. (2013) is considered as an organic horizon and not as an A horizon.

However, in this study the OR label was used also for A horizons having > 75% in volume of roots. This choice was justified in order to supply to a nomenclature gap, as root-rich horizons were often organo-mineral layers (A) and not organic ones. The forthcoming key of humus forms (https://www.researchgate.net/project/HUMUSICA-a-new-humus-manual) fills this gap and introduces the concept of rhizic horizon, this latter being either Oi, Oe, Oa or A.

In summary, among terrestrial humus forms, the structure of A horizons may result from different factors: the soil decomposer community, the texture and the root-associated processes. Other physical processes, such as frost/thaw cycles, are also likely, but they were not observed in this study. Waterlogging conditions are fundamental as well, as a massive structure was associated to almost all Anmoors recorded (Figure 5.6).

By saying that the decomposer community is not the unique driving factor of the structure of A horizons, it implies that the latter would not be anymore an indicator of the decomposition efficiency. This is the key to understand the presence of microstructured A (indicating a Moder or Mor according to Jabiol *et al.*, 2013) in absence of Oa, Oe and with pH of A horizon > 5 (indicating a Mull). This discrepancy between the A structure and the horizon sequence leads to some reflections. In an alpine environment, part of the litter may be removed by the combined action of steep terrains, strong winds, snow melting, which tend to creeping and transporting plant material downwards or accumulating it in depressions, or litter may be locally grazed by cattle or wild ungulates before dying. These processes, combined to a low productivity, regulate the low leaf litter input into the soil, compared to forest ecosystems. The absence of thick Oe and Oa layers may indicate that the decomposition of these small amounts of remaining litter is efficient, despite of the absence of earthworms and the presence of micro-granular structure of A horizons, normally typical of Moder forms. Finally, the snowpack may protect the soil from frozen temperatures and enhance an effective decomposition during winter (Saccone *et al.*, 2013). In this case, such humus forms would be functionally closer to Mulls than Moders, even if the structure of A horizons is micro-granular.

To conclude, we can hypothesize the existence of a sort of a disconnection between organic and organo-mineral layers in alpine ecosystems. The occurrence and thickness of organic layers could be mainly linked to the vegetation productivity, degradability of plant species, decomposer organisms, and to a series of disturbances leading to the accumulation/removal of the litter. A horizons, instead, would be influenced by the soil texture, alkalinity, root abundance and the decomposer community. As mentioned in the introduction (Chapter 1), the root : shoot ratio in the alpine grasslands is > 6 (Yang *et al.*, 2009), meaning that the highest part of plant biomass is represented by roots in the alpine environment. The root biomass enters the soil system directly in the A horizon, and thus does not participate to the formation of Oi, Oe and Oa horizons. This further amplifies the disconnection of OM cycling between organic and organo-mineral layers.

5.6 Conclusions

The present chapter gives an extensive overview of the diversity of soils and humus forms in the subalpine and alpine belts of the Swiss Alps. Taking advantage of the large variability in soil parent materials, topography, plant communities and climate, it was possible to discuss the influence of each of these factors on properties of humus forms. In the context of this study, with a few exceptions, three main groups of interactions were observed: 1) calcareous parent material - Cambisols - Mull humus forms - calcicole plants; 2) siliceous parent material – Podzols - Moder or Mor humus forms - calcifuge plants; 3) waterlogging conditions - hydromorphic soils - Anmoor humus forms - snowbed vegetation.

Therefore, the parent material and topography seems to act as attracting poles (Beisner *et al.*, 2003), shaping soils and humus forms. The influence of climate on the distribution of humus forms may be as much important as the parent material; however, their interdependence stemming from the present sampling design prevents to assess their singular role.
In any case, despite the harsh climatic conditions, typical of the subalpine-alpine belt, Mull humus forms were widely observed up to 2697 m. This fact indicates that an effective litter decomposition was possible under certain conditions in the alpine belt.

Furthermore, the root system was shown to play a primary role in the subalpine-alpine humus forms. Decomposition patterns of roots, and relative exudates, must be investigated in the future in order to better understand plant-soil interactions in the alpine environment.

Finally, the study of decomposer organisms, as meso-fauna and micro-flora communities, their specific requirements in terms of temperature, humidity, acidity, and grain-size distributions, would allow the alpine OM dynamics to be better characterized. This information is needed also in order to adapt keys for classification of humus forms to the alpine environment, as it is presently based on forest ecosystem.

6 Drivers of organic matter stability

6.1 Abstract

Our understanding of mechanisms governing soil organic matter (OM) stability is evolving. It is gradually becoming accepted that soil OM stability is not primarily regulated by the molecular structure of plant inputs, but instead by the biotic and abiotic properties of the edaphic environment. Moreover, several experimental studies conducted in artificial systems have suggested that mechanisms regulating OM stability may differ with depth in the soil profile. Up to now however, there is very limited field-scale evidence regarding the hierarchy of controls on soil OM dynamics and their changes with soil depth.

In this study, we take advantage of the high heterogeneity of ecological conditions occurring in the alpine belt to identify the major determinants of OM stability and how their significance varies with soil depth. For this purpose, 46 soil profiles spanning a wide range of soil types have been investigated. Aboveground litter, mineral topsoil, and subsoil samples were analysed using Rock-Eval Pyrolysis, a technique that investigates the thermal stability of OM, which can be considered as a proxy for OM transformation processes.

Our results show a clear divergence of controls on OM thermal stability in the litter, topsoil, and subsoil layers. The composition of plant inputs influences OM thermal stability in the litter layer but not in mineral soil horizons, where the supply rate of fresh organic material and the physical and chemical characteristics of the pedogenic environment appear important instead. This study offers direct confirmation that soil OM dynamics are controlled by different ecosystem properties in each soil layer. This has important implications for our understanding of carbon cycling in soils under a changing climate.

This chapter is an excerpt from the paper:
Matteodo M, Grand S, Sebag D, Rowley M, Vittoz P, Verrecchia EP (submitted) Decoupling of topsoil and subsoil controls on organic matter stability.

The Introduction and part of the Material and Methods have been removed from the paper and they were included in Chapter 1, 3, and 4.

6.2 Aims

In this study the following questions are targeted:

1. what are the major determinants of soil OM thermal stability
2. how does their significance vary with soil depth?

6.3 Materials and methods

Thermal stability of OM from litter (Oi horizon), topsoil mineral (A horizons), and subsoil mineral layers (including E, B, and C horizons) of 46 subalpine-alpine soil profiles was assessed using Rock-Eval pyrolysis. We focused on the R-Index as defined in Sebag et al. (2016), which refers to the proportion of refractory compounds within the pyrolysed OM, as an indicator of OM thermal stability. The soil profiles represented a broad spectrum of environmental conditions, spanning eight vegetation types, a wide range of soil pH (between 3 and 7.9) and moisture conditions (Table 6.1). Study sites are extensively described in Chapter 2, and methods in Chapter 3.

Table 6.1 – Description of the vegetation types associated to a soil profile. List of the eight vegetation types among which the 46 soil profiles are distributed and description of their main features: list of the dominant plant species (nomenclature according to Aeschimann et al., 1996), range of elevation, mean summer temperatures, annual precipitations, monthly moisture index, and the daily average of global potential shortwave radiation during summer months, claculated for the period 1961-1990 (Zimmermann and Kienast, 1999), study sites where the vegetation types were observed, number of soil profiles within each plant community, soil types (nomenclature according to IUSS Working Group, 2006) and humus forms encountered (nomenclature according to Jabiol et al., 2013). Values in brackets refer to medians.

Vegetation type	**Description**	**Dominant species**	**Elevation [m]**	**Summer temperature [°C]**	**Annual precipitations [mm]**	**Monthly moisture index [mm/month]**	**Summer solar radiations [KJ/m^2*day]**	**Site(s)**	**No. of soil profiles**	**Soil type(s)**	**Humus form types**
Calcareous grasslands	Generally steep and south-exposed slopes of the subalpine-lower alpine belt	*Carex sempervirens, Sesleria caerulea, Helianthemum nummulariums. s.l.*	1698-2099 (1774)	7.9-10.0 (9.6)	1590-1742 (1631)	715-918 (765)	27030-28545 (27879)	Morteys	10	Calcaric, Dystric and Eutric Cambisol	Oligomull, Dysmull
Subalpine pastures	Calcareous bedrock. Subalpine, mesotrophic to eutrophic pastureland	*Alchemilla vulgaris aggr., Poa alpina, Ligusticum mutellina*	1900-1981 (1945)	8.5-9 (8.7)	1661-1697 (1685)	838-1016 (953)	19512-28243 (20795)	Morteys	4	Dystric Cambisol	Eumesoamphi, Oligomull, Mesomull
Windy ridges	Mostly on calcareous bedrock. Wind exposed, short snow cover	*Elyna myosuroides, Agrostis alpina, Sesleria caerulea,* high lichens cover	2430-2697 (2595)	5.5-7.1 (6.1)	1396-1564 (1486)	806-945 (868)	21535-28447 (26233)	Rechy	4	Calcaric and Eutric Cambisol, Leptosol	Oligomull, Dysmull
Calcareous snowbeds	Calcareous bedrock. Concave topography and/or north aspect, long snow cover (> 9 months)	*Dryas octopetala, Ranunculus alpestris, Salix reticulata*	1966-2232 (2180)	7.2-8.6 (7.5)	1694-1773 (1742)	960-1022 (1011)	17080 - 27564 (25985)	Morteys	4	Dystric and Eutric Cambisol, Leptosol	Mesomull, Dysmull, Hyperlithic Parahumus
Siliceous subalpine grasslands	Siliceous bedrock. Subalpine pastureland below treeline	*Nardus stricta, Festuca rubra aggr., Anthoxanthum odoratum aggr.*	2312-2348 (2326)	6.4-6.6 (6.5)	2010-2024 (2019)	1188-1219 (1199)	27984-28902 (28574)	Grimsel	4	Entic and Umbric Podzol	Hemimoder, Dysmoder, Humimor
Siliceous alpine grasslands	Siliceous bedrock. Alpine grasslands above treeline	*Carex curvula, Leontodon helveticus, Helictotrichon versicolor*	2310-2682 (2560)	4.8-6.6 (5.9)	1482-2218 (2080)	832-1511 (1244)	20949-28418 (27207)	Grimsel, Rechy	9	Albic and Entic Podzol, Leptosol	Hemimoder, Dysmoder, Humimor
Typical snowbeds	Siliceous bedrock. Concave topography and/or north aspect, long snow cover (>9 months)	*Salix herbacea, Gnaphalium supinum, Carex foetida,* high bryophytes cover	2313-2685 (2489)	5.6-7.0 (6.6)	1422-2158 (1436)	779-1384 (855)	23479-27933 (25748)	Grimsel, Rechy	7	Albic and Entic Podzol, Gleysol, Leptosol, Regosol, Stagnosol	Oligomull, Hemimoder, Euanmoor
Wet snowbeds	Siliceous bedrock. Running water brought by small rivers or firn melting, or next to a lake, long snow cover	*Carex bicolor, Salix herbacea, Taraxacum alpinum,* high bryophytes cover	2468-2650 (2568)	5.8-6.8 (6.2)	1432-1513 (1482)	784-964 (911)	18153-26819 (26110)	Rechy	4	Gleysol, Leptosol	Euanmoor, Hemimor

Table 6.2 – Eighteen potential drivers of OM thermal stability subdivided following thematic categories, with the scale for the ordinal drivers and the units for the continuous ones, their range and indications on whether they were included in the linear mixed models (LMM) specific to each soil horizon, and their relative importance calculated with the IT-AIC analysis. Some drivers were excluded from the models to avoid collinearities or because they were not relevant in the soil horizon considered.

Category	**Potential drivers of OM thermal stability**	**Remarks**	**Scale or unit**	**Range (median)**	**Relative importance in litter horizons**	**Relative importance in mineral topsoil**	**Relative importance in mineral subsoil**
Site conditions	Mean summer temperature	Monthly average temperature (period 1961-1990)	°C	4.8-10 (6.6)	<0.01	0.08	<0.01
	Monthly moisture Index	Precipitation - potential evapotranspiration (period 1961-1990)	mm/month	715-1511 (866)	0.01	0.05	<0.01
	North-South gradient	Equals to *0 - cosinus [radian (Aspect)]*	-	From -1 (North) to 1 (South) (-0.03)	Collinear with solar radiation and Vegetation PC2 scores	0.03	<0.01
	Summer solar radiations	Global potential shortwave radiation	KJ/m^2*day	17080-28902 (27030)	Collinear with North-South gradient and Vegetation PC2 scores	<0.03	<0.01
Vegetation type	Vegetation PC1 scores	Proportion of acidophilous species	Scores on the PC1 axis of a PCA based on species composition	From -0.3 to 0.2 (0.05)	<0.01	Collinear with pH	0.49
	Vegetation PC2 scores	Proportion of hygrophilous species	Scores on the PC2 axis of a PCA based on species composition	From -0.2 to 0.2 (-0.01)	0.7	0.08	0.02
Soil properties	pH	For the litter layers, is the value of the first A horizon in the corresponding soil	-	3 - 7.9 (5.4)	Collinear with Vegetation PC1 scores	0.05	<0.01
	Presence of carbonates	For the litter layers, it corresponds to the presence of carbonates within the soil profile	0 (absence), 1 (presence)	-	0.03	0.04	0.01
	Clay	Mineral particles < 0.002 mm diameter	% of fine earth fraction	1.1-48.5 (4.3)	Not relevant	Collinear with Sand	Collinear with Sand
	Silt	Mineral particles 0.002-0.063 mm diameter	% of fine earth fraction	31.7-87.1 (57.7)	Not relevant	0.06	0.46
	Sand	Mineral particles 0.063-2 mm diameter	% of fine earth fraction	3.2-65.4 (22.9)	Not relevant	0.04	0.54
Humus form properties	Humus Index	Modified from Ponge *et al.,* 2002	2 (Mesomull & Euanmoor), 3 (Oligomull), 4 (Dysmull), 5 (Hemimoder & Amphi), 7 (Dysmoder), 8 (Hemimor & Humimor)	2-8 (4)	0.02	0.03	<0.01
	Waterlogged conditions	Presence of Anmoor humus forms (Jabiol *et al.*, 2013)	0 (absence), 1 (presence)	-	0.01	0.03	<0.01
	Rhizic humus form	Presence of more than 25% of dead or living roots in the total volume of the O and A horizons combined (Jabiol *et al.*, 2013)	0 (absence), 1 (presence)	-	Not relevant	<0.03	0.01
OM properties	TOC	Total organic Carbon concentration	% of fine earth fraction	0.45-59 (6.2)	<0.01	1	<0.01
	Hydrogen Index (HI)	Amount of hydrocarbons (HC) released relative to TOC	mg HC/g TOC	44.9-524.5 (267.3)	0.36	0.03	0.4
	Oxygen Index (OI)	Amount of CO and CO_2 released relative to TOC	mg CO+CO2/g TOC	107.8-464.6 (216.2)	<0.01	0.03	0.02
	C/N	Total Carbon / Total Nitrogen	-	7.3-70.2 (14.7)	0.73	0.08	Not relevant

6.3.1 Potential drivers of OM thermal stability

A total of eighteen quantitative variables in five categories (site conditions, vegetation type, soil properties, humus forms and OM properties) were chosen for their potential impact on OM stability (Table 6.2). The mean air temperature in summer (June to September included), the average summer solar radiation and the mean annual moisture index (precipitation-evapotranspiration) were extrapolated for each soil location from the Swiss meteorological stations (www.MeteoSwiss.ch) according to Zimmermann and Kienast (1999). The aspect was measured in the field with a compass and then converted to a "North-South (NS) gradient" by the formula:

$$NS_{gradient} = 0 - \cos\llbracket[radian(Aspect)]\rrbracket.$$

The vegetation type was taken into account by performing a principle component analysis (PCA) based on the species composition and cover (after Hellinger transformation) recorded at each study point. Scores on the first two axes (Appendix G2) were retained for subsequent analyses. The two resulting variables were respectively called Vegetation PC1 scores and Vegetation PC2 scores. Landolt ecological indicator values (Landolt *et al.*, 2010) expressing plant-specific requirements for soil pH (R) and moisture (F) were associated to each plant species of the dataset. Then, mean indicator values per plant inventory were calculated with the species cover as a weight. Finally, the Pearson's r correlation between the mean indicator values and the PC1 and PC2 scores of each plant inventory were calculated.

Soil properties included pH_{H_2O}, clay (<2 µm), silt (2-63 µm) and sand (63–2000 µm) percentages, the occurrence of carbonate (presence/absence of 10% HCl reaction). The humus form, i.e. the sequence of organic and underlying topsoil mineral horizons, represents the integrated effects of plant and decomposer communities, soil climate, pH, and root distribution. In this study, the humus form was represented by the Humus Index (modified after Ponge *et al.,* 2002) spanning from 2 (Mull) to 8 (Mor). The presence of waterlogged and rhizic conditions (binary variables) was assigned, respectively, to the histic Anmoor humus forms (Jabiol *et al.*, 2013) and to humus forms having more than 25% of dead or living roots in the total volume (Jabiol *et al.*, 2013). The OM properties consisted in the TOC concentration and three indices of OM quality: the HI and OI indices from Rock-Eval pyrolysis and the C/N ratio.

Finally, the relation between class variables and OM thermal stability was also investigated. Class variables included the soil parent material, pedogenic processes and horizon type (see Figure 6.4d, Appendix G6 & G8). The soil parent material was assigned using our field observations as well as existing geological and geomorphological maps (www.swisstopo.admin.ch). Pedogenic processes and horizon types were assigned on the basis of field description and results of soil lab analyses.

6.3.2 Statistical analysis

The litter (Oi horizon), topsoil mineral (A horizon) and subsoil mineral layers (set of E, B and C horizons) were considered separately in the statistical analyses. The Oe and Oa horizons were excluded because of their low frequency in the data set (respectively 6 and 4% of the samples).
An information theoretic framework based on the Aikaike's information criterion (IT-AIC, Burnham and Anderson, 2002) was employed in order to find the dominant factors influencing OM thermal stability in each layer. Contrary to the traditional null hypothesis testing (Anderson *et al.*, 2000), the IT-AIC approach fundamentally explores range of alternative hypotheses (a "model set") potentially associated to a certain phenomenon and highlights the strongest associations worthy of further investigations (Symonds and Moussalli, 2011).

In the present study, a model set of linear mixed-effects models (LMM) was built with the R-Index as dependent variable and the potential drivers of Table 6.2 as independent variables. The study sites were set as random effects in order to account for their potential influence on the dependent variable.
The independent variables (predictors) to be included in the models were scrutinised in order to avoid problematic collinearities. For each layer, groups of variables having a Spearman's rank correlation coefficient higher than 0.7 were identified, and only the most ecologically relevant variable within each group was retained. The model set was composed of every possible combination of the variables, including an intercept-only model. According to Harrell (2001), the number of predictor variables simultaneously considered in each model should not exceed 1/10 of the sample size to avoid over-parameterization. As the sample size of the litter layers was 33, the maximal number of predictors simultaneously considered in each model was set to 3. The same maximum number of predictors was used for mineral topsoil and subsoil horizons, although the number of samples was higher (77 and 69, respectively), to ensure that each analysis operated under similar constraints.

The models composing the set were then simultaneously compared and ranked by their AIC_C (modified version of AIC recommended for small sample sizes). The approximation power of each model was expressed as the difference (ΔAIC_C) between the AIC_C of the best model (the lowest AIC_C value) and the AIC_C value for each of the other models. The ΔAIC_C was then used to calculate the Aikaike weight (w_i) representing, for a given model, the probability to be the best approximating model within the model set. In this study, a "top model set" was created by subsetting the models that had a cumulative Aikaike weight of ≤0.95. Then, within the top model set, the relative importance of each variable was calculated by summing the Aikaike weights of the model(s) containing that variable. The factors having the strongest effect on the response variable were those with the highest summed Aikaike weights, i.e. having a relative importance tending towards 1 (Burnham and Anderson, 2002).

The relationship between the response variable (R-Index) and the factors having the highest relative importance was measured by the Pearson's correlation coefficient and its 95% confidence intervals. The lower the confidence interval width, the higher the probability of the Pearson's correlation coefficient to correctly reflect population correlation.

Finally, the role of class variables (soil parent material, pedogenic process, horizon type) on OM thermal stability, which could not be evaluated through the IT-AIC analysis, was investigated using a one-way analysis of variance (ANOVA).

Diagnostics for assumptions of normality, homoscedasticity, and goodness-of-fit were performed on residual plots. For significant effects, pairwise t-test without adjustment for multiple inferences (Webster, 2007) were performed to identify significant differences between R-Index means. The alpha level for significance was set to α = 0.05 for all tests.

6.4 Results

6.4.1 Thermal stability of the OM increases with depth in the soil profile

The R-Index, i.e. the proportion of refractory compounds in the pyrolysed OM, increased with depth in the soil profile, from litter to topsoil and subsoil mineral layers (Figure 6.1). In contrast, the I-index, a proxy for preservation of "fresh" or "labile" compounds (Sebag *et al.*, 2016), decreased with depth. This progressive increase in OM thermal stability with depth was observed in each of the eight vegetation types (Appendix G1).

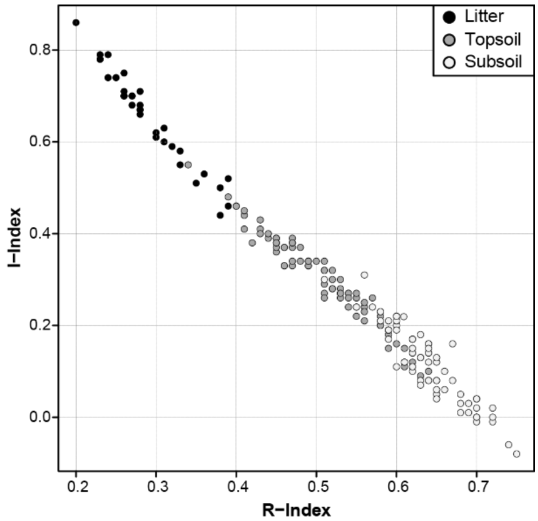

Figure 6.1 - Co-variation of the R- and I-indices through the different soil layers with increasing depth. Rock-Eval I/R plot (Sebag et al., 2016) of samples from litter (Oi horizons), topsoil mineral (A), and subsoil mineral layers (E, B and C horizons). The I-Index and R-Index represent the proportion of 'labile' and 'refractory' compounds in pyrolysed OM, respectively.

6.4.2 Factors influencing OM thermal stability in the litter layer

According to the IT-AIC analysis, OM thermal stability in the litter layer was mainly related to the OM stoichiometry (C/N ratio and hydrogen index, HI) and vegetation type (Figure 6.2).

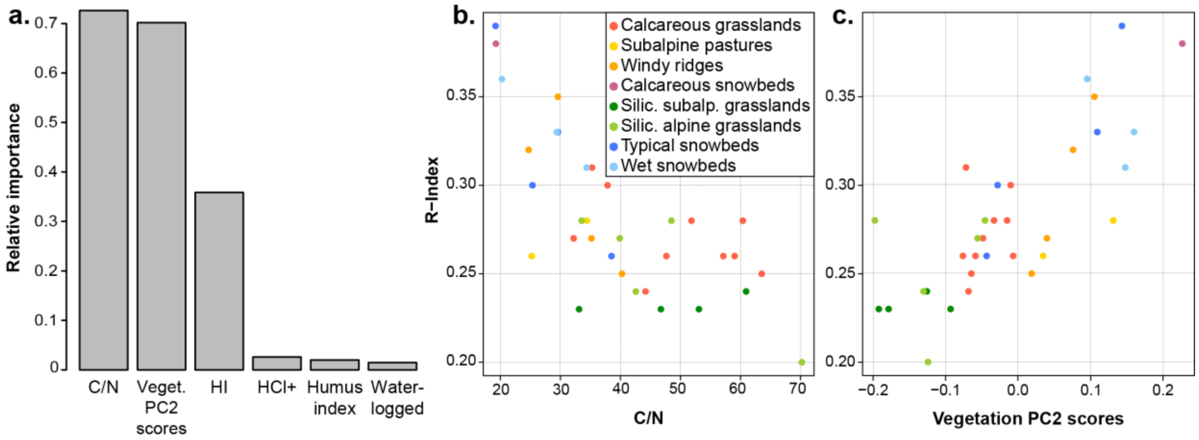

Figure 6.2 - Drivers of OM thermal stability in the litter layer. **(a)** The six main predictor variables influencing the R-Index in the litter layers, ranked by their relative importance. “Veget. PC2 scores”: scores on the 2nd axis of a principle component analysis based on vegetation composition and cover, corresponding to a gradient of increasing contribution of hygrophilous species; “HI”: Hydrogen Index, amount of hydrocarbons released relative to the total organic C content; “HCl+”: visible effervescence upon strong acid addition due to the presence of carbonate in the soil; **(b and c)** R-Index values plotted against the two most important predictors, C/N and Vegetation PC2 scores. Colours represent the eight plant communities. “Silic.”: siliceous. “subalp.”: subalpine.

The vegetation type in our analysis was represented by two variables, namely “Vegetation PC1 scores” and “Vegetation PC2 scores”, corresponding to the first two principal components of a multivariate dataset containing plant species composition and cover (Appendix G2). To facilitate interpretation of these principal components, we calculated the Pearson’s correlation coefficient between Landolt ecological indicator values (Landolt *et al.*, 2010) and vegetation PC1 and PC2 scores. Landolt’s R value, corresponding to an increasing preference for alkaline soils, correlated strongly and negatively with Vegetation PC1 scores (Pearson’s r= -0.88, 95% confidence interval = -0.93 < r < -0.80). Landolt’s F value, corresponding to increasing requirement for soil moisture, was positively correlated with Vegetation PC2 scores (r= 0.54, -0.30 < r < -0.72). Vegetation PC1 scores were thus mainly related to the proportion of acidophilic species and separated plant communities typically associated with calcareous versus siliceous substrates. Instead, Vegetation PC2 scores reflected in part the contribution of hygrophilous species and distinguished grasslands from snowbeds.

The R-Index of the litter samples correlated negatively with the C/N ratio (r = -0.72, -0.85 < r < -0.50) and positively with Vegetation PC2 scores (r = 0.79, 0.61 < r < 0.89). The Hydrogen Index (HI), representing the proportion of hydrogen (H) relative to C atoms in OM, ranked as the third most important factor. Similarly to C/N, the relationship between HI and the R-Index was negative (r = -0.65,

-0.81 < r < -0.39; Appendix G3). The litter from snowbeds showed the lowest C/N ratios and HI values but the highest OM thermal stability.

6.4.3 Factors influencing OM thermal stability in the mineral topsoil

In the topsoil (A horizons), thermal stability of the OM was predominantly related to its concentration (Figure 6.3).

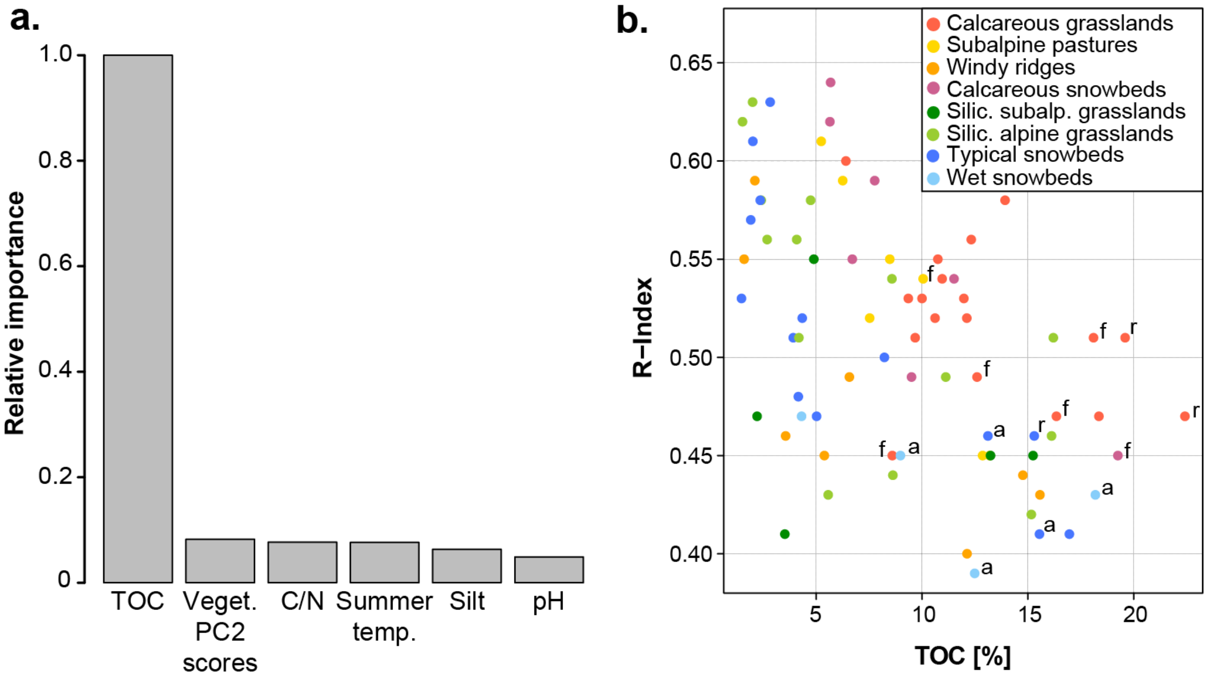

Figure 6.3 - Drivers of OM thermal stability in the mineral topsoil. **(a)** The six main predictor variables influencing the R-Index in the topsoil, ranked by their relative importance. “TOC”: total organic C concentration; “Summer temp.”: mean summer temperature; “Silt”: % of mineral particles having a diameter between 0.002 and 0.063 mm **(b)** R-Index values plotted against the most important variable, the organic C concentration (TOC %). Colours represent the eight plant communities, while letters represent peculiarities of the A horizon. “a”: hydromorphic A (Anmoor in Jabiol et al. (2013); “r”: rhizic humus form, presence of > 25 % of dead and living roots in the total volume of O and A horizons combined (Jabiol et al., 2013); “f”: fragmented litter homogeneously mixed with fine earth fraction.

The correlation between the R-Index and total organic C (TOC) concentration was negative and relatively weak (r = -0.51, -0.66 < r < -0.32). When the topsoil was OM-rich (TOC > 10%), the OM thermal stability was relatively low. In some cases, these OM-rich A horizons were water-saturated for more than six months per year and displayed a hydromorphic humus type (classified as Anmoor; Jabiol et al., 2013). In others cases, the OM-rich A horizons had a large proportion of roots, and finally some of them presented a certain amount of fragmented litter homogeneously mixed with the fine earth fraction, likely resulting from bioturbation.

It has to be noted that 28 of the 46 soil profiles presented several A horizons. In these cases, the OM of the most surficial A horizon systematically had a lower thermal stability than the underlying one (Appendix G4), indicating increasing proportions of thermally stable OM with depth. When only the topmost A horizons were considered in the IT-AIC analysis, the relative importance of OM concentration decreased but it still remained the primary factor influencing OM thermal stability (not shown).

6.4.4 Factors influencing OM thermal stability in the mineral subsoil

The OM thermal stability in the subsoil was negatively related to the sand content and positively to the proportion of acidophilic species (Vegetation PC1 scores; Figure 6.4b and c), but the correlation remained weak in both cases ($r = -0.33$, $-0.52 < r < -0.10$ and $r = 0.25$, $0.01 < r < 0.46$, respectively). Silt and HI ranked respectively as third and fourth most important predictors (Figure 6.4a; Appendix G5).

The correlation between the R-Index and the texture variables (sand and silt proportion) and HI was mainly driven by three eluvial (E) horizons, which were particularly sandy. If these three samples were removed from the analysis, the importance of texture and HI was reduced and Vegetation PC1 scores became the most important predictor, followed by sand and silt proportions (not shown).

This study taking place in the alpine environment, with little human activity, the respective vegetation type reflected each site's ecological conditions. Vegetation PC1 scores could thus be considered as a proxy for soil geochemistry, as determined by the nature of the geological substrate and pedogenic trajectory (Appendix G6). The nature of the geological substrate indeed explained 74% of the variance in Vegetation PC1, while the pedogenic trajectory explained 62% of the variance in Vegetation PC1. This interpretation is confirmed by the correlation between Vegetation PC1 and soil pH (Appendix G7).

Soil geochemistry was best represented by class variables that were not suited to the IT-AIC analysis. We therefore conducted a separate analysis of variance to test the effect of geological and soil classes on the R-index of subsoil horizons (Appendix G8). Geological classes explained 19% of the variance in the R-index, with samples associated with Si-rich lithologies having a significantly higher R-index than samples associated with calcareous or mixed lithologies. Soil classes explained 26% of the variance in the R-index, with ferric podzols having a significantly higher R-index than other soils.

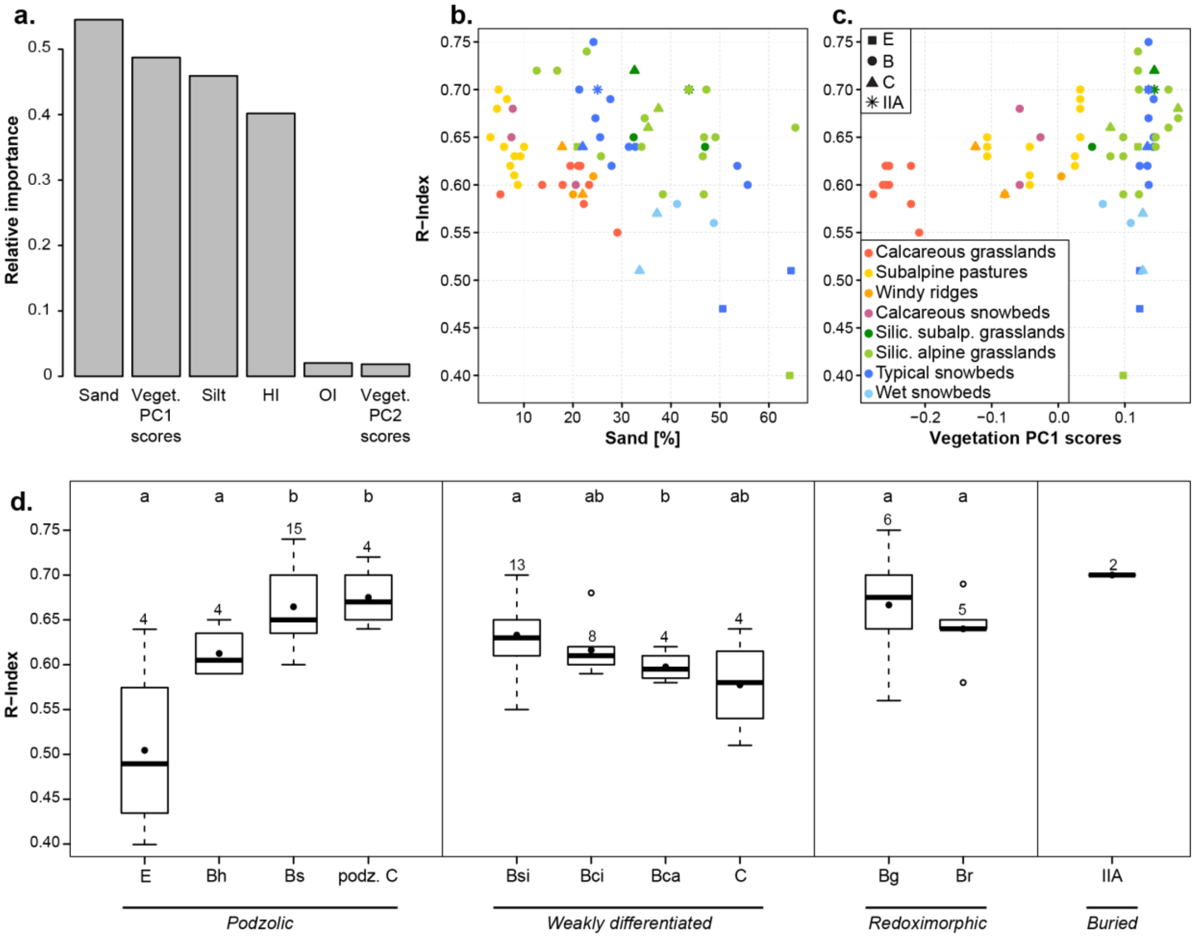

Figure 6.4 - Drivers of OM thermal stability in the mineral subsoil **(a)** The six main predictor variables influencing the R-Index in the subsoil, ranked by their relative importance. “Veget. PC1 scores”: scores on the 1st axis of a principle component analysis based on vegetation composition and cover, corresponding to gradient of increasing contribution of acidophilous species and here considered as proxy for soil geochemistry. **(b and c)** R-Index values along the gradient of the two most important variables, Sand proportion and Vegetation PC1 scores. Colours represent the eight plant communities and symbols represent the horizon categories. **(d)** Boxplots of R-Index by mineral horizon types. The first four horizon types represent the podzolic soil sequence, including “E” (eluvial horizon); “Bh” (illuvial accumulation of organic matter), average pH = 4.7; “Bs” (illuvial accumulation of sesquioxides), average pH = 4.9; “podzolic C” (horizon weakly affected by pedogenic processes and underlying a podzolic profile). The next four horizon types are found in weakly-developed solums, such as Cambisols, Leptosols, and Regosols, and include: “Bsi” (siliceous, low Ca saturation), average pH=5.7; “Bci” (absence of Ca-carbonate but high Ca saturation), average pH = 6.7; “Bca” (presence of calcium (Ca) carbonate), average pH = 7.5; “C” (underlying horizon weakly affected by pedogenic processes). The next two horizon types are found in soils with expressed redoximorphic features and include “Bg” (stagnic conditions) and “Br” (strong reducing conditions) horizons. The last class “IIA” refers to buried A horizons (FAO, 2006). Black dots represent the mean values, the black line is the median, and boxes are limited by 1st and 3rd quartiles. Numbers of observations are indicated above boxplots. Letters above boxplots indicate significant differences (p-value < 0.05) within each group of horizons, calculated by pairwise t-test.

Moreover, thermal stability of subsoil layers varied according to the type of horizon considered (Figure 6.4d) and the pattern was not reducible to horizon depth, as could be observed in the topsoil (Appendix G4).

E horizons showed the lowest R-Index values, reaching the same range of thermal stability displayed by the A horizons (Figure 6.3), while buried A horizons (IIA; corresponding to fossil soils) showed among the highest R-index values. B and C horizons showed intermediate values on average. Significant differences could be noted according to the different pedogenic processes at work: in podzolic profiles, OM thermal stability increased dramatically from eluvial (E) to illuvial horizons and was highest in horizons dominated by the accumulation of sesquioxides (E ~ Bh < Bs ~ podzolic C). In moderately developed soils, thermal stability slightly increased from carbonate-rich to non-carbonate horizons (Bca < Bsi). In redoximorphic horizons, OM thermal stability was generally variable and within range of other acid B and C horizons.

The horizon type and the associated pedogenic process were therefore shown to affect the OM thermal stability of the mineral subsoil layers.

6.5 Discussion

Due to its complex topography, geology, and geomorphology, the Alpine environment generates steep natural gradients of vegetation, soil moisture, texture, and geochemistry over very short spatial scales. This natural variability was used to explore controls on OM thermal stability.
Study sites displayed a small climatic gradient (restricted region in the Alps and limited elevation range) and climate-related variables (mean summer temperature, moisture index, and solar irradiance) were not found to be important predictors of OM dynamics in the data set. Furthermore, anthropogenic impact on these soils could be discounted as they have never been ploughed, but have been used only for extensive pasture.

The stability of OM was represented by the Rock-Eval R-index, which gives a snapshot of the proportion of thermally refractory compounds found within the OM. The use of Rock-Eval pyrolysis allowed us to evaluate OM properties similarly across all soil layers without applying any pre-treatment, and thus eliminated the risk of creating experimental artefacts. As expected from results of other studies employing Rock-Eval analysis (Sebag *et al.*, 2016 and references therein), we found that the contribution from thermally stable OM progressively increased with depth in the soil profile (Figure 6.1). This is in accordance with the generally accepted idea that in the absence of perturbations, soil OM stability and residence time tends to increase with depth (van der Voort *et al.*, 2016).

However, the R-index of subsoil horizons retained significant variability (Figure 6.4d and Appendix G1). Moreover, differences in subsoil horizons could not be predicted from differences observed in the litter layer or even the A horizon. As an example, wet snowbeds had relatively high R-index values in the litter layer, but showed the lowest values in mineral horizons; siliceous subalpine grasslands had among the lowest R-index values in the litter and topsoil horizons, but they showed the highest values in the subsoil (Appendix G1). This indicates that soil OM transformation, as represented by changes in OM thermal properties, follows diverging trajectories with depth in different edaphic environments. In the next sections, we will explore the factors influencing OM thermal stability in each major soil layer (litter, topsoil, and subsoil).

6.5.1 Litter layer

In the litter layer, thermal stability of OM varied according to its stoichiometry (C/N and Hydrogen Index – HI) and to the plant community producing it (Vegetation PC2 scores). Variability of the C/N and HI in the litter layer can be inherited from the initial biochemical OM composition (Barré *et al.*, 2016; Sebag *et al.*, 2016), or rather be a result of the litter mineralisation degrees.

The variations in C/N ratios recorded in this study were driven by differences in N contents (Appendix G9). The N enrichment in some litter types might stem from various plant properties, such as highly efficient N uptake mediated by mycorrhizal fungi or N-fixing capacity. These characteristics were observed in some plant species of snowbeds (Mullen *et al.*, 1998) and mosses (Woolgrove and Woodin, 1996a), furtherly enhanced by N accumulation in the snowpack, acting as a scavenger of air pollution (Knutson *et al.*, 1976).

Furthermore, as N accumulation (Aber and Melillo, 1982; Manzoni *et al.*, 2008) and OM dehydrogenization (loss of H bonds) typically occur during decomposition (Barré *et al.*, 2016), low C/N and HI values may also indicate a more advanced mineralisation degree. The simultaneous increase of the litter thermal stability and the proportion of hygrophilous species may indeed indicate that longer periods of snow cover favour decomposition (Baptist *et al.*, 2010; Hobbie and Chapin, 1996) and selectively preserve thermally resistant components (Sebag *et al.*, 2016). The increase in the R-index, concomitant with the increase in N and decrease in H content of the litter, corroborates the conventional view, according to which OM properties are controlled by the quality of the inputs, modulated by selective preservation of certain compounds.

6.5.2 Mineral topsoil layer

In the A horizons, the main factor influencing OM thermal stability was the amount of soil OM, which is in turn related to the balance between mechanisms governing the fresh OM inputs and those hampering its mineralization or deep translocation.

This study showed that when topsoil layers were water saturated for long periods, as indicated by the presence of hydromorphic humus forms (Figure 6.3), the OM remained in a thermally labile state, probably because of a limited access to oxygen, and therefore a reduced activity of some enzymes essential for OM decomposition, such as phenol oxidase (Freeman *et al.*, 2001). Similarly, the OM stability was low when relatively high amounts of fresh organic material was delivered to the topsoil layers via plant roots and fragmented litter. In the same way, Sebag *et al.* (2006) observed lower Rock-Eval R-indices in soil layers under dense plant cover (large inputs) comparing to sparse vegetation (low inputs). Therefore, quantity of the inputs, instead of quality, appears to determine the OM stability in topsoils.

A possible explanation involves the efficiency of the decomposer community. Even if litter contains biochemical resistant substances, the soil decomposer community and the type of enzymes produced are generally well-suited for their decomposition (Ekschmitt *et al.*, 2005). However, it has been suggested that above a certain amount of substrate availability, the enzyme efficiency could reach saturation, and the energy gain from decomposition products would be insufficient to sustain enzyme production (Schimel and Weintraub, 2003). As a consequence, in the presence of large inputs of litter, the soil OM may accumulate in the topsoil in a labile form.

On the other hand, when plant litter inputs do not exceed the threshold for maximum enzyme efficiency, decomposition could be relatively effective. In this case, labile components can be rapidly mineralised, while the remaining recalcitrant components would instead be decomposed by slow-growing microbial types (Fontaine *et al.*, 2003). This could explain why, in our study, topsoils with > 15% TOC showed low average OM thermal stability, while topsoils with lower concentrations in TOC had higher and more variable OM thermal stability (Figure 6.3).

Moreover, the potential for OM stabilization by interactions with mineral surfaces increases at low organic loadings (Six *et al.*, 2002). The effective preservation of partially oxidized, thermally stable compounds, on mineral surfaces could contribute to the increasing thermal stability of samples with low TOC.

Overall, our results indicate that thermal stability of OM in the topsoil mineral layers is mainly an emergent property stemming from the pedogenic environment, rather than an intrinsic property of OM molecular structure.

6.5.3 Mineral subsoil layers

In subsoil mineral layers, OM thermal stability was mainly influenced by the texture and the soil geochemical characteristics (as represented by Vegetation PC1). An additional analysis of variance confirmed that geological and pedogenic classes had a strong explanatory power on variations in the R-index of the subsoil (Appendix G8).

This result concords with a recent study of instantaneous OM mineralisation rates (represented by soil-surface efflux, also known as soil respiration) in mountain soils, which found that 17% of the variation in whole-soil respiration could be explained by soil classes (Grand *et al.*, 2016). In the subsoil, chemical properties of the mineral matrix are thus likely to be critical drivers of OM stability; yet, they are conspicuously absent from most models of soil OM cycling. Interestingly, we found that texture (% sand, silt, or clay) only had a very minor effect on the R-index of OM in subsoil layers once special pedogenic dynamics were accounted for, such as that associated with the E horizons of podzols.

Moreover, significant differences in OM thermal stability were observed between subsoil horizon types (Figure 6.4d). Differences between horizons could not be simply explained by an increase in the R-index with depth. We instead hypothesize that various stabilisation mechanisms, associated to specific pedogenic processes, could be responsible for the observed variations.

According to von Lützow *et al.* (2008), stabilisation mechanisms are indeed horizon-specific in Podzols. The potential for organo-mineral interactions is thought to be low in eluvial horizons, where long-chain alkyl structures could accumulate (Rumpel *et al.*, 2004), perhaps as a result of hydrophobic separation from decomposers. Complexation of organics with Al and Fe has been proposed as the main stabilization mechanism in Bh horizons while Bs and podzolic C horizons typically contain highly oxidized OM stabilised by organo-mineral interactions, such as ligand-exchange (Rumpel et al., 2004; Lützow et al., 2008). Interestingly, thermal stability of Podzol mineral layers measured in this study increased in the order E < Bh < Bs layers, however the difference between E and Bh horizons was not significant (Figure 6.4d). In accordance with the conceptual model outlined by Rumpel *et al.* (2004), a possible interpretation is that E horizons contained mostly C and H-rich, thermally unstable moieties (Appendix G10), while Bh and Bs horizon were enriched in partially dehydrogenated, thermally stable molecules. Moreover, our results might suggest that OM interaction with metals, believed to dominate in Bh horizons, have a weaker effect on OM properties than interactions with poorly crystalline oxides and aluminosilicates, expected in Bs horizons.

A potential stabilisation mediated by Ca was less apparent (Figure 6.4d), but OM present in Ca-rich horizons (Bca) was more thermally labile, and thus perhaps less processed, than the OM present in Ca-poor horizons (Bsi). This may indicate that aggregation (Muneer and Oades, 1989), and the heterogeneous protection of both thermally labile and refractory OM by occlusion within aggregates (Popleau et al., *in review*), were more pronounced in Ca-rich horizons. Redoximorphic processes (Bg and Br horizons) were not associated with a specific OM thermal signature, perhaps due to the typically seasonal nature of waterlogging in alpine soils.

Overall, our result strongly support a dominant role of the geochemical properties of the mineral matrix on OM dynamics in the subsoil. Further detailed investigation is needed to establish whether the thermal resistance measured by Rock-Eval pyrolysis is indeed reflective of the type of organo-mineral association involved.

6.5.4 The decoupling

As previously proposed by Salomé *et al.* (2010), this study confirms a substantial decoupling between organic, topsoil, and subsoil mineral horizons in terms of factors governing OM dynamics. This study also confirms the repeated findings of litter bag experiments (e.g. Preston *et al.*, 2009) showing that the

intrinsic properties of OM (litter source, stochiometry) play a role at the beginning of the OM decomposition continuum (Lehmann and Kleber, 2015), in the litter layer, before any pervasive opportunity for interaction with the mineral matrix.
However, in the topsoil and subsoil mineral layers, OM properties are determined by the pedogenic environment, rather than being an intrinsic property driven by its initial composition. In these layers, the vegetation type plays an indirect role on soil OM thermal stability by determining the rate of plant inputs entering the soil system and its vertical distribution along the soil profile (Jobbagy and Jackson, 2000), rather than by determining its quality. As observed in many studies (Kögel-Knabner *et al.*, 2008; Rumpel *et al.*, 2002), soil OM stability in subsoil horizons seems to be driven by the types and intensity of organo-mineral interactions and physical protection from decomposers.

Building upon the theoretical framework of Schmidt et al. (2011), field observations and Rock-Eval pyrolysis have illustrated that OM dynamics in soils are related to biological (amount of plant roots, presence of bioturbation), and edaphic properties (conditions of water saturation, presence of polyvalent cations, reactive mineral surfaces). By taking into account the biological (plant species inventories), geological and geochemical contexts, this study broadly demonstrated that OM dynamics resulted from a complex interplay between ecosystem properties and those horizon-resolved; consequently, multi-disciplinary approaches are key to the understanding and the prediction of soil OM fate in a changing world.

6.5.5 Long-term implications

It is generally thought that global warming will increase organic C mineralisation in soils (Leifeld *et al.*, 2009; Schimel, 1995). The present study suggests that the effects of climate change will not be reducible to changes in OM mineralisation rates as a result of the temperature-dependency of enzymatic degradation (Q10-effects); indeed, pure Q10-effects are likely to be of minor importance when compared to broader ecosystem consequences.
For instance, higher temperatures and the consequent shortening of snow cover may affect the soil OM mineralization rates in contradicting ways. The reduction of insulation by the snowpack might reduce mineralization in the winter season (Saccone *et al.*, 2013). However, by reducing the duration of waterlogging conditions, hydromorphic topsoils could progressively dry out and OM degradation could increase. Moreover, the way in which changes in climatic conditions will affect OM dynamics in the deep soil, where interactions with the mineral matrix are of prime importance, is highly uncertain. Changes in pedogenic trajectories could indeed result in drastically altered conditions for OM stabilisation in the subsoil. This constitutes a critical research gap which undermines our capacity to predict the future of OM storage in soils.

Aknowledgments

We thank Marie-José Petétot for her help in plant inventories and soil descriptions of the Morteys site, and analysis of the relative soil samples. We thank also Loïc Liberati, Swanee Messerli, Jessica Rion, Aurélie Rubin, Ayumi Koishi, Yohan Ancey and Jérémy Tritz for their help in the field, pH measurements and sample preparations. Dr. Thierry Adatte (ISTE, University of Lausanne) performed Rock-Eval and CHNS analyses. We are grateful to Aline Buri for her suggestions on statistical analyses. The “Fondation Herbette” kindly supported Dr. David Sebag during his stays at the University of Lausanne.

7 Synthesis

As I write these lines, Switzerland is experiencing in 2017 the 3rd warmest summer since the beginning of weather measures in 1864 (www.meteosuisse.admin.ch), with a mean summer temperature 1.9 °C higher than the reference period 1981-2010. Only the summers 2003 and 2015 have been warmer (+3.6 and 2.3 °C, respectively). In the Swiss Alps, December 2016 was the driest since 1864 and the sunniest since 1959. As a consequence of this dry and mild weather, the snowline in the Alps in December 2016 was at ca. 2000 m, and the snow depth at 2500 m amounted to 20-30 cm only (MétéoSuisse, 2016). These data do not represent isolated records, but they witness a trend of increasing temperatures and decreasing snow precipitations that started already at the end of the XXth century, and that is projected to continue in the present century, especially at high elevations (Pepin *et al.*, 2015). High elevation ecosystems are considered particularly vulnerable to climate change (IPCC, 2014). Modest changes in mean annual temperature may significantly alter the elevation-controlled distribution of plants and vegetation (Theurillat *et al.*, 1998). Climatic parameters being fundamental in the maintenance of several mountain ecosystems, these are quite sensitive and highly vulnerable to climate changes. Deterioration of alpine ecosystems may bring important biodiversity losses and socioeconomic consequences (Diaz *et al.*, 2003).

Most of the long-term studies on climate change effects focused on upper alpine and nival belts or the treeline ecotone. Conversely, the subalpine-alpine herbaceous plant communities have been poorly investigated so far. Furthermore, these ecosystems were also poorly known under a soil perspective. Soils are worth to study as they generate a significant diversity of ecosystem services, including physical support to plants, nutrient and organic C cycling, hydrological control, biodiversity and biological activity (FAO, 2015). These functions are currently threatened in mountain ecosystem, which are affected by climate and land-use changes in a unprecedented way (FAO, 2015). Mountain soils represent also extremely rich OM-stocks (Leifeld *et al.*, 2009; Sjogersten *et al.*, 2011), whose sensitivity to recent climate changes is still unclear. Within the soil profile, the humus form represents the centre of plant-soil interactions, litter degradation, and is a pathway to most geochemical cycles. The study of alpine humus forms, soil OM properties, and the main environmental factors influencing them, may significantly improve our understanding of the subalpine-alpine ecosystem functioning and, thus, its response to climate changes.

This research aimed to assess the response of different subalpine-alpine vegetation types to recent climate changes and to estimate the consequences of such responses on soil organic matter dynamics and on the distribution of humus forms. The main outcomes are highlighted by thick arrows in Figure 7.1.

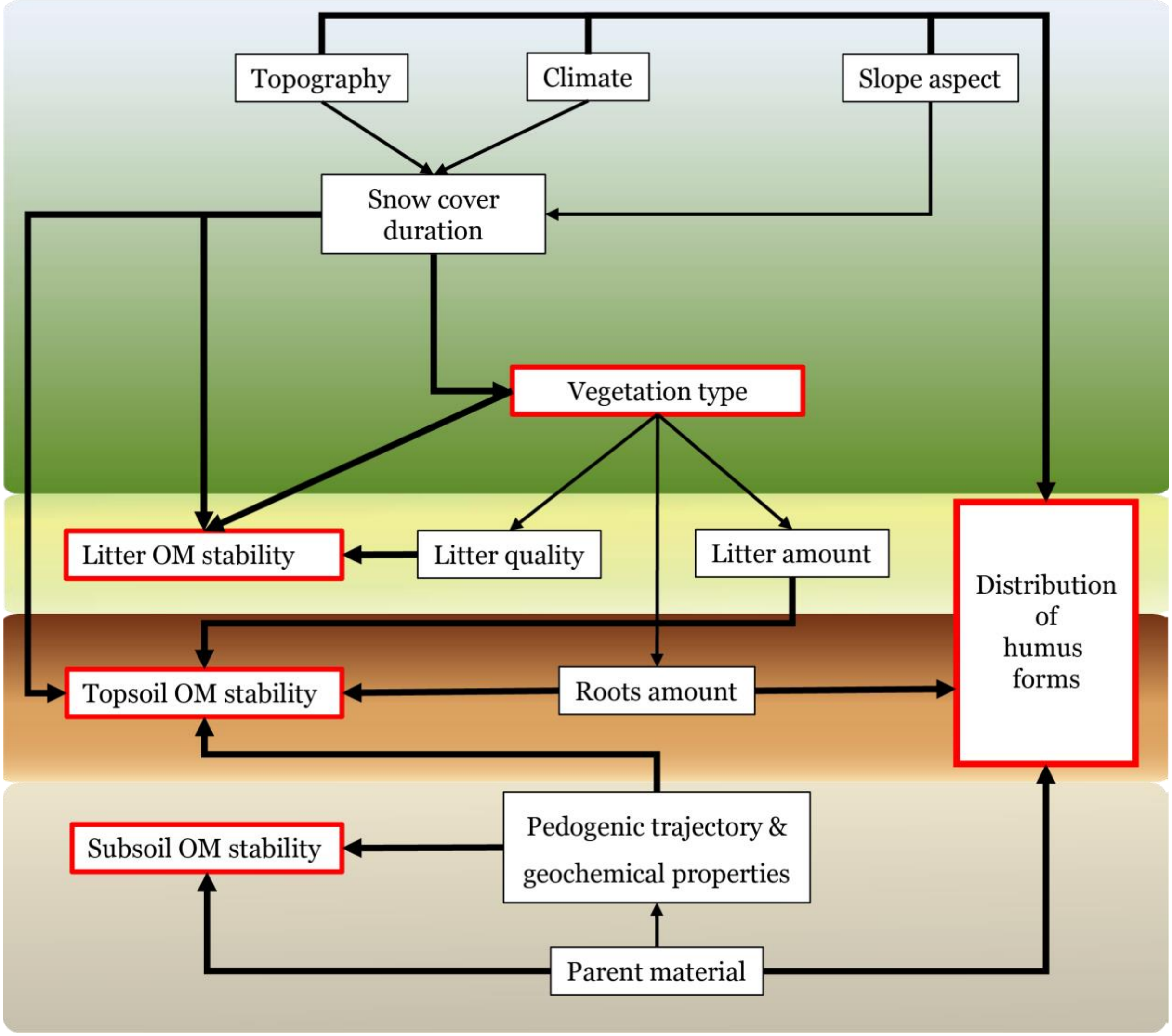

Figure 7.1 – Summary diagram reporting the main findings of this study. Red boxes : objects targeted by this study and for which the main drivers were investigated. Black boxes : ecosystem factors having an effect on the targeted objects. Thick arrows : relationships between targeted objects and ecosystem factors that were highlighted by this study. Thin arrows : relationships between components that were assumed and not demonstrated by this study.

The main changes were observed in vegetation types closely related to the snow cover duration: the typical snowbeds showed a marked shift of species composition and cover towards the siliceous alpine grasslands, while the wet snowbeds tended towards the typical snowbeds. This was likely a consequence of climate warming and reduced snow precipitations that, combined, induced earlier snowmelt dates. It is certain that the snow cover duration is also related to topography and slope aspect, however, being these parameters unchangeable in the short to middle term, the climate remains the unique driver of snow cover duration.

Recent climate changes appeared to have no direct effects on those vegetation types less related to the snow cover duration. Indeed, calcareous and siliceous grasslands demonstrated a stability of species composition and cover, whatever the bedrock type. The dense plant cover and the important belowground phytomass characterizing the grassland vegetation increase the competition for light and soil resources, which hampers the establishment of new seedlings. Moreover, grasslands plant species are characterized by high longevity, clonal growth, and persistent shoots and root systems. These properties induce long-term persistence and continuous recolonization of existing gaps.

The distribution of humus forms was mainly controlled by climate, lithology of the soil's parent material, topography and slope aspect. Mulls were mostly found on calcareous parent materials, at lower elevations, south-exposed, and therefore warmer sites. On the contrary, Moder and Mors were associated to siliceous materials and colder sites. Roots were abundant in humus forms located on slopes, while humus forms presenting waterlogging conditions were exclusively found in depressions. Interestingly, the vegetation type appeared to play a secondary role in the humus form distribution, but it still influenced the litter quality, here expressed by the C/N ratio. Indeed, both calcareous and siliceous grasslands were characterized by higher C/N values in their litter samples than any other plant communities. With such high C/N values, a low degradability potential is expected for the grassland litter. However, Mull forms, indicating efficient decomposition, were observed in association with calcareous grasslands. This furtherly confirmed that the humus form development weakly depends on the litter degradability, but rather on environmental factors.

The study of OM thermal stability provided consistent results with the study of humus forms. Indeed, the vegetation type and the litter quality (here represented by the C/N ratio) were the main environmental controls of OM thermal stability in the litter layer, whereas they were of minor importance in the top- and subsoil horizons. Litter from snowbeds showed the highest levels of thermal stability, while those from siliceous grasslands the lowest. It was hypothesized that litter degradation in the snowbed was relatively efficient because of an initial OM biochemical composition favourable to degradation (role of litter quality) and because of the protection from freezing temperature provided by the snowpack (role of snow cover duration). As a consequence, the mineralisation degree of snowbed litter samples, collected in summer, after snowmelt, was probably at an advanced stage. On the contrary, grassland litter, inherently more resistant to degradation (high C/N) and less protected by the long snow cover, was probably less degraded at the collection period and thus still richer in thermally labile compounds.

OM thermal stability in the topsoil mineral horizons was influenced instead by the balance between factors controlling its inputs and those hampering its mineralisation or deep translocation. Thermal stability was relatively low when large amounts of fresh OM were provided into the topsoil by plant roots, their exudates, and fragmented litter (role of litter and root amount). Similarly, thermal stability was low when waterlogging conditions, consequence of a long snow cover, prevented its transformation and decomposition. In absence of these conditions (water saturation, litter and root abundance), OM likely undergoes decomposition and the most thermally resistant components accumulate and/or are protected by interactions with mineral surfaces.

In subsoil layers, the geochemical properties of the mineral matrix exerted the major control on OM thermal stability. This was not homogeneous among subsoil horizons and significantly varied according to the specific pedogenic process at work. Specific stabilisation mechanisms, associated to the different pedogenic processes, were suggested as responsible of the observed variations.

This research clearly indicated a substantial decoupling between organic, topsoil, and subsoil mineral horizons in terms of factors driving OM dynamics. It was confirmed by field observations that the inherent properties of OM, linked to the vegetation type, are of minor importance for the OM dynamics in the mineral soil. However, if the vegetation type does not influence the OM dynamics by determining its quality, it does by determining the rate of plant inputs entering the soil system and its vertical distribution along the soil profile (Jobbagy and Jackson, 2000).

Building on the outcomes illustrated so far, it seems appropriate to return once more to the main questions of this study. Firstly, it was asked "how did subalpine-alpine vegetation respond to recent climate changes?" The response would be "it depends on the vegetation type considered". Indeed only snowbed vegetation showed pronounced changes. The second question was "what are the consequences of the potential vegetation shifts on soil OM dynamics?" As grassland vegetation did not show large shifts in species composition and cover, there is not evident reason to discuss how soil OM dynamics could evolve in these ecosystems. Instead, in the case of snowbed vegetation, the answer would be "soil OM dynamics can be affected by the vegetation shifts depending on the soil layer considered".

Indeed, it was demonstrated that the vegetation type was not an important driver of OM thermal stability in the mineral soil. Pedogenic processes and soil OM protection mechanisms were fundamental instead. Changes in vegetation will likely have an effect only at the litter level. The expansion of grassland species in the snowbeds will probably increase the mean C/N ratio of the litter and thus reduce its degradability potential. However, this does not directly imply a litter accumulation, since this will also depend on the soil insulation from extreme temperatures operated by the snowpack. As demonstrated by Serquet *et al.* (2013) the snowfall/precipitation ratio decreased by ca. 0.25% per year at the beginning and the end of the snow season from 1961 to 2008. Beniston *et al.* (2003) predicted that, with a temperature rise of 4°C in 2071-2100 (Christensen *et al.*, 2002), the snow volume in the Alps at 2000 m may be reduced by 50% and the melting season advanced by 50-60 days. With such projections, snowbed soils will experience progressively shorter periods of thermal insulation. This, combined with the supposed decrease in litter degradability potential (higher C/N ratios), may consequently reduce the litter degradation in snowbeds (Saccone *et al.*, 2013).

At the topsoil level, reduction of snow cover period may diminish frequency and magnitude of waterlogging conditions. Water saturation being a constraint on OM decomposition in the topsoil, the gradual drying of snowbed soils may make important amounts of fresh OM available to oxidation. Moreover, the expansion of some grassland species with particularly well developed root systems (e.g. *Nardus stricta, Carex curvula*), may provide large amounts of fresh, and labile, OM in the topsoils of snowbeds. The abundance of root exudates may also enhance the OM mineralisation in the rhizosphere by two mechanisms: first, root exudates represent a large source of labile C that can sustain the degradation activity of soil microorganisms (priming effect; Kuzyakov 2002); and second, some root exudates, such as oxalic acid, may liberate organic compounds from protection by mineral associations (Keiluweit *et al.*, 2015).

Vegetation changes will likely have very small effects on the subsoil OM dynamics. There, the OM thermal stability is mainly controlled by the pedogenic environment and the type of stabilisation mechanism. These factors are likely independent from the plant species composition. In order to discuss the future of deep soil OM, it would be more informative to identify controls of OM stabilisation and destabilisation processes (Sollins *et al.*, 1996; von Lutzow *et al.*, 2006).

What is the impact of the observed vegetation changes on the humus form distribution? As discussed above, changes in plant species composition of the snowbeds and a reduced snow cover period may lead to lower litter degradation rates. Will this favour the development of Moder and Mor forms? According to the present results, the humus form is mostly influenced by the lithology of the soil parent material and the climatic parameters. Therefore, a reduction of litter degradability should not determine a shift in the humus form, provided other environmental variables constant. The Mull forms associated to the calcareous grasslands despite their low litter degradability, confirm such hypothesis. The importance of climatic variables for the humus form development may question on the future of humus form under a warmer climate. However, the sampling strategy of this study does not allow to draw conclusions in this sense. Indeed, warmer sites (lower elevations) were all on calcareous parent materials, while higher and colder sites were mostly on siliceous ones. This correlation among lithology and climate prevent the assessment of their respective influence on the humus forms. Further studies investigating the influence of climate changes on humus forms should be careful to avoid this issue.

Finally, based on the present findings, what is the impact of climate changes on the soil organic C cycling in mountain ecosystems? Despite the assessment of soil organic C stock was not targeted by this research, some general considerations may be proposed. Subalpine-alpine grasslands did not display significant vegetation changes. Important variations of the C cycling in such ecosystem is therefore unlikely in short to middle term. Conversely, ecosystems related to long snow cover were identified as extremely sensitive to recent warming and snow precipitations decline. The expansion of grassland plant species, and the consequent progressive shift towards less degradable litter, may cause the OM accumulation at the soil surface, enhancing the C sink capacity of such soils. Moreover, the reduction of insulation by the snowpack might increase frost events, and therefore reduce mineralisation under snow. On the other hand, the release of waterlogging conditions will likely liberate considerable proportions of OM that will be available for oxidation. This can transform snowbed soils into a CO_2 source instead.

Aside from changes in soil water regimes, recent and projected climate changes include an increase in temperature. Temperature sensitivity of C stabilisation processes is still not well understood and not accurately quantified by the scientific community. Experimental approaches allowed the identification of a cohort of processes working simultaneously, such as accessibility of microorganisms to substrates, pH, water, oxygen and nutrient limitations (von Lutzow and Kogel-Knabner, 2009). This study confirms that factors influencing the outcome of OM in soils are numerous, horizon and soil specific, and highly interconnected. Multi-disciplinary approaches, as the present research, are key to understand and forecast soil OM fate in a changing world.

8 General conclusions and perspectives

The aim of this research was to investigate the relationships between subalpine-alpine vegetation and soil OM dynamics in the context of recent climate changes. In particular, the following questions were targeted in separate chapters:

- Chapter 5: (1) are there observable changes in the subalpine-alpine vegetation over the last 25-50 years in species richness and community composition in the Alps? (2) Do the magnitude and direction of changes vary across different plant communities and how? (3) What environmental factors best explain the observed changes?
- Chapter 6: (4) which soils and humus forms are associated to the main subalpine-alpine plant communities? (5) What are the determinants of their distribution in the alpine environment? (6) Are the existing classification criteria adapted to the alpine humus forms?
- Chapter 7: (7) what are the major determinants of OM thermal stability and how does their significance vary with soil depth?

The present research provided the following answers, respectively:

1. The species richness and composition of the subalpine-alpine vegetation did show changes over the last 25-50 years in the Alps.
2. Not all subalpine-alpine vegetation types reacted to recent climate changes. Both calcareous and siliceous grasslands showed high stability in terms of plant species composition and cover. On the other hand, vegetation types linked to long snow cover (snowbeds) showed pronounced changes. Several species, coming from the surrounding grasslands increased in frequency and cover.
3. The observed vegetation changes are likely a consequence of earlier melting dates and longer growing seasons.
4. The eight vegetation types displayed ten main groups of soil references and the same number of humus forms.
5. The plant community type played a secondary role in the humus form distribution, which was in contrast mostly defined by the lithology of the soil's parent material, the climate and the topography. Mull forms were observed along the whole elevation gradient of this study (1698-

2697 m), but mostly on lowest-elevation sites and on calcareous parent material. Moder and Mor forms, instead, were associated to the highest elevations and the siliceous parent materials. The concave topography was determinant for the occurrence of Anmoor forms. Roots were abundant in the investigated soils, particularly on steep slopes.

6. The existing keys for humus form identification proved partly unsuitable for the alpine ecosystem and some adaptations were suggested.
7. Ecosystem controls on soil OM dynamics differed substantially according to the soil layer considered. The vegetation type influenced OM stability in the litter layer, but not in the topsoil and subsoil. There, the supply rate of fresh organic material and the physical and chemical characteristics of the pedogenic environment appeared important instead.

The plant resurvey method, the one employed in this research, was suitable to identify vegetation types and plant species that are reacting more strongly to recent climate changes. However, the same method does not allow the understanding of mechanisms underlying such changes or, on the contrary, their absence. For example, why did the grassland communities show so little changes during the last decades? The dense plant cover characterizing this vegetation type has often been raised as a factor hampering the establishment of new seedlings (Choler *et al.*, 2001). In order to verify this hypothesis, plant seeds from lower elevations belt than the one under study could be sowed in grasslands with increasing plant cover, and the proportion of germination success recorded after a certain period. Moreover, the grassland stability may result from the presence of obstacles for the seed dispersion, such as a forest belt that separates sources of potential colonizers from the sink plant communities. This could be verified by comparing the proportion of species from low elevation grasslands (source) present in supplementary reinventoried subalpine-alpine grasslands (sink) distributed along a gradient of connection with montane grasslands. It is also possible that the weak vegetation changes observed so far represent just a first phase of the response to warming; and a second phase, characterized by strong and sudden changes, could follow after forest colonisation, successive years of drought, development of diseases (Ayres and Lombardero, 2000), or the arrival of new herbivores (Pellissier et al., 2014). A regular monitoring of alpine grasslands, based on permanent plots, as the ones established in this study, would allow this question to be addressed.

In the present study, a drought stress was hypothesized to explain several observations of dried turfs of *Elyna myosuroides* in, or around, the studied plots. However, it is difficult to evaluate the real desiccation stress at which alpine plants are submitted, as precipitations at these high elevations are rarely a limiting factor and alpine plants exhibit extreme tolerance to desiccation (Körner, 2003). The plant water supply also depends on the pattern of the rainfall distribution during the growing season, the soil structure, the plant cover, and the exposition to wind (Körner, 2003). Researches in this direction could be very pertinent in light of the increasing frequency of extreme drought events expected globally by the end of the 21st century (Calanca, 2007).

In snowbed vegetation types, the arrival of species from surrounding grasslands was interpreted as the consequence of earlier snowmelt dates. However, why were some grassland species better colonizers than others? The same question was addressed by many authors studying the upward movement of plant species in alpine summits, and some answers came from the analysis of plant functional traits (Matteodo *et al.*, 2013; Tackenberg and Stocklin, 2008; Vittoz *et al.*, 2009a). The same approach could be followed in snowbeds by comparing plant functional traits of good vs weak colonizing species. The functional plant traits represent a connection between the plant C strategy and biogeochemical cycling (Cornwell *et al.*, 2008; De Deyn *et al.*, 2008). Therefore, the study of plant functional traits could be relevant also for the understanding of present and predicted litter decomposition potentials among different vegetation types.

Many questions concerning the humus forms functioning are still pending because out of the scope of this research, or due to an inappropriate sampling design. First, what are the composition and functions of the macro-, meso-, and micro-fauna inhabiting the alpine topsoils in different vegetation types? Are there fluctuations in microbial population during the year?
The study of soil fauna and microorganisms could be addressed in several ways: directly by soil fauna extraction or DNA sequencing, followed by determination of taxa, and indirectly, by micromorphological observations of the fecal pellets, whose size and shape are family-specific (Bullock *et al.*, 1985). Thin layer sections of humus form horizons could be very helpful in this regards, as they provide a snap-shot of litter degradation status, with images of plant residues, fecal pellets, and mineral components and their spatial arrangement. Repeated observations of such thin layers during the growing season, and under different ecological conditions, could be highly informative on the functioning of humus forms.
The sampling strategy of this study was based on the availability of historical vegetation surveys. This, together with orogenic processes resulting in calcareous mountain ranges being at lower elevations than siliceous ones (Pfiffner, 2014; Stampfli, 2001), led to alkaline soils being mostly described at lower elevations (warmer temperatures) and acidic ones mostly at high elevations (lower temperatures). Mull forms appeared as mainly associated to calcareous parent materials and thus to warmer temperatures, while Moders and Mors to colder and siliceous sites. What is the respective influence of temperature and soil parent material in the humus form distribution? The study of humus forms of high alpine calcareous soils and subalpine siliceous grasslands would allow this question to be answered.

Both the description of humus forms and the study of OM thermal stability suggested the importance of the root system in the alpine carbon cycling. Is the belowground biomass contributing more than the aboveground one to the soil OM pool in the alpine ecosystems? Are there differences among vegetation types? What degradability (C/N) and thermal stability do the dead roots have? Are they determining the thermal stability signature of the topsoil OM? Are there differences of thermal stability between coarse and fine roots?

An attempt to answer these questions was made in this study, but was finally discarded for lack of time. Litter, aboveground and belowground biomasses were collected in 12 study plots, evenly distributed among three vegetation types (calcareous grasslands, siliceous alpine grasslands and typical snowbeds). Preliminary results indicated that the root density (Kg/m^2) was higher in calcareous grasslands than in other plant communities, and it exceeded aboveground biomass by a factor of 8 in each plant community. The difference with litter density was even higher, especially in siliceous alpine grasslands and typical snowbeds, where the root density was 35 and 24 times higher than litter one, respectively (only 7 times higher in calcareous grasslands). Rock-Eval and CHN analyses on the biomass, litter and root samples (coarse and fine separately) would then allow the thermal stability and the degradability of the three OM pools to be characterized.

Studying the belowground biomass is a challenging task, especially in the alpine ecosystem where soils are generally rich in skeleton and the root system is very dense. The root extraction from soil monoliths by washing-sieving procedure was employed in this study. This method is time-consuming and a large proportion of fine roots is inevitably lost during the process (Oliveira *et al.*, 2000), thus leading to underestimation of the belowground biomass. An alternative indirect method to study root biomass is the ground penetrating radar, which allows relatively large surfaces to be investigated in a non-destructive way. However, this method generally requires well drained sandy soil, with low OM and ion content, for an optimum accuracy (Addo-Danso *et al.*, 2016). These conditions are not fulfilled in the alpine soils, and several tests and calibrations would be needed prior to implement the method in the alpine system. In order to study root production, mini-rhizotrons are increasingly employed. This method, capturing root images at time intervals in a constant position, has the advantage to be non-destructive, time-efficient and allows studying root production along the year (Blume-Werry *et al.*, 2016).

As for aerial plant parts, root functional traits strongly influence ecosystem processes, such as C and nutrient cycling, and are crucial for soil formation and structural stability (Bardgett *et al.*, 2014). Their study in the alpine ecosystems would bring important knowledge on the biogeochemical cycles characterizing these soils.

The present research highlighted the importance of organo-mineral interactions for the thermal stability of OM in the deep soil. What will be the effect of climate warming on this stabilized fraction? What are the respective effects of warming and snow cover changes on the C stabilization mechanisms? Elevated CO_2 concentration in the atmosphere are considered to increase the amount of root exudates (Carney et al., 2007). Among the root exudates, the oxalic acid has been shown to unravel organo-mineral association, thus enhancing the microbial access to organic compounds and finally, their mineralisation (Keiluweit et al., 2015). Considering the high amount of roots present in the alpine soils, are these particularly prone to C loss? On the other hand, roots and their exudates likely represent an important C input for alpine soil. Is this input important enough to counterbalance the C output stimulated by root exudates?

In order to better understand the role of climate on soil OM dynamics, a study of soils along an elevation gradient, from mountainous forest to alpine grasslands, would be very informative. Research sites should be selected on homogeneous parent material, in order to discard its relative influence on the OM stabilisation processes.

Besides improving our knowledge of the alpine ecosystem functioning, the above mentioned research lines are crucial to forecast impacts of climate change on alpine vegetation and soils. Moreover, as a natural experimental laboratory, the alpine environment may provide findings and clues that can be, at least in part, extrapolated to a larger scale, also beyond boundaries of high elevation ecosystems.

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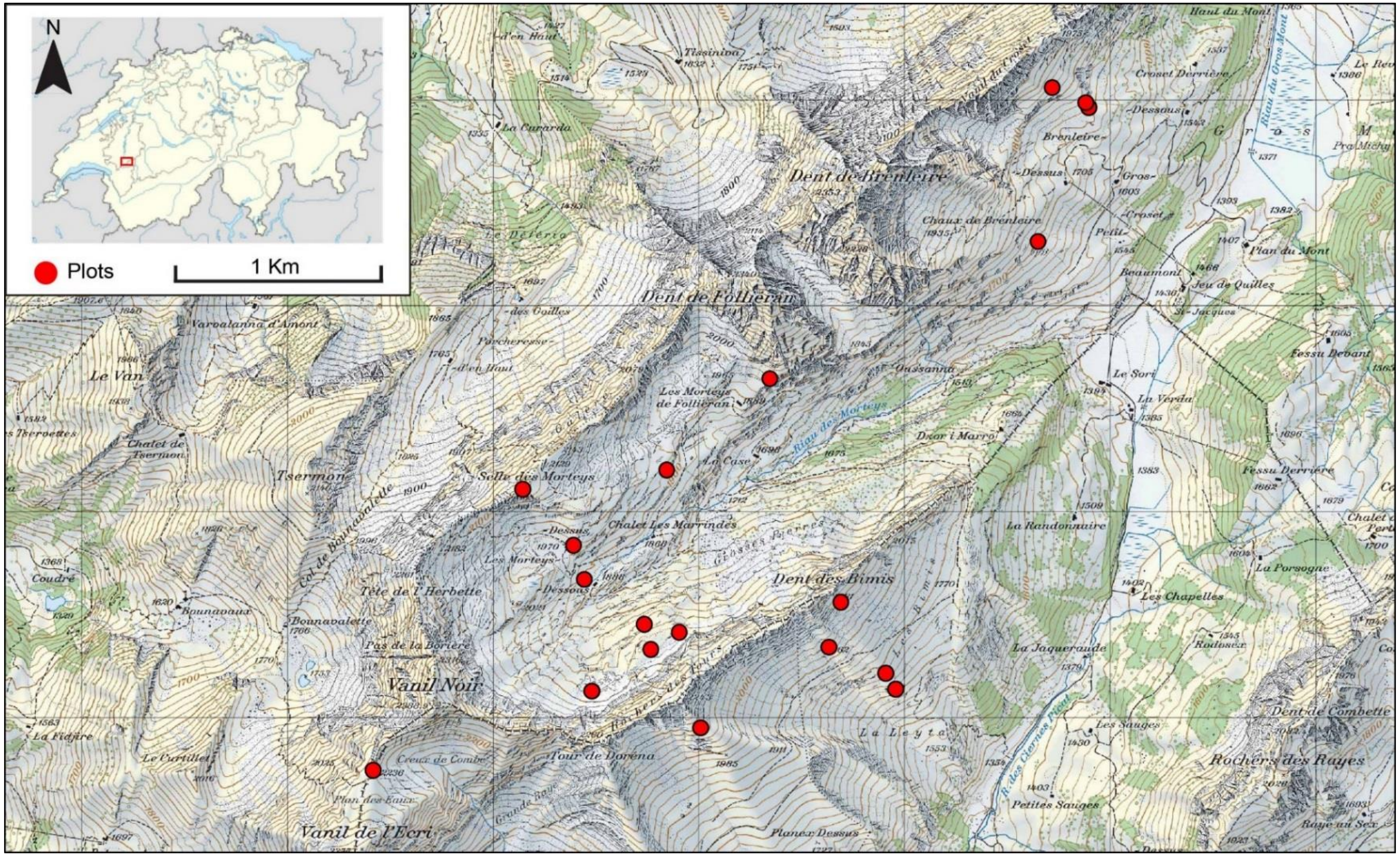
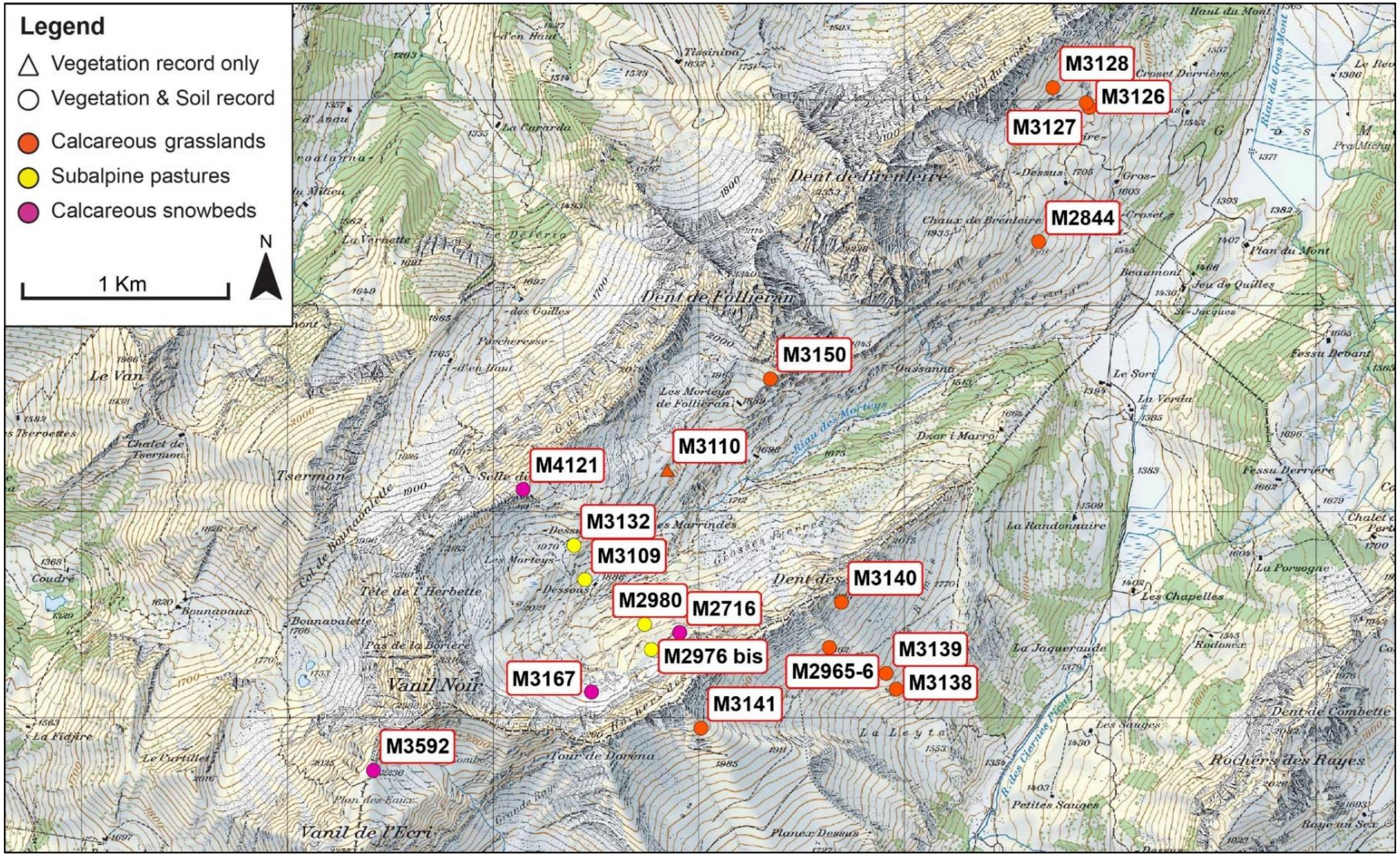
Zimmermann NE, Kienast F (1999) Predictive mapping of alpine grasslands in Switzerland: Species versus community approach. Journal of Vegetation Science **10**, 469-482.

10 Appendices

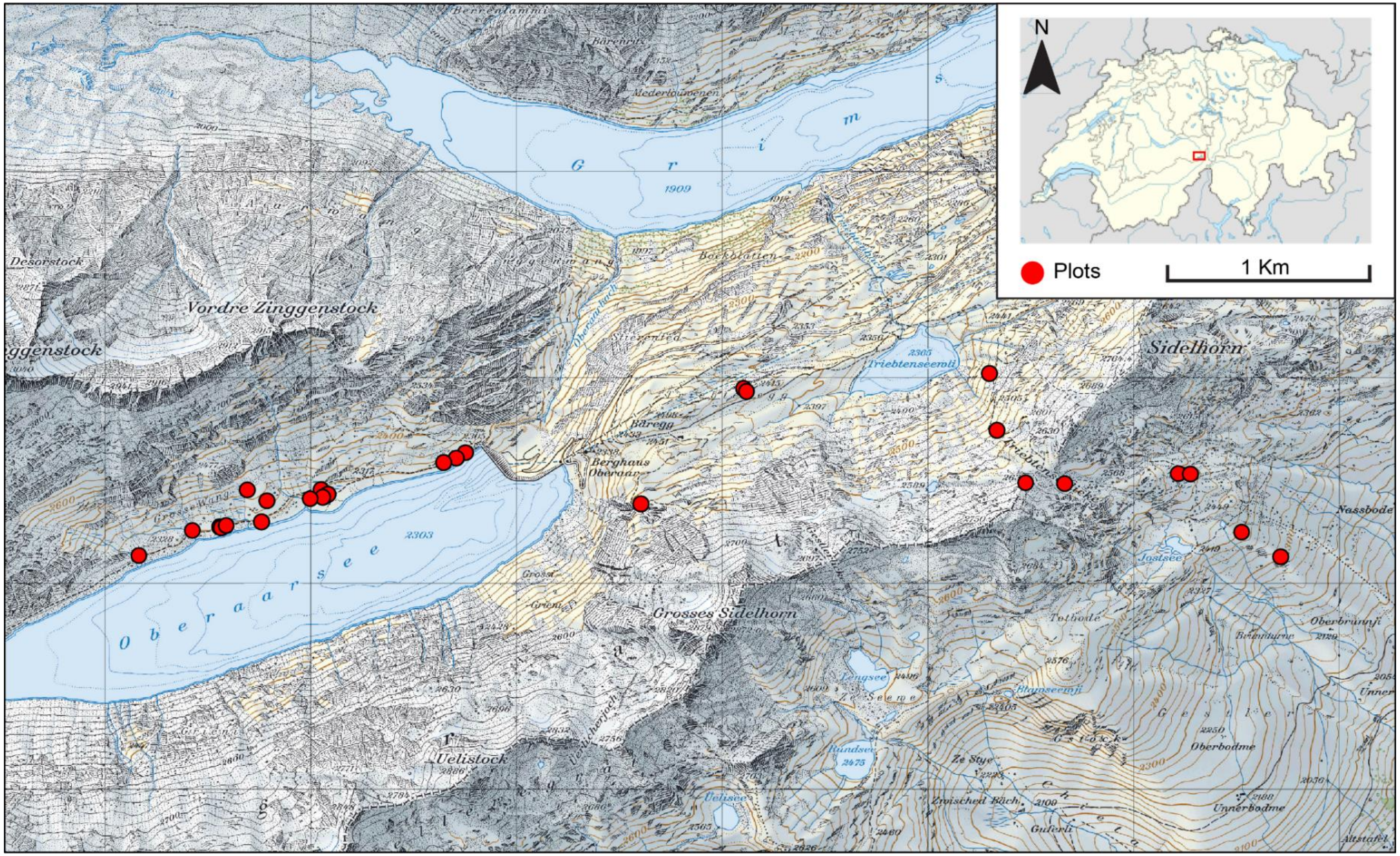
A. Plot location



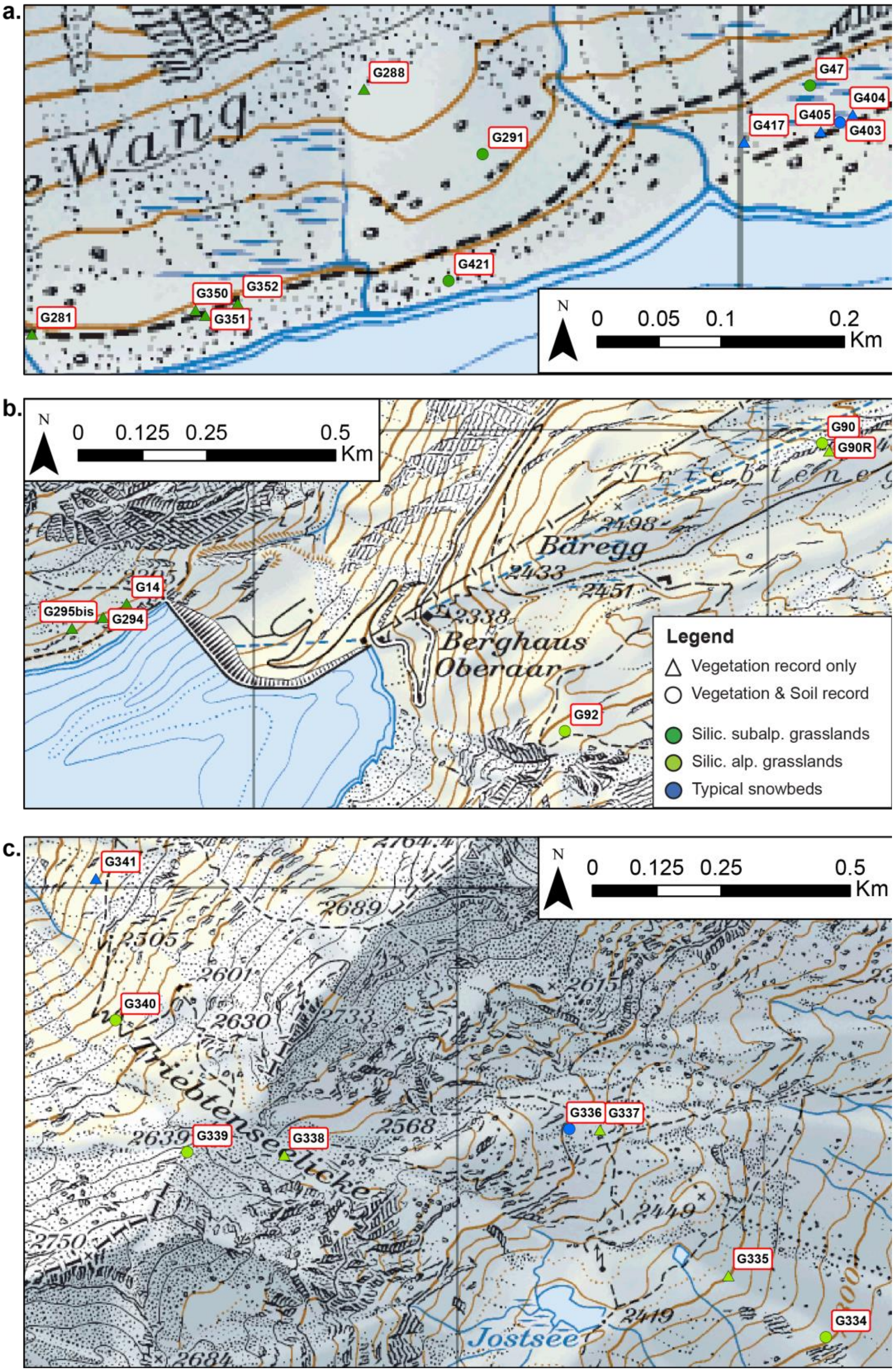
Appendix A1 – Topographical map of the Morteys plots.



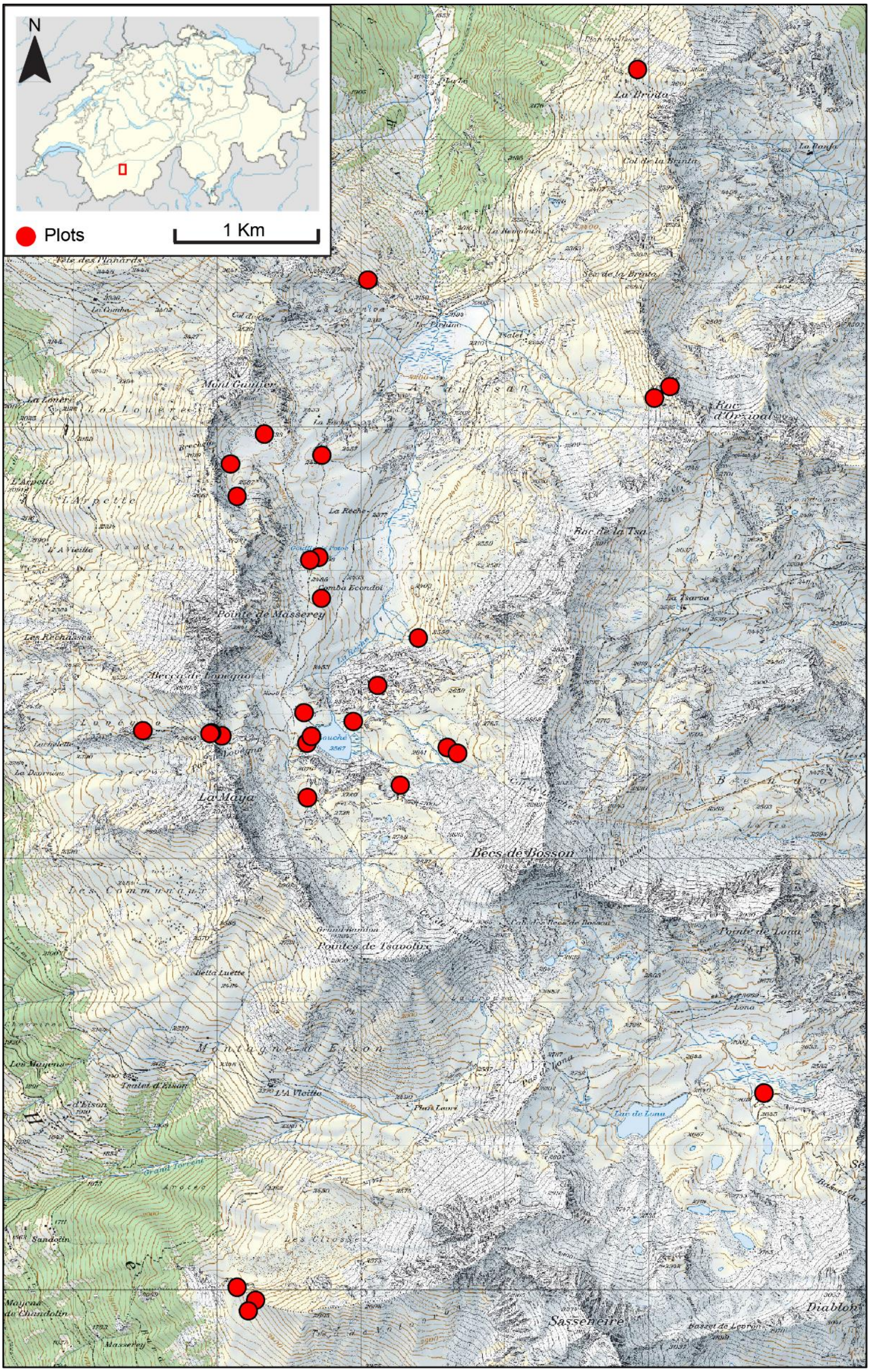
Appendix A2 – Topographical map of the Morteys plots. Colours represent the vegetation type, and symbols whether a vegetation record was accompanied by a soil description and sampling (circles) or not (triangles).



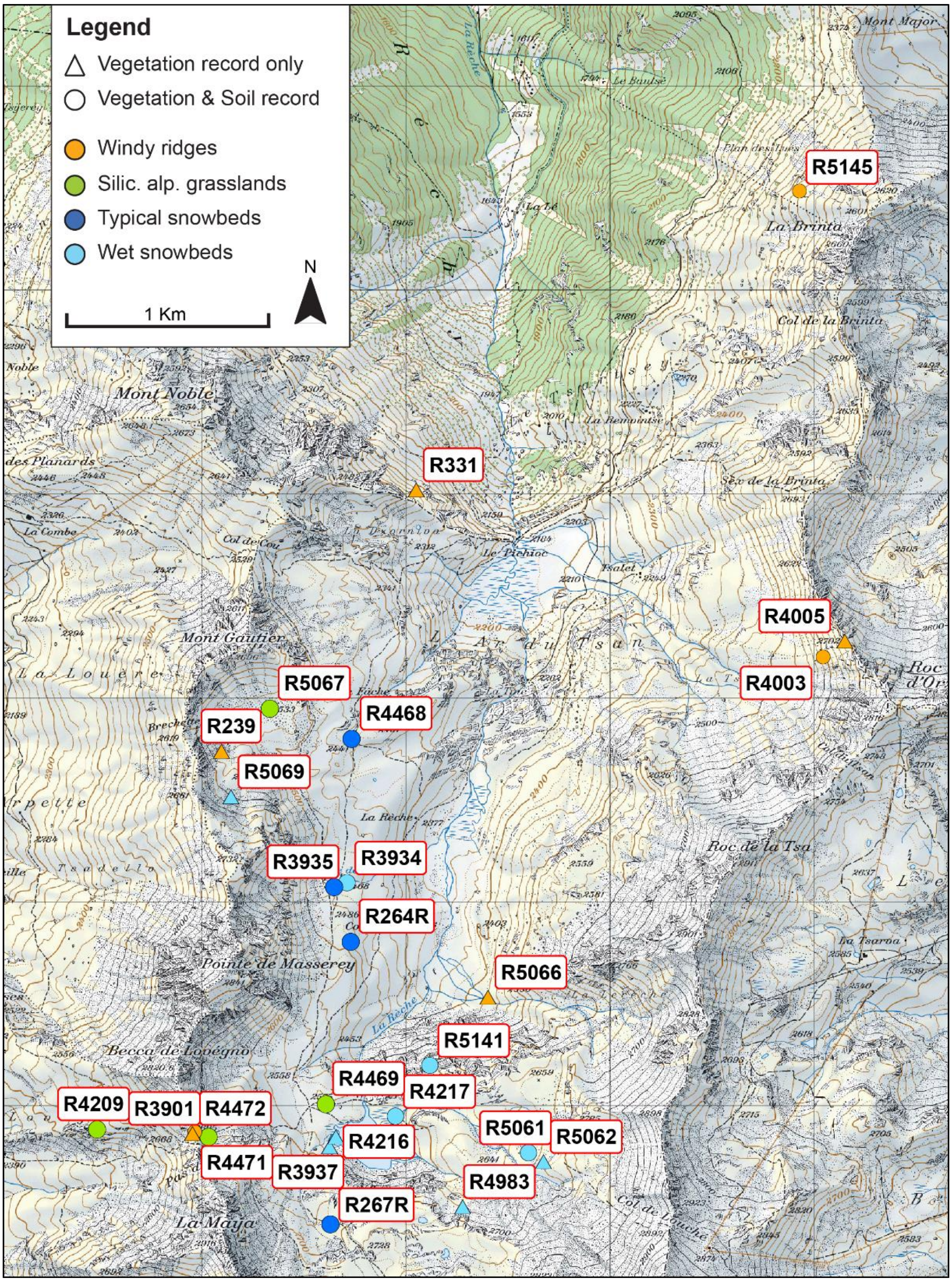
Appendix A3 – Topographical map of the Grimsel plots.



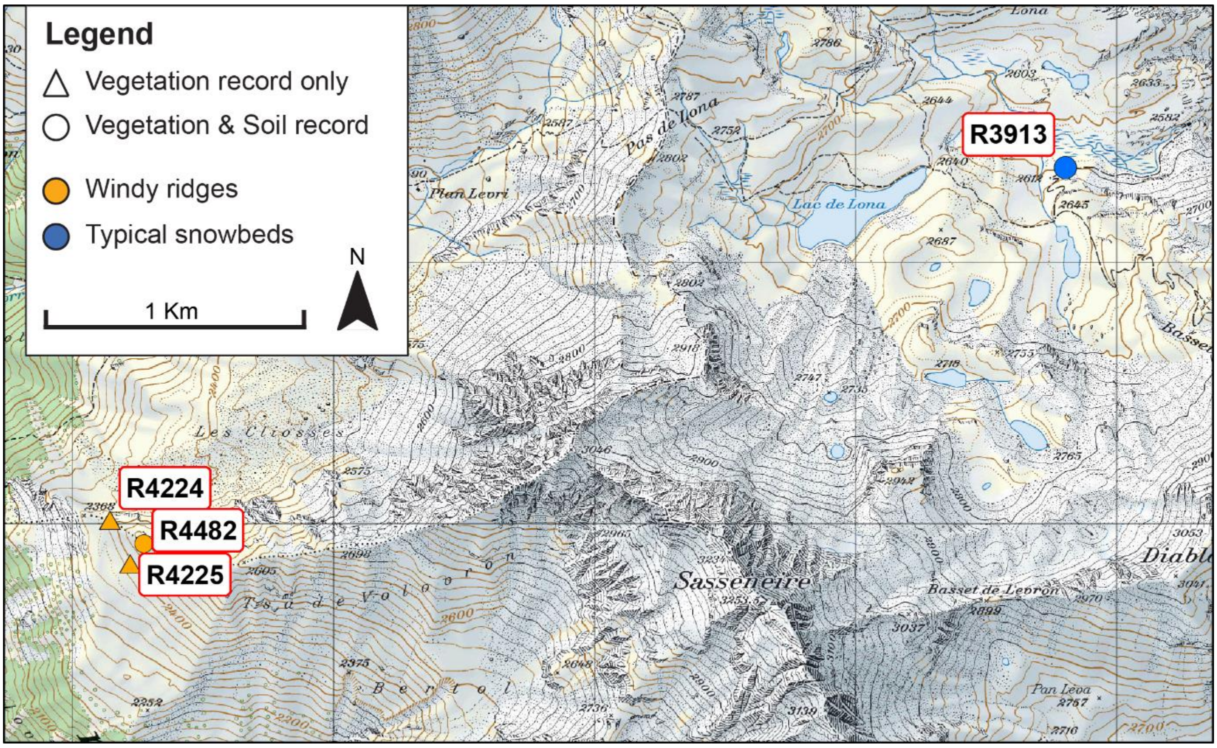
Appendix A4 – Topographical map of the Grimsel plots. Focus on the Western (a), Central (b) and Eastern (c) part. Colour and symbol meaning as in Appendix A2.



Appendix A5 – Topographical map of the Réchy plots.

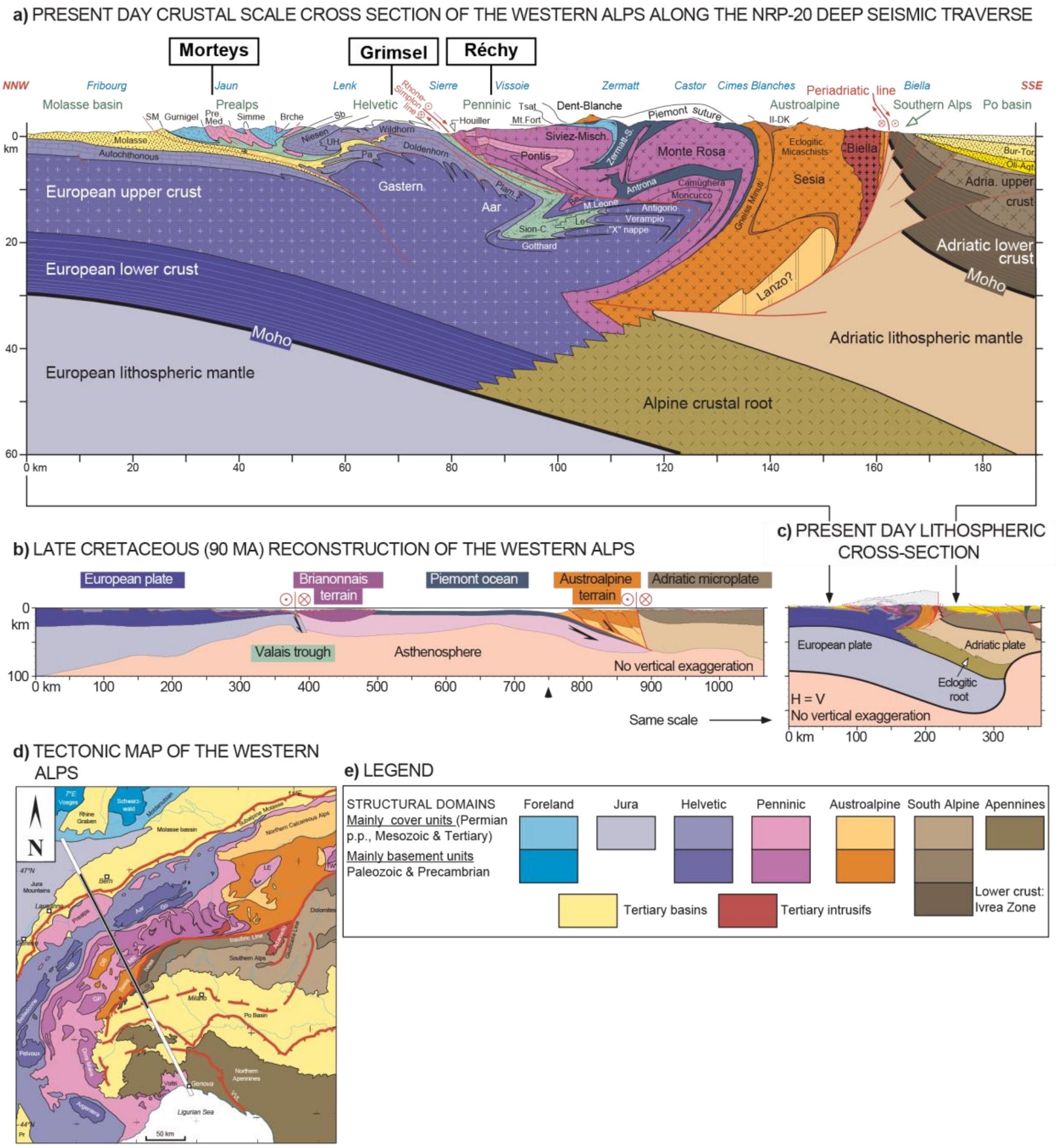


Appendix A6 – Topographical map of the Réchy plots. Focus on the Northern part. Colour and symbol meaning as in Appendix A2.

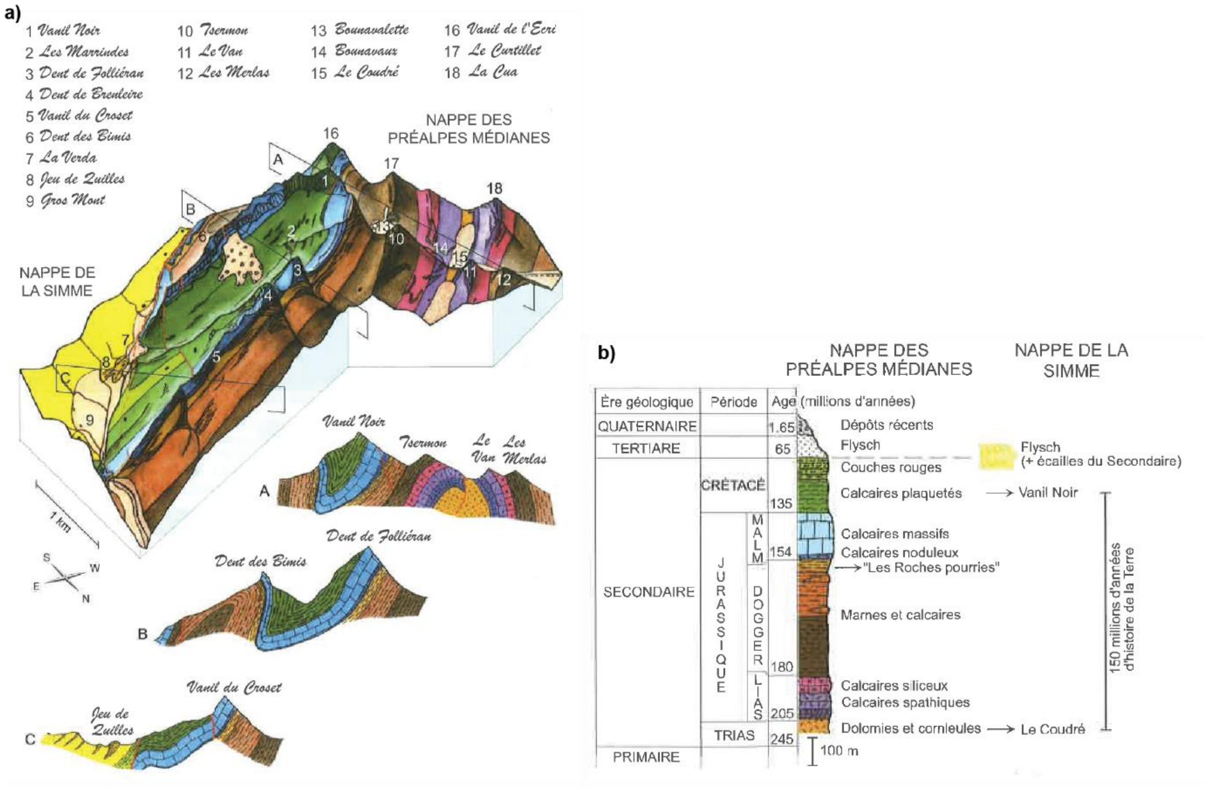


Appendix A7 – Topographical map of the Réchy plots. Focus on the Southern part. Colour and symbol meaning as in Appendix A2.

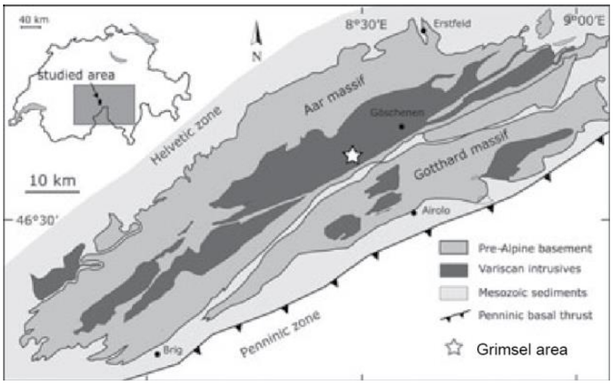
B. Tectonic and geological maps



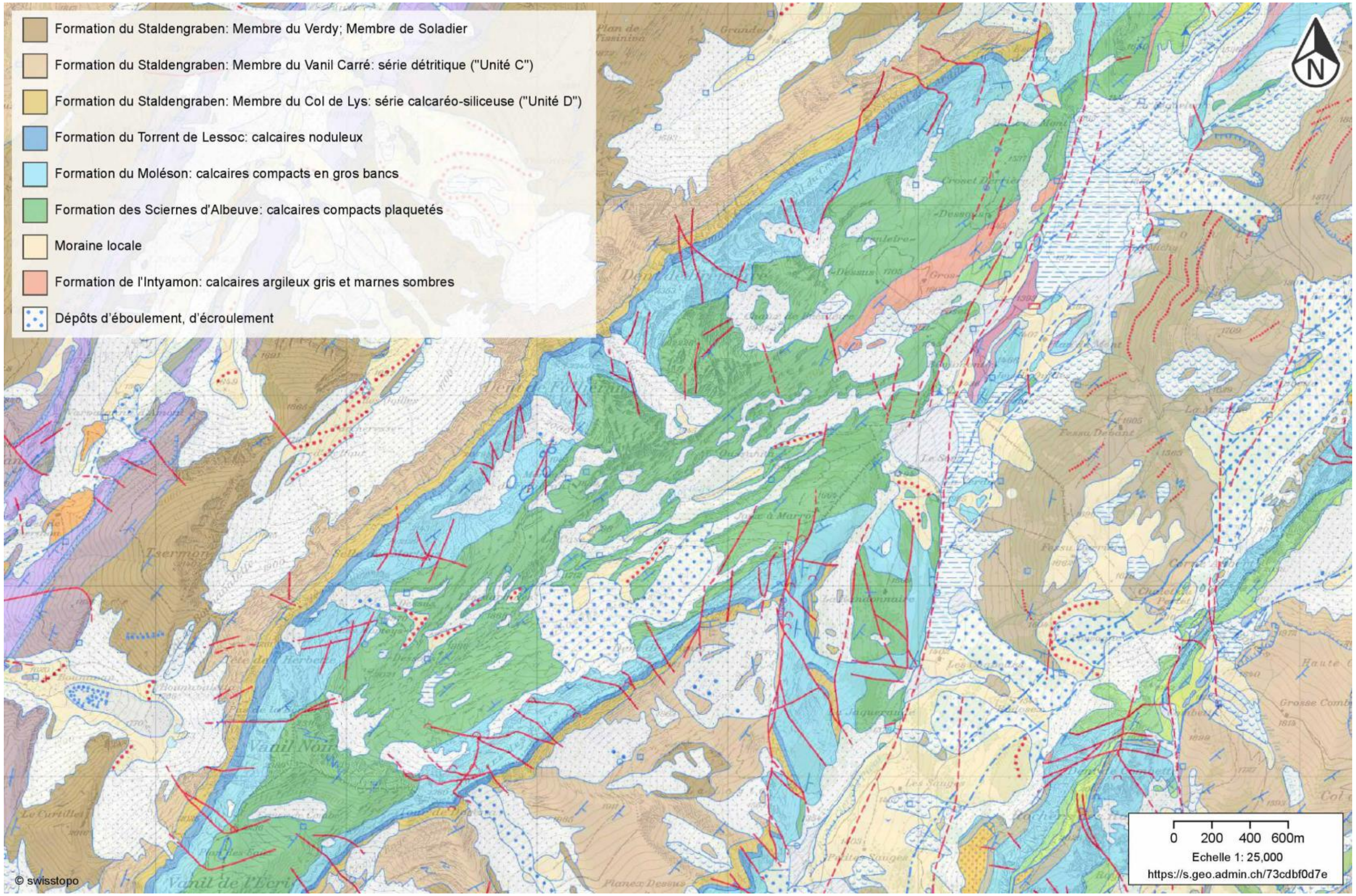
Appendix B1 - (a) Cross section of the Western Swiss Alps on transect of figure (d), and simplified palinspastic model **(b and c)**, modified from Marchant 1993 and Marchand & Stampfli (1997) in Stampfli (2001; p. 7). The estimated location of the three study areas is indicated in (a). **(d)** Tectonic map of the Western Alps modified from Berthelsen (1992) in Stampfli (2001; p. 6). Ao = Adamello intrusions; DB = Dent Blanche nappe; Go = Gotthard massif; GP = Grand Paradis massif; LE = Lower Engadine window; MB = Mont Blanc massif; MR = Monte Rosa nappe; Pr = Provence basin; TW = Tauern window; VVL = Villalvernia-Varzi-Levanto line. Thin black line: cross-section of the western Alps (a). **(e)** Color legend. All figures are taken from Stampfli (2001).



Appendix B2 - **(a)** Tectonic profile of the Morteys valley and tree cross sections (A, B and C). The study area is represented by the cross section B. **(b)** Stratigraphic chart and color legend. Figures taken from Lehmann (2006).



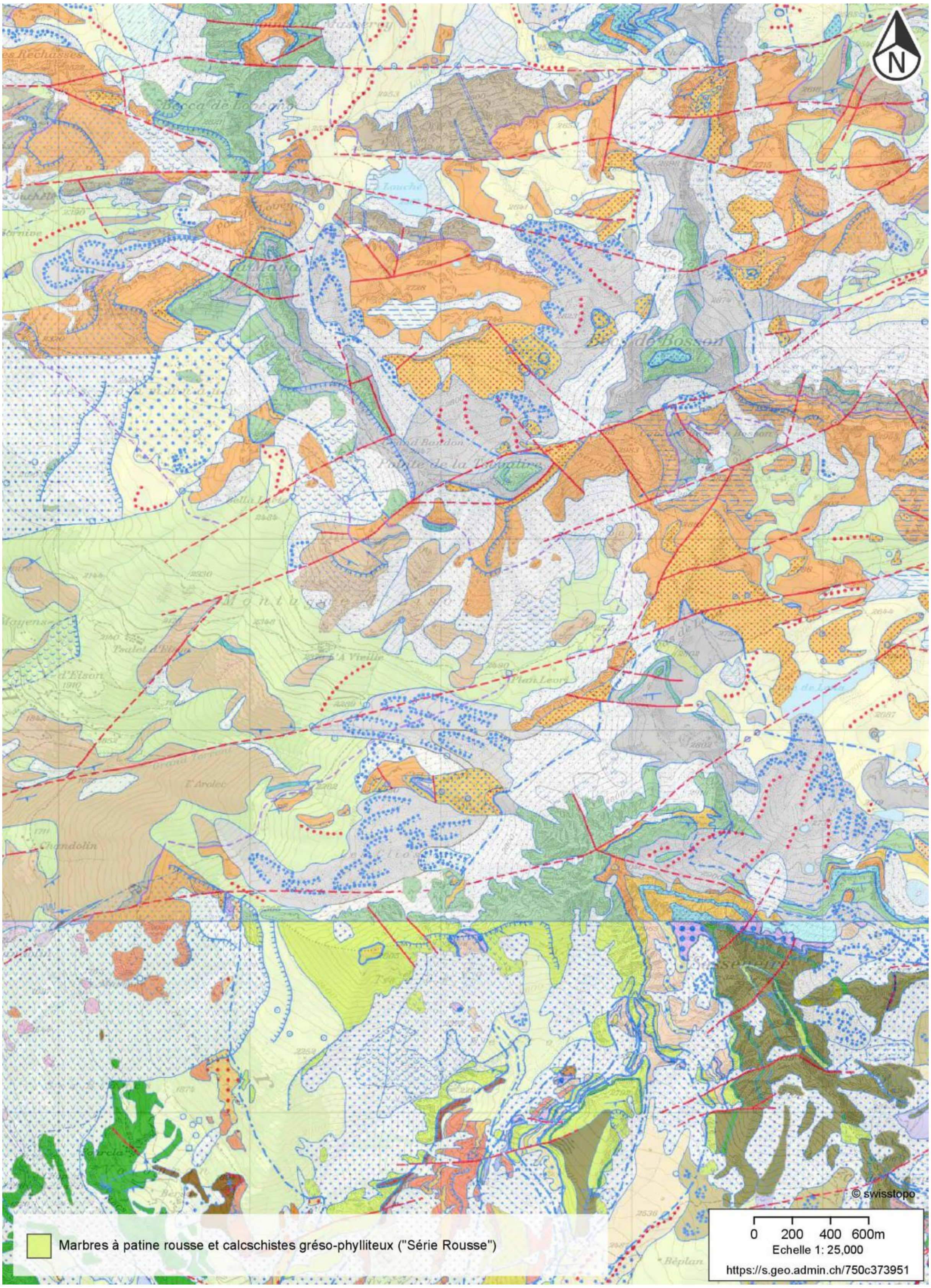
Appendix B3 - Tectonic map of the Central Alps, modified from Goncalves *et al.* (2012). The Grimsel study area is represented by the star.



Appendix B4 - Geological map of the Morteys area and partial legend, extracted from Swisstopo (https://map.geo.admin.ch).

Appendix B5 - Geological map of the Grimsel area and partial legend, extracted from Swisstopo (https://map.geo.admin.ch).

Appendix B6 - Geological map of the Réchy area and partial legend, extracted from Swisstopo (https://map.geo.admin.ch). Focus on the Northern part.



Appendix B7 - Geological map of the Réchy area and partial legend, extracted from Swisstopo (https://map.geo.admin.ch). Focus on the Southern part.

C. Historical and recent plant inventories

Appendix C1 - List of the 134 inventories (67 historical and 67 recent) included in the vegetation study, with the corresponding author's names, time span of survey, spatial coordinates in m (according to the Swiss reference system for geographical coordinates, CH1903+), elevation (“Elev.”), slope, aspect, surface (“Surf.”), plant community (phytosociological alliance), herbs, mosses and/or lichens (“M. & L.”), litter, rock and bare soil covers, and current land use. Covers are given in %, except values with * for which the Braun-Blanquet's scale was used (Table 4.1). Author names are abbreviated as follows: Jean-Louis Richard (JLR), Klaus Ammann (KA), Benoît Bressoud (BB), Olivier Duckert (OD), Magalì Matteodo (MM), Pascal Vittoz (PV), Marie-José Petétot (MJP), Loïc Liberati (LL), and Swanee Messerli (SM).

Plot name	Author(s)	Date	Coord X	Coord Y	Elev. [m]	Slope [°]	Aspect [°]	Surf. [m^2]	Vegetation type	Herbs [%]	M. & L. [%]	Litter [%]	Rocks [%]	Bare soil [%]	Grazed
M2844_1	JLR	25.06.1972	580651	155309	1700	37	SSE	25	Seslerion						
M2844_2	PV & MM	01.07.2013	580651	155309	1698	28	122	25	Seslerion	90	0	1	6	3	no
M3110_1	JLR	15.07.1973	578884	154197	1910	31	SSE	20	Seslerion						
M3110_2	PV & MM	22.07.2013	578845	154201	1926	31	135	20	Seslerion	94.9	0.1	1	2	2	yes
M3126_1	JLR	20.07.1973	580901	155948	1710	45	ESE	100	Seslerion						
M3126_2	PV & MM	04.07.2013	580896	155961	1716	48	108	85	Seslerion	89	1	2	8	0	no
M3127_1	JLR	20.07.1973	580901	155948	1730	39	ESE	100	Seslerion						
M3127_2	PV & MM	04.07.2013	580883	155984	1738	35	125	70	Seslerion	92	0.5	3	4	0.5	no
M3128_1	JLR	20.07.1973	580728	156076	1850	39	SSE	100	Seslerion						
M3128_2	MM	05.07.2013	580720	156058	1843	38	150	100	Seslerion	85	1	3	8	3	no
M3138_1	JLR	18.08.1973	579954	153138	1720	31	SE	60	Seslerion						
M3138_2	PV & MJP	16.07.2013	579959	153138	1715	33	130	60	Seslerion	90.9	0.1	3	5	1	no
M3139_1	JLR	18.08.1973	579919	153178	1750	27	SE	50	Seslerion	100					
M3139_2	PV & MJP	16.07.2013	579910	153214	1771	27	145	50	Seslerion	96.5	0	2	1	0.5	no
M3140_1	JLR	18.08.1973	579682	153564	2010	39	SE	20	Seslerion	80					
M3140_2	PV & MM	15.07.2013	579691	153559	1997	35	136	20	Seslerion	75	0	7	13	5	no
M3141_1	JLR	18.08.1973	579004	152955	2100	27	SE	100	Seslerion	100					
M3141_2	PV & MM	17.07.2013	579009	152948	2099	27	135	100	Seslerion	95.9	0	4	0	0.1	no
M3150_1	JLR	22.08.1973	579352	154639	1950	33	SW	30	Seslerion	100					
M3150_2	PV & MJP	22.07.2013	579347	154645	1951	31	210	30	Seslerion	93	0.1	4.5	2	0.4	no
M2976_1	JLR	29.08.1972	578727	153322	1960	0	N	2	Poion alpinae						
M2976bis_2	MM	28.08.2014	578769	153331	1981	0	0	2	Poion alpinae	92	3	5	0	0	yes
M2980_1	JLR	01.09.1972	578770	153439	1950	6	N	NA	Poion alpinae						
M2980_2	PV & MJP	24.07.2013	578735	153453	1945	10	340	12	Poion alpinae	96	0.9	2	0.1	1	yes
M3109_1	JLR	15.07.1973	578462	153689	1900	27	SSE	10	Poion alpinae						
M3109_2	MM	19.07.2013	578445	153669	1900	39	146	9	Poion alpinae	90	0	0	7	3	yes
M3132_1	JLR	25.07.1973	578405	153834	1970	11	E	NA	Poion alpinae						
M3132_2	PV & MJP	18.07.2013	578392	153835	1972	11	165	42	Poion alpinae	96.9	0.5	0.1	2	0.5	yes
M3592_1	JLR	06.08.1975	577370	152715	2230	17	N	5	Elynion	90					
M3592_2	MM	05.09.2013	577417	152744	2232	18	20	6	Elynion	70	7.5	0.5	20	2	no
M4121_1	JLR	02.07.1979	578142	154115	2180	50	N	10	Elynion	70					
M4121_2	PV & MM	25.07.2013	578145	154108	2180	50	330	12	Elynion	65	7	2	33	3	no
R239_1	BB	02.08.1990	604100	115760	2550	25	WNW	100	Elynion	85	0				
R239_2	MM	06.08.2014	604095	115740	2550	30	61.5	81.9	Elynion	75	1.5	0.5	22	1	no
R331_1	OD	1990	604970	117030	2340	35	E	5x5	Elynion	30	10				
R331_2	MM & PV	14.07.2014	605050	117020	2328	37	22	25	Elynion	77	10	6	2	5	no
R3901_1	JLR	16.08.1977	603945	113878	2695	6	W	10	Elynion	90	0				
R3901_2	MM	12.08.2014	603963	113870	2697	6	251	9.86	Elynion	80	16	2	1.5	0.5	no
R4003_1	JLR	19.8.1978	607069	116182	2600	35	WSW	10	Elynion	100	0				
R4003_2	PV	15.07.2014	607042	116199	2595	35	240	10	Elynion	88	3	6	1	2	yes
R4005_1	JLR	19.08.1978	607139	116283	2690	11	WSW	5	Elynion	30	0				

Plot name	Auth or(s)	Date	Coord X	Coord Y	Elev. [m]	Slope [°]	Aspect [°]	Surf. [m^2]	Vegetation type	Herbs [%]	M. & L. [%]	Litter [%]	Rocks [%]	Bare soil [%]	Grazed
R4005_2	MM & PV	15.07.2014	607150	116278	2694	20	238	4	Elynion	81	8	8	2	1	no
R4224_1	JLR	30.8.1979	604156	109976	2380	17	W	5	Elynion	90	0				
R4224_2	MM & PV	03.07.2014	604144	110013	2386	20	284	5	Elynion	80	6	8	2	4	yes
R4225_1	JLR	30.8.1979	604225	109876	2400	39	SW	25	Elynion	80	0				
R4225_2	PV	03.07.2014	604220	109846	2400	36	232	25	Elynion	85	1	7.9	0.1	6	yes
R4472_1	JLR	29.7.1981	603945	113878	2695	6	W	40	Elynion	90	0				
R4472_2	MM & SM	22.08.2014	603953	113865	2694	10	243	40	Elynion	86.5	7	1	5	0.5	no
R4482_1	JLR	18.9.1981	604364	109876	2460	31	WSW	25	Elynion	0	0				
R4482_2	PV	03.07.2014	604272	109921	2450	30	225	25	Elynion	75	7	10	2	6	yes
R5066_1	JLR	24.8.1989	605403	114580	2420	11	WNW	15	Elynion	60	50				
R5066_2	MM	07.08.2014	605402	114532	2422	18	298	15.08	Elynion	70	15	1	5	0	yes
R5145_1	JLR	18.8.1990	606928	118484	2430	31	WNW	20	Elynion	80	0				
R5145_2	MM	17.07.2014	606927	118485	2430	36	275	20	Elynion	80	8	2	10	0	?
G14_1	KA	24.07.1964	663765	155640	2315	45	S	100	Nardion	5*	1*	+*	0	0	
G14_2	PV, MM, LL	13.08.2013	663753	155633	2320	45	155	25	Nardion	92	2	4	1	1	no
G281_1	KA	19.09.1967	662425	155215	2320	15	SSE	50	Nardion	5*	1-2*	1*	0	1*	
G281_2	MM & LL	07.08.2013	662426	155254	2320	20	216	35	Nardion	75	7	3	15	0	no
G288_1	KA	19.09.1967	662700	155450	2368	10	S	6	Nardion	5*	1*	+*	0	0	
G288_2	MM & LL	6.08.2013	662694	155451	2370	10	146	6	Nardion	50	15	34	1	0	no
G291_1	KA	24.09.1967	662785	155390	2345	5	SE	50	Nardion	5*	+*	0	0	0	
G291_2	PV & LL	16.08.2013	662789	155399	2348	5	140	50	Nardion	85	3	7	4	1	no
G294_1	KA	25.09.1967	663705	155625	2325	45	SE	100	Nardion	5*	+*	0	0	0	
G294_2	PV, MM, LL	13.08.2013	663707	155606	2320	42	140	77	Nardion	92	1.5	3	2	1.5	no
G295_1	KA	25.09.1967	663660	155610	2335	40	SE	100	Nardion	5*	+*	+*	0	0	
G295 bis_2	PV, MM, LL	13.08.2014	663646	155585	2329	37	155	98	Nardion	95	0.5	3	1	0.5	no
G343_1	KA	24.08.1972	662160	155150	2330	30	S	25	Nardion	5*	1*	1*	0	1*	
G343_2	MM & LL	09.08.2013	662167	155133	2330	30	175	24	Nardion	65	15	3	10	7	no
G350_1	KA	24.08.1972	662550	155275	2320	10	S	25	Nardion	3*	+*	+*	0	0	
G350_2	MM & LL	07.08.2013	662558	155273	2326	18	160	22.5	Nardion	60	10	3	25	2	no
G351_1	KA	24.08.1972	662565	155280	2320	10	S	25	Nardion	3*	1*	+*	0	2*	
G351_2	MM & LL	6.08.2013	662566	155269	2318	18	164	25	Nardion	65	5	4	25	1	no
G352_1	KA	24.08.1972	662585	155290	2320	10	S	25	Nardion	5*	+*	+*	0	+*	
G352_2	MM & LL	6.08.2013	662592	155279	2320	10	178	23.5	Nardion	80	3	7	10	0	no
G421_1	KA	27.08.1973	662770	155295	2315	0	-	25	Nardion	5*	1*	+*	0	1*	
G421_2	MM & LL	5.08.2013	662762	155297	2312	20	167	16	Nardion	60	3	10	20	7	no
G47_1	KA	31.08.1964	663040	155440	2315	10	S	100	Nardion	5*	1*	1*	0	0	
G47_2	MM	29.08.2013	663052	155454	2317	30	180	98	Nardion	78	2	3	15	2	no
G334_1	KA	30.08.1970	667725	155110	2300	20	S	25	Caricion curvulae	5*	1*	1*	0	1*	
G334_2	PV, MM, LL	15.08.2013	667715	155127	2310	20	145	27	Caricion curvulae	83	4	6	5	2	yes
G335_1	KA	30.08.1970	667520	155275	2410	10	S	25	Caricion curvulae	5*	1*	1*	0	+*	
G335_2	PV, MM, LL	15.08.2013	667526	155246	2410	15	160	25	Caricion curvulae	86	4	3	5	2	yes
G337_1	KA	30.08.1970	667250	155515	2495	5	N	25	Caricion curvulae	5*	1*	1*	0	1*	
G337_2	PV & LL	15.08.2013	667276	155529	2500	10	300	25	Caricion curvulae	50	36	2	10	2	yes
G338_1	KA	30.08.1970	666675	155485	2600	20	SSE	9	Caricion curvulae	4*	1-2*	2*	0	1*	
G338_2	PV, MM, LL	14.08.2013	666664	155481	2603	25	120	12	Caricion curvulae	22	15	1	60	2	no
G339_1	KA	30.08.1970	666500	155500	2640	0	-	9	Caricion curvulae	2*	2*	1*	0	3*	
G339_2	PV & LL	14.08.2013	666476	155486	2650	5	45	18	Caricion curvulae	30	19	1	15	35	no
G340_1	KA	30.08.1970	666330	155740	2560				Caricion curvulae	0	0	0	0	0	
G340_2	PV, MM, LL	14.08.2013	666337	155742	2560	20	320	17.5	Caricion curvulae	30	25	15	30	0	no
G90_1	KA	24.09.1965	665105	155945	2370	5	SE	25	Caricion curvulae	4*	1*	2*	0	0	
G90 R_2	MM	28.08.2013	665119	155930	2441	10	150	25	Caricion curvulae	70	12	5	5	8	no
G92_1	KA	03.08.1965	664610	155380		-	-	4	Caricion curvulae	2*	4-5*	0	0	1*	

Plot name	Author(s)	Date	Coord X	Coord Y	Elev. [m]	Slope [°]	Aspect [°]	Surf. [m^2]	Vegetation type	Herbs [%]	M. & L. [%]	Litter [%]	Rocks [%]	Bare soil [%]	Grazed
G92_2	MM & LL	08.08.2013	664605	155385	2511	0	0	4	Caricion curvulae	60	20	0	10	10	no
R4209_1	JLR	15.08.1979	603597	113878	2600	11	S	100	Caricion curvulae	80	several lichens				
R4209_2	MM & SM	18.08.2014	603487	113884	2581	14	207	99	Caricion curvulae	75	19.5	1	4	0.5	no
R4471_1	JLR	29.07.1981	604014	113878	2695	11	ENE	20	Caricion curvulae	70	0				
R4471_2	MM & SM	19.08.2014	604033	113848	2682	22	64	19.8	Caricion curvulae	63	15	1	20	1	no
R5067_1	JLR	25.08.1989	604291	115880	2520	0	0	10	Caricion curvulae	70	0				
R5067_2	MM	05.08.2014	604333	115949	2528	8	20	9.6	Caricion curvulae	74.5	20	2	3	0.5	yes
G336_1	KA	30.08.1970	667250	155515	2495	-	-	5	Salicion herbaceae	+*	5*	r*	0	0	
G336_2	PV, MM, LL	15.08.2013	667218	155531	2497	0	0	6	Salicion herbaceae	10	68	15	3	4	yes
G341_1	KA	30.08.1971	666310	156030	2460	20	N		Salicion herbaceae	5-4*	1-2*	0	0	0	
G341_2	PV, MM, LL	14.08.2013	666299	156018	2460	25	285	2.7	Salicion herbaceae	88	6	2	0	4	?
G404_1	KA	27.08.1973	663080	155425	2315	5-10	NNE	4	Salicion herbaceae	5*	1*	0	0	0	
G404_2	MM	27.08.2013	663086	155430	2313	5	340	4	Salicion herbaceae	75	15	5	2	3	no
G405_1	KA	27.08.1973	662040	155410	2320	5-10	NNE	4	Salicion herbaceae	5*	1-2*	0	0	0	
G405_2	PV, MM, LL	16.08.2013	663061	155417	2313	7	330	4.5	Salicion herbaceae	85	11.9	3	0.1	0	no
G417_1	KA	27.08.1973	663015	155400	2315	3	S	10	Salicion herbaceae	4-5*	+*	0	0	2*	
G417_2	PV, MM, LL	16.08.2013	662999	155408	2315	3	145	10.5	Salicion herbaceae	73	0	7	20	0	no
R264_1	BB	1979	6047	1148	2470	0	0	4	Salicion herbaceae	100	10				
R264R_2	MM	04.08.2014	604728	114805	2489	0	0	4	Salicion herbaceae	70	27	2	1	1	yes
R267_1	BB	1979	604650	1134	2690	5	W	2	Salicion herbaceae	90	0				
R267R_2	MM	28.07.2014	604629	113420	2685	5	242	2.25	Salicion herbaceae	80	5	15	0	0	no
R3935_1	JLR	25.08.1977	604639	115079	2470	11	N	2	Caricion bicolori-atrofuscae	25	100				
R3935_2	MM	16.07.2014	604647	115072	2468	10	340	2.25	Salicion herbaceae	50	37	8	2	3	yes
R4468_1	JLR	27.7.1981	604708	115780	2450	0	0	2	Salicion herbaceae	80	0				
R4468_2	PV	16.07.2014	604733	115800	2440	3	342	5	Salicion herbaceae	70	10	20	0	0	yes
R3934_1	JLR	25.08.1977	604708	115079	2467	0	0	2	Caricion bicolori-atrofuscae	50	0				
R3934_2	MM	04.08.2014	604710	115093	2468	5	116	2.25	Caricion bicolori-atrofuscae	80	15	0	1	4	yes
R3937_1	JLR	25.08.1977	604640	113779	2567	0	0	2	Caricion bicolori-atrofuscae	20	0				
R3937_2	MM	08.08.2014	604627	113800	2569	0	0	2	Caricion bicolori-atrofuscae	67	30	1	2	0	no
R4216_1	JLR	29.08.1979	604640	113879	2567	0	0	?	Caricion bicolori-atrofuscae	25	30				
R4216_2	MM & SM	21.08.2014	604656	113848	2567	0	0	3	Caricion bicolori-atrofuscae	35	52	0.5	2.5	10	no
R4983_1	JLR	19.08.1988	605404	113779	2630	22	N	3	Caricion bicolori-atrofuscae	20	80				
R4983_2	MM	14.08.2014	605278	113505	2659	15	17	2.8	Caricion bicolori-atrofuscae	24	25	1	50	0	no
R5061_1	JLR	24.8.1989	605543	113779	2650	17	WNW	5	Caricion bicolori-atrofuscae	70	75				
R5061_2	MM	14.08.2014	605601	113769	2650	18	299	5	Caricion bicolori-atrofuscae	70	24	2	3	1	no
R5062_1	JLR	24.8.1989	605682	113779	2670	17	WNW	10	Caricion bicolori-atrofuscae	0	0				
R5062_2	MM	15.08.2014	605673	113726	2677	17	290	10	Caricion bicolori-atrofuscae	25	15	0.2	59.8	0	no

Plot name	Author(s)	Date	Coord X	Coord Y	Elev. [m]	Slope [°]	Aspect [°]	Surf. [m^2]	Vegetation type	Herbs [%]	M. & L. [%]	Litter [%]	Rocks [%]	Bare soil [%]	Grazed
R5069_1	JLR	25.8.1989	604152	115479	2600	22	N	20	Caricion bicolori-atrofuscae	10	60				
R5069_2	MM	05.08.2014	604143	115515	2602	30	20	20	Caricion bicolori-atrofuscae	25	22	2	50	1	yes
R5141_1	JLR	17.8.1990	605126	114179	2560	35	N	5	Caricion bicolori-atrofuscae	70	0				
R5141_2	MM & SM	20.08.2014	605116	114197	2567	32	340	5	Caricion bicolori-atrofuscae	65	9.5	0.5	25	0	no

Appendix C2 - List of the 22 recent plant inventories discarded from the vegetation study, with the corresponding author's names, time span of survey, spatial coordinates in m (according to the Swiss reference system for geographical coordinates, CH1903+), elevation, slope, aspect, surface, herbs, bryophytes and/or lichens, litter, rock and bare soil covers, and current land use. Author names are abbreviated as follows: Magalì Matteodo (MM), Pascal Vittoz (PV), Loïc Liberati (LL), and Swanee Messerli (SM). The vegetation type, defined only for the plant inventories included in the Soil and OM studies, are reported in Table 5.2.

Plot name	Author(s)	Date	CoordX	CoordY	Elevation [m]	Slope [°]	Aspect [°]	Surface [m^2]	Herbs [%]	Mosses & lichens [%]	Litter [%]	Rocks [%]	Bare soil [%]	Grazed
M2716	MM	03.09.2013	578907	153414	1966	30	320	20.8	63	20	0	15	2	no
M2965-6	PV & MM	23.07.2013	579633	153341	1932	45	180	15	75	0	10	5	10	?
M2976	MM	02.09.2013	578771	153332	1981	0	-	15	96.5	2	0.5	0.5	0.5	yes
M3167	MM	4.09.2013	578474	153131	1979	28	50	10	65	10	1	20	4	no
M3167R	MM	4.09.2013	578498	153057	2014	30	0	10	10	23	0	65	2	no
G38	MM	26.08.2013	663073	155423	2313	0	-	2	70	10	10	5	5	no
G39	MM	26.08.2013	663070	155424	2313	5	340	1	40	38	10	10	2	no
G90	MM	28.08.2013	665112	155927	2441	10	156	24	70	12	3	8	7	no
G283	MM & LL	09.08.2013	662350	155272	2332	38	154	17.5	65	5	5	20	5	no
G286	MM & LL	06.08.2013	662635	155305	2324	16	159	24	75	3	17	0	5	no
G401	MM	27.08.2013	663082	155427	2313	30	330	4	25	60	2	10	3	no
G403	MM	27.08.2013	663076	155424	2313	20	0	4	75	15	5	0	5	no
R264	MM	04.08.2014	604715	114805	2489	5	101	4.1	88	10	1	1	0	yes
R267	MM	28.07.2014	604641	113402	2690	8	255	2.1	70	25	2	3	0	no
R3900	MM	13.08.2014	604623	113169	2734	20	4	2.2	30	45	2	23	0	no
R3912	MM	27.07.2014	607802	111367	2598	12	7	2.2	70	23	1	5	1	yes
R3913	MM	27.07.2014	607804	111364	2599	20	3	2.2	50	30	5	15	0	yes
R4217	MM & SM	21.08.2014	604949	113947	2568	0	-	25	60	32	5	3	0	no
R4469	MM	13.08.2014	604607	114009	2578	18	182	4	75	19	0.5	4	1.5	no
R4470	MM	27.08.2014	604624	113856	2568	0	-	10.1	20	10	0.3	69	0.7	no
R5140	MM & SM	20.08.2014	605101	114322	2500	40	343	10	75	20	1	3	1	no
R5144	MM	18.07.2014	607080	118778	2380	30	300	20	60	5	2	25	8	no

Appendix C3 - Plant species list of the inventories of *Seslerion*, *Poion alpinae* and *Elynion* vegetation types, and corresponding cover classes of Braun-Blanquet (1964; see Table 4.1 for details). Within each vegetation type, plant species are classified into characteristic, companion and casual.

Plot name							M2844_1	M2844_2	M3110_1	M3110_2	M3126_1	M3126_2	M3127_1	M3127_2	M3128_1	M3128_2	M3138_1	M3138_2	M3139_1	M3139_2	M3140_1	M3140_2	M3141_1	M3141_2	M3150_1	M3150_2	M2976_1	M2976bis_2	M2980_1	M2980_2	M3109_1	M3109_2	M3132_1	M3132_2	M3592_1	M3592_2	M4121_1	M4121_2	R239_1	R239_2	R331_1	R331_2	R3901_1	R3901_2	R4003_1	R4003_2	R4005_1	R4005_2	R4224_1	R4224_2	R4225_1	R4225_2	R4472_1	R4472_2	R4482_1	R4482_2	R5066_1	R5066_2	R5145_1	R5145_2
Species number							73	76	61	67	73	77	70	77	71	65	63	73	59	72	38	50	59	73	60	66	24	32	27	48	62	52	35	46	20	41	23	34	34	59	36	55	38	45	34	31	11	29	26	42	27	44	37	61	34	33	27	55	28	51
	ind. Val	p-value	freq. (1)	freq. (2)	freq. (3)	freq. tot.	*Seslerion caeruleae*																				*Poion alpinae*								*Elynion myosuroidis*																									
Characteristic species of *Seslerion caeruleae* (1)																																																												
Anthyllis vulneraria subsp. alpestris	0.493	0.001	20	1	19	40	+	1	+	+	+	1	+	+	+	+	+	+	+	+	+	2	+	+	1	1	.	.	.	.	+	.	.	.	.	r	.	r	.	+	+	+	.	+	2	2	.	+	.	+	.	+	+	1	+	1	+	1	2	1
Carex sempervirens	0.519	0.001	20	2	16	38	4	2	2	2	3	2	3	2	2	3	3	2	3	2	3	2	3	2	3	2	.	+	.	.	.	.	1	.	+	2	2	1	.	r	.	.	.	.	1	+	.	2	1	+	2	2	.	r	3	2	.	1	.	.
Lotus corniculatus	0.414	0.001	20	5	8	33	1	2	+	1	+	+	1	1	+	+	+	1	+	+	1	1	+	+	1	1	.	.	.	+	1	+	+	+	.	.	.	.	2	+	+	+	.	.	.	.	.	.	.	.	.	+	.	+	.	.	+	.	+	.
Phleum hirsutum	1.000	0.001	20	0	0	20	+	+	1	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phyteuma orbiculare	0.800	0.001	20	2	0	22	+	1	+	+	+	+	+	1	+	+	+	+	+	+	+	+	+	+	+	+	.	.	.	.	r	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pulsatilla alpina s.str.	0.950	0.001	20	1	0	21	1	+	2	1	1	1	1	1	2	+	r	+	2	2	1	+	2	2	2	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Galium anisophyllon	0.264	0.003	19	5	21	45	+	+	+	+	+	+	+	+	+	+	1	+	.	+	1	+	+	+	+	+	.	.	.	+	1	+	+	+	.	+	.	.	1	1	+	+	+	+	1	+	.	r	.	+	+	+	+	+	1	+	+	+	1	+
Leucanthemum adustum	0.622	0.001	19	3	0	22	+	+	+	+	+	+	+	+	+	+	+	+	.	+	+	+	+	+	+	+	.	.	.	.	+	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Scabiosa lucida	0.619	0.001	19	3	5	27	+	1	+	1	+	+	+	1	.	1	1	+	1	+	1	+	1	+	+	+	.	.	.	r	+	1	.	.	+	1	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carduus defloratus s.str.	0.713	0.001	18	2	1	21	+	+	.	1	+	+	+	+	+	+	+	+	.	+	+	+	+	+	+	2	.	.	.	.	+	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Helianthemum nummularium s.l.	0.762	0.001	18	0	8	26	1	1	2	2	.	2	1	2	1	2	1	2	1	1	2	2	2	1	.	2	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	+	1	+	.	+	1	2	.	.	.	.
Gentiana lutea	0.563	0.001	17	3	0	20	r	1	+	2	+	.	+	r	+	+	+	+	+	1	.	.	+	r	+	+	.	.	.	.	+	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium pratense s.str.	0.392	0.001	16	5	0	21	.	+	+	.	+	2	+	1	1	+	.	+	+	+	.	1	+	+	1	1	.	.	.	1	2	+	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Euphorbia cyparissias	0.750	0.001	15	0	0	15	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gymnadenia conopsea	0.739	0.001	15	0	0	15	+	r	.	+	+	.	+	+	+	+	+	+	+	r	.	r	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium villosum	0.750	0.001	15	0	0	15	r	+	+	1	+	r	+	r	+	r	.	.	+	.	+	r	r	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hippocrepis comosa	0.726	0.001	15	1	0	16	.	+	+	.	+	+	+	+	.	.	+	+	.	+	+	+	+	+	+	+	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Linum catharticum	0.750	0.001	15	0	0	15	.	r	+	r	.	+	+	+	+	+	+	+	+	+	+	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Paradisea liliastrum	0.750	0.001	15	0	0	15	1	+	.	+	r	+	+	+	+	+	+	+	+	1	.	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus montanus aggr.	0.313	0.001	15	5	1	21	.	.	.	1	+	1	1	1	1	+	+	+	+	+	+	1	.	.	+	+	.	+	.	+	+	+	.	1	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Traunsteinera globosa	0.750	0.001	15	0	0	15	+	r	+	+	+	.	+	r	+	.	+	+	+	+	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla conjuncta aggr.	0.636	0.001	14	0	2	16	+	+	+	1	+	1	.	.	.	.	.	.	+	+	+	+	+	+	+	r	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bupleurum ranunculoides s.str.	0.700	0.001	14	0	0	14	.	.	.	.	+	+	+	1	1	.	+	1	+	1	+	.	+	+	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca ovina aggr.	0.526	0.001	14	0	5	19	.	+	.	+	1	1	+	2	+	1	.	1	.	1	.	r	.	+	1	1	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	+	1	.	.	.	.
Helictotrichon pubescens	0.700	0.001	14	0	0	14	1	1	+	+	+	1	+	+	r	1	.	.	.	.	.	.	r	r	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Laserpitium latifolium	0.700	0.001	14	0	0	14	2	2	1	+	1	2	+	2	1	2	+	1	.	.	.	.	.	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygala chamaebuxus	0.700	0.001	14	0	0	14	r	.	.	.	+	2	+	1	+	+	1	2	1	1	+	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Prunella grandiflora	0.700	0.001	14	0	0	14	1	1	1	2	1	1	2	1	1	1	2	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Thymus pulegioides s.str.	0.535	0.001	14	2	0	16	+	+	.	1	+	1	+	1	+	+	.	r	.	.	.	+	+	.	+	+	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium murorum aggr.	0.650	0.001	13	0	0	13	.	.	+	r	.	.	+	+	+	.	.	r	.	+	+	r	+	+	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygala alpestris	0.413	0.001	13	2	1	16	+	+	+	+	.	+	.	+	.	+	.	+	.	+	.	.	+	r	r	+	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Serratula tinctoria subsp. monticola	0.650	0.001	13	0	0	13	1	1	.	.	+	+	+	+	+	+	+	1	1	1	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stachys pradica	0.545	0.001	13	1	0	14	+	+	+	+	+	+	.	+	+	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Astrantia major	0.600	0.001	12	0	0	12	+	+	.	+	+	+	+	+	.	.	.	+	2	1	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Briza media	0.600	0.001	12	0	0	12	+	+	.	.	+	+	+	+	+	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex flacca	0.600	0.001	12	0	0	12	1	+	.	.	+	.	+	.	.	.	1	1	2	+	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Linum alpinum	0.600	0.001	12	0	0	12	+	.	+	.	.	+	.	.	+	r	r	r	.	.	+	.	+	+	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Peucedanum austriacum	0.600	0.001	12	0	0	12	+	1	.	.	1	2	+	1	1	+	+	1	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium montanum	0.600	0.001	12	0	0	12	1	+	.	.	1	1	1	2	1	1	+	+	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calamagrostis varia	0.550	0.001	11	0	0	11	.	r	.	.	+	.	.	+	.	.	+	1	+	1	1	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirsium acaule	0.550	0.001	11	0	0	11	+	r	.	+	.	.	.	r	.	+	.	.	+	+	.	1	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cuscuta epithymum	0.550	0.001	11	0	0	11	.	r	.	+	+	.	1	+	+	r	r	.	+	.	.	r	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Geranium sylvaticum	0.345	0.001	11	2	0	13	1	+	+	.	+	+	+	+	+	.	.	.	.	r	.	.	.	+	.	+	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Laserpitium siler	0.550	0.001	11	0	0	11	.	+	.	.	3	3	3	4	3	3	2	3	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla crantzii	0.369	0.001	11	0	7	18	.	.	.	+	+	+	.	+	+	+	+	+	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	+	+	+	+	+	.	.	.	.
Senecio doronicum	0.537	0.001	11	0	1	12	.	.	+	+	.	.	.	.	+	r	r	r	.	.	+	r	.	r	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.
Acinos alpinus	0.479	0.001	10	1	0	11	.	+	+	1	.	1	r	+	+	+	.	+	.	.	.	+	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Primula veris subsp. columnae	0.500	0.001	10	0	0	10	.	.	.	.	+	+	r	1	+	+	+	+	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Thesium alpinum	0.288	0.005	10	0	2	12	.	.	.	+	.	.	+	r	.	.	+	+	.	+	+	.	+	r	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trollius europaeus	0.389	0.001	10	2	1	13	+	+	.	.	.	.	+	r	.	+	.	.	.	1	.	.	1	1	+	1	.	.	.	.	r	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carlina acaulis subsp. caulescens	0.180	0.009	9	0	0	9	+	+	+	1	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dianthus superbus	0.450	0.001	9	0	0	9	.	.	.	.	+	+	+	+	+	+	.	.	.	.	.	.	+	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene vulgaris s.str.	0.263	0.003	9	2	0	11	.	+	+	+	+	.	.	+	+	.	.	.	.	.	+	r	.	.	.	+	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Viola hirta	0.450	0.001	9	0	0	9	.	.	.	.	+	1	+	+	+	1	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanula thyrsoides	0.400	0.002	8	0	0	8	r	.	.	+	+	+	+	.	+	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Centaurea montana	0.400	0.001	8	0	0	8	+	+	.	.	r	.	.	.	+	.	.	.	.	.	.	.	+	1	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Centaurea scabiosa s.l.	0.400	0.001	8	0	0	8	+	+	+	.	.	.	+	+	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Euphrasia hirtella	0.240	0.003	8	2	0	10	.	.	.	.	+	.	+	.	+	.	1	+	+	.	.	.	.	.	+	+	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhinanthus alectorolophus	0.400	0.001	8	0	0	8	+	+	.	.	1	+	1	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene nutans s.str.	0.245	0.002	8	0	0	8	.	.	r	.	+	1	.	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anemone narcissiflora	0.350	0.001	7	0	0	7	.	.	.	1	.	.	+	+	.	.	.	.	1	1	.	.	+	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aposeris foetida	0.350	0.001	7	0	0	7	+	+	+	.	.	.	.	.	.	.	.	.	r	1	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lilium martagon	0.350	0.002	7	0	0	7	.	.	r	r	r	r	.	.	r	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pimpinella major	0.225	0.001	7	2	0	9	.	+	1	+	.	.	.	+	+	.	.	.	.	.	.	.	.	.	1	+	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cotoneaster integerrimus	0.300	0.001	6	0	0	6	.	.	.	.	+	+	.	+	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Plot name							M2844_1	M2844_2	M3110_1	M3110_2	M3126_1	M3126_2	M3127_1	M3127_2	M3128_1	M3128_2	M3138_1	M3138_2	M3139_1	M3139_2	M3140_1	M3140_2	M3141_1	M3141_2	M3150_1	M3150_2	M2976_1	M2976bis_2	M2980_1	M2980_2	M3109_1	M3109_2	M3132_1	M3132_2	M3592_1	M3592_2	M4121_1	M4121_2	R239_1	R239_2	R331_1	R331_2	R3901_1	R3901_2	R4003_1	R4003_2	R4005_1	R4005_2	R4224_1	R4224_2	R4225_1	R4225_2	R4472_1	R4472_2	R4482_1	R4482_2	R5066_1	R5066_2	R5145_1	R5145_2
Crepis pyrenaica	0.221	0.009	6	1	0	7	+	.	1	+	.	.	.	.	+	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Knautia dipsacifolia s.str.	0.300	0.001	6	0	0	6	.	r	+	.	.	.	.	.	.	.	.	.	.	.	+	+	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Onobrychis montana	0.300	0.004	6	0	0	6	1	2	.	.	.	.	.	.	.	.	.	.	+	+	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pedicularis foliosa	0.300	0.002	6	0	0	6	+	.	+	.	.	.	.	.	.	.	.	.	1	+	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantago media	0.300	0.002	6	0	0	6	1	1	.	.	r	+	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium rubens	0.300	0.001	6	0	0	6	.	.	.	.	+	.	.	.	+	.	1	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanula glomerata s.str.	0.250	0.002	5	0	0	5	.	.	.	.	+	r	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex montana	0.250	0.002	5	0	0	5	2	2	.	.	.	.	.	.	.	.	.	+	.	2	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Euphrasia salisburgensis	0.185	0.008	5	0	2	7	.	.	.	.	.	.	+	.	+	.	.	.	.	.	1	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Globularia cordifolia	0.152	0.031	5	0	2	7	.	.	.	1	.	+	.	+	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	2	.	.	.	.	.	.	.	.
Globularia nudicaulis	0.250	0.001	5	0	0	5	.	.	.	.	.	.	.	.	.	.	2	2	1	1	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Helictotrichon pratense	0.250	0.001	5	0	0	5	.	.	.	.	.	+	+	2	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium pilosum	0.231	0.003	5	1	0	6	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	+	.	+	+	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Origanum vulgare	0.250	0.004	5	0	0	5	.	+	.	.	+	.	+	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantago lanceolata	0.250	0.001	5	0	0	5	1	.	+	.	r	.	.	.	.	.	.	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhinanthus glacialis	0.171	0.006	5	1	0	6	.	.	1	+	.	.	.	.	.	.	1	.	1	.	.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sanguisorba minor s.str.	0.250	0.002	5	0	0	5	+	1	.	.	+	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tephroseris capitata	0.250	0.002	5	0	0	5	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	r	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Turritis glabra	0.250	0.004	5	0	0	5	r	.	.	.	+	+	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Allium schoenoprasum	0.200	0.005	4	0	0	4	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	r	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Buphthalmum salicifolium	0.200	0.002	4	0	0	4	.	.	.	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carlina biebersteinii	0.200	0.008	4	0	0	4	.	.	.	.	.	.	+	.	.	.	r	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dactylis glomerata	0.200	0.013	4	0	0	4	.	2	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lathyrus pratensis	0.200	0.009	4	0	0	4	.	.	.	.	.	+	r	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygonatum odoratum	0.200	0.011	4	0	0	4	.	.	.	.	+	+	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla erecta	0.145	0.044	4	1	0	5	1	+	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium medium	0.200	0.013	4	0	0	4	.	1	.	.	.	.	.	.	.	+	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Allium lusitanicum	0.150	0.01	3	0	0	3	.	.	.	.	.	.	.	.	+	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arrhenatherum elatius	0.150	0.014	3	0	0	3	.	.	.	.	.	.	+	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Chaerophyllum villarsii	0.111	0.048	3	1	0	4	+	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crepis bocconei	0.150	0.017	3	0	0	3	+	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium prenanthoides aggr.	0.150	0.018	3	0	0	3	+	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Listera ovata	0.150	0.017	3	0	0	3	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pedicularis ascendens	0.150	0.019	3	0	0	3	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rosa pendulina	0.150	0.012	3	0	0	3	.	.	.	.	.	+	.	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Teucrium montanum	0.150	0.023	3	0	0	3	.	.	.	.	.	r	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Valeriana officinalis aggr.	0.150	0.015	3	0	0	3	.	.	.	.	r	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Geranium sanguineum	0.100	0.042	2	0	0	2	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lathyrus occidentalis	0.100	0.043	2	0	0	2	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Characteristic species of *Poion alpinae* (2)																																																												
Alchemilla vulgaris aggr.	0.786	0.001	7	8	0	15	.	r	+	+	.	.	.	.	.	.	.	.	r	r	.	r	.	r	.	.	+	1	1	1	3	3	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ligusticum mutellina	0.576	0.001	1	8	3	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	2	1	2	2	+	+	1	2	1	+	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantago alpina	0.658	0.001	0	8	3	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	3	2	1	+	2	1	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.
Plantago atrata s.str.	0.716	0.001	9	8	6	23	1	1	+	1	.	.	.	+	.	+	.	+	.	.	.	+	.	+	.	.	2	+	1	+	1	1	1	2	.	.	.	.	1	+	.	.	.	.	.	.	.	r	.	.	.	.	.	r	.	.	1	1	.	.
Soldanella alpina	0.707	0.001	5	8	11	24	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	+	+	r	+	2	1	2	2	1	+	1	+	1	+	.	.	2	2	.	+	.	.	1	.	.	.	.	r	.	+	.	.	.	.	1	1	.	+
Cirsium spinosissimum	0.463	0.001	0	7	4	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	1	+	+	+	1	.	.	.	.	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
Leontodon hispidus s.str.	0.609	0.001	3	7	7	17	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	.	+	+	2	2	1	2	2	.	+	.	.	.	+	+	1	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	r	.	1
Phleum alpinum aggr.	0.495	0.001	1	7	0	8	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	1	.	+	+	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sagina saginoides	0.406	0.001	0	7	2	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	+	r	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	r	.	.
Trifolium badium	0.471	0.001	3	7	2	12	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	r	+	+	1	.	2	1	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Trifolium thalii	0.842	0.001	0	7	0	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	2	2	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca violacea aggr.	0.203	0.021	9	6	13	28	.	.	2	2	.	.	.	.	1	+	.	.	.	.	.	2	+	1	1	2	1	+	1	1	.	+	1	.	+	2	.	+	1	+	2	2	.	.	.	.	.	+	.	.	.	+	.	+	.	.	.	+	3	2
Poa alpina	0.263	0.01	3	6	20	29	.	.	.	+	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	1	+	2	2	2	2	+	.	.	+	1	+	+	+	+	1	1	+	+	+	+	.	+	.	+	1	.	.	1	1	1	1
Carex atrata aggr.	0.357	0.002	0	5	5	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	+	r	.	.	+	.	.	+	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.
Crepis aurea	0.502	0.001	0	5	2	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	2	2	.	1	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Deschampsia cespitosa	0.520	0.001	0	5	0	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	1	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana bavarica	0.248	0.005	0	5	4	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	.	.	1	.	.	.	.	.	+	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
Ranunculus tuberosus	0.461	0.001	7	5	0	12	.	1	+	r	.	.	.	.	.	.	.	.	.	.	.	r	.	+	+	+	.	.	.	r	+	+	+	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rumex alpestris	0.581	0.001	0	5	0	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	+	+	r	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula spicata s.l.	0.186	0.018	0	4	4	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	+	.	+	+	.	r	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.
Ranunculus acris subsp. friesianus	0.450	0.001	1	4	0	5	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	2	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica serpyllifolia subsp. humifusa	0.500	0.001	0	4	0	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis capillaris	0.237	0.004	9	3	0	12	+	+	.	.	+	+	+	+	+	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	+	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex ferruginea	0.244	0.002	3	3	0	6	.	+	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	r	2	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium fontanum subsp. vulgare	0.375	0.001	0	3	0	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crocus albiflorus	0.274	0.004	7	3	0	10	+	.	.	+	.	r	.	r	r	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	1	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana purpurea	0.265	0.002	0	3	0	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa supina	0.304	0.001	0	3	0	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Primula elatior s.str.	0.239	0.001	2	3	0	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	r	.	.	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Adenostyles alliariae	0.217	0.001	0	2	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dactylorhiza fuchsii	0.160	0.013	2	2	0	4	r	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum maculatum s.l.	0.188	0.009	1	2	0	3	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus aconitifolius	0.250	0.003	0	2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Taraxacum officinale aggr.	0.250	0.002	0	2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veratrum album s.l.	0.114	0.047	1	2	0	3	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Characteristic species of *Elynion myosuroides* (3)																																																												
Sesleria caerulea	0.588	0.001	19	0	25	44	1	.	+	+	1	2	2	1	2	+	1	1	1	1	1	+	2	1	1	1	.	.	.	.	.	.	.	.	+	+	3	2	2	2	2	1	.	+	3	3	+	1	1	2	3	3	+	1	3	2	2	2	2	+

Plot name							M2844_1	M2844_2	M3110_1	M3110_2	M3126_1	M3126_2	M3127_1	M3127_2	M3128_1	M3128_2	M3138_1	M3138_2	M3139_1	M3139_2	M3140_1	M3140_2	M3141_1	M3141_2	M3150_1	M3150_2	M2976_1	M2976bis_2	M2980_1	M2980_2	M3109_1	M3109_2	M3132_1	M3132_2	M3592_1	M3592_2	M4121_1	M4121_2	R239_1	R239_2	R331_1	R331_2	R3901_1	R3901_2	R4003_1	R4003_2	R4005_1	R4005_2	R4224_1	R4224_2	R4225_1	R4225_2	R4472_1	R4472_2	R4482_1	R4482_2	R5066_1	R5066_2	R5145_1	R5145_2
Polygonum viviparum	0.221	0.017	13	6	23	42	1	+	+	1	+	.	+	+	.	.	.	.	+	+	.	.	+	1	1	+	2	1	1	1	+	.	1	.	1	1	1	2	2	2	1	+	1	+	1	+	.	+	1	r	1	+	1	.	+	+	1	+	.	+
Elyna myosuroides	0.793	0.001	0	0	21	21	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	+	.	3	3	3	2	2	2	2	+	2	+	3	3	2	r	2	2	3	1
Pedicularis verticillata	0.704	0.001	2	0	20	22	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	+	+	+	1	1	+	+	1	+	2	1	.	+	+	.	.	.	1	+	+	+	+	+	.	+
Gentiana verna	0.427	0.001	7	2	19	28	+	.	.	+	.	.	r	r	.	.	.	+	.	.	.	.	.	.	+	r	.	.	.	.	+	+	.	.	.	.	+	.	.	+	.	+	+	+	1	1	+	+	.	1	.	+	+	+	+	+	1	+	+	+
Festuca quadriflora	0.647	0.001	1	0	18	19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	1	1	.	1	.	.	2	1	2	2	.	1	1	2	1	2	1	1	2	2	.	.	2	1
Ligusticum mutellinoides	0.463	0.001	0	0	17	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	1	+	1	.	.	r	+	r	.	.	+	+	+	.	+	+	+	+
Silene exscapa	0.275	0.003	0	0	15	15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	+	1	+	+	.	+	1	r	.	.	+	1	.	.	+	1	+	+
Agrostis alpina	0.348	0.001	1	0	14	15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	.	1	.	.	1	2	2	1	.	+	2	1	.	+	1	1
Androsace obtusifolia	0.344	0.002	0	0	14	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	r	1	+	+	+	.	+	.	r	.	.	+	+	.	.	.	+	+	+
Salix reticulata	0.519	0.001	0	0	14	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	1	+	2	+	2	2	.	.	.	.	2	3	.	.	.	.	+	+	.	.	.	.	3	2
Saxifraga paniculata	0.463	0.001	0	0	14	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	r	.	r	+	1	.	.	.	.	.	+	1	+	+	+	+	+	.	.	1	r
Minuartia verna	0.399	0.001	0	0	12	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	1	+	+	+	.	.	.	+	+	+	+	+	+	+	.	.	.	.
Aster alpinus	0.276	0.003	5	0	11	16	.	.	+	.	.	.	.	.	.	.	.	r	.	.	.	.	1	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	+	.	.	+	.	1	.	+	+	1	r	.	.	+	.
Bartsia alpina	0.164	0.037	2	3	11	16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	1	r	+	.	.	.	.	.	.	.	.	1	+	+	1	.	.	.	.	1	1	.	.	.	.	.	.	+	.	1	1	1	+
Dryas octopetala	0.423	0.001	0	0	11	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	3	.	.	+	+	.	.	.	.	.	.	3	2	+	+	+	.	.	.	.	.	2	2
Parnassia palustris	0.218	0.007	0	0	11	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	r	.	.	+	.	.	.	.	.	.	.	+	+	2	+	.	.	1	+	.	.	1	+
Salix retusa	0.303	0.001	0	2	11	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	5	3	2	1	2	2	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3	.	1
Draba aizoides	0.302	0.001	0	0	10	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	+	+	.	+	.	r	r	.	+	+	.	.	.	r	.	.
Erigeron uniflorus	0.221	0.003	0	0	10	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	+	+	+	.	r	.	.	.	.	+	+	.	.	.	+	.	.
Gentiana brachyphylla	0.262	0.003	0	0	10	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	r	.	r	.	.	+	+	.	.	.	.	+	.	.	+	.	+	r	.	.	.	.	.
Gentiana nivalis	0.319	0.001	0	0	10	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	+	.	+	+	1	.	.	.	.	.	+	.	.	+	+	r	.	+	.	.
Antennaria carpatica	0.257	0.005	0	0	9	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	r	.	.	+	2	.	.	.	.	+	.	.	.	1	2	.	.	.	.	+	+
Aster bellidiastrum	0.160	0.041	7	3	9	19	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	+	+	1	+	+	.	r	.	+	r	.	.	.	.	+	.	.	1	+	+	1	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	+	.	2
Gentiana campestris s.str.	0.142	0.045	5	1	9	15	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	.	.	+	+	.	.	.	.	.	r	.	.	.	.	+	.	.	.	.	+	.	.	r	+	.	.	.	.	.	+	.	.	+	+	r	.	r	.	.
Salix serpillifolia	0.143	0.044	0	0	9	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	+	.	+	.	+	+	1	+	.	.	.	.	.
Silene acaulis	0.223	0.005	0	0	9	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	+	2	.	.	.	+	.	.	.	+	.	+	.	.	.	+	.	.	.	+	.	.	.	.
Leontopodium alpinum	0.308	0.001	0	0	8	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	+	+	.	.	.	.	1	+	.	.	1	1	.	.	.	.
Arenaria ciliata	0.162	0.018	0	0	7	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	1	.	.	.	.	+	.	.	.	+	.	.	.	r	.	r
Saxifraga exarata subsp. moschata	0.209	0.007	0	0	7	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	1	1	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.
Carex ericetorum	0.231	0.004	0	0	6	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	+	1	+	.	.	1	2	.	.	.	.
Potentilla frigida	0.231	0.005	0	0	6	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	+	+	.	.	.	r	.	.
Ranunculus alpestris	0.149	0.01	0	1	6	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	2	2	2	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga aizoides	0.133	0.029	0	0	6	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	r	+	.	+	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.
Sedum atratum	0.231	0.005	0	0	6	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	r	.	.	.	+	.	.	+	+	.	.
Carex ornithopodioides	0.192	0.01	0	0	5	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	2	+	.	.	.	.	.	.	.	.	1	+	.	.
Lloydia serotina	0.192	0.01	0	0	5	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	2	r	.	.	.	.	.	.	.	.	+	.
Polygala alpina	0.183	0.007	0	0	5	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	r	.	+	.	.	.	+	.	+	.	.
Sempervivum arachnoideum	0.150	0.016	0	0	5	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.
Veronica aphylla	0.192	0.003	0	0	5	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	1	.	+
Oxytropis campestris s.str.	0.154	0.029	0	0	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	.	.	.	.	.	.	.	.	2	2	.	.	.	.	.	.
Oxytropis lapponica	0.154	0.024	0	0	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.
Gentiana tenella	0.115	0.038	0	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.
Pedicularis oederi	0.115	0.039	0	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Companion species																																																													
Campanula scheuchzeri	0.258	0.001	5	8	18	31	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	+	.	1	.	+	r	+	+	+	+	+	+	.	+	.	.	+	+	.	+	.	r	1	+	.	+	1	+	+	+	.	+	+	+	+	+	.	+
Anthoxanthum odoratum aggr.	0.366	0.001	18	5	5	28	1	+	1	1	1	r	+	+	1	1	+	+	+	+	.	.	+	1	1	1	.	.	.	1	2	1	+	1	.	+	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+
Festuca rubra aggr.	0.419	0.001	15	7	0	22	+	1	1	1	1	+	.	+	.	1	+	.	1	1	.	.	+	2	+	2	.	2	1	2	1	2	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga oppositifolia	0.340	0.001	0	0	19	19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	1	+	+	r	+	.	+	.	2	+	+	r	+	r	+	+	.	.	+	+	.	.
Homogyne alpina	0.115	0.445	3	2	12	17	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	+	.	1	.	.	.	.	+	+	.	.	1	+	+	1	.	.	+	.	.	.	.	r	.	r	.	.	.	.	+	+	.	1
Myosotis alpestris	0.093	0.39	5	3	9	17	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	r	.	.	+	+	.	.	+	.	+	+	.	.	+	+	+	+	2	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+
Selaginella selaginoides	0.192	0.024	0	2	12	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	+	.	.	.	+	+	+	.	.	.	+	.	.	r	+	.	+	.	r	.	.	+	+	.	+
Sempervivum montanum	0.236	0.008	0	0	12	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	1	+	+	+	.	.	.	+	.	.	+	+	.	.	.	+	+	+
Botrychium lunaria	0.153	0.033	5	1	5	11	r	.	.	.	.	r	.	r	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	r	+	+	.	.	.	.	.	.	r	+	.	.	.	.	.	.
Euphrasia minima	0.462	0.001	0	2	9	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	r	.	.	.	+	+	+	+	.	.	r	.	.	.	.	.	.	.	+	.	.	.	+	.	r
Helictotrichon versicolor	0.310	0.001	0	0	10	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	+	+	.	.	.	+	.	.	.	.	+	.	.	.	+	+	1
Pulsatilla vernalis	0.161	0.036	0	0	10	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	+	+	+	+	.	+	+	+	.	.	.	r
Carex ornithopoda	0.072	0.278	3	2	4	9	.	.	.	+	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	r	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	1	.	1	.	.	.	1	.	.	.	.	.
Potentilla aurea	0.375	0.001	1	4	4	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	1	.	r	+	.	.	.	.	.	r	.	r	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Veronica fruticans	0.164	0.033	1	0	8	9	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	1	1	+	+	.	.	.	+	.	.	+	+	.	.	.	.	.	.
Carex parviflora	0.338	0.001	0	0	8	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	r	.	.	1	1	.	.	.	.	+	.	.	.	2	+	.	.
Cerastium arvense subsp. strictum	0.222	0.007	2	1	5	8	.	.	.	.	.	+	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	r	.	r	+	r	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Coeloglossum viride	0.236	0.002	4	2	2	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	r	+	.	.	.	.	+	.	.	+	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Nigritella rhellicani	0.169	0.023	8	0	0	8	.	.	r	r	.	.	.	.	.	+	.	.	.	.	.	r	r	r	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Erigeron alpinus	0.116	0.054	4	0	3	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.
Luzula alpinopilosa	0.190	0.033	0	4	3	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.	+	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Arabis ciliata	0.077	0.191	4	1	1	6	.	.	.	.	.	.	r	r	.	r	.	.	.	.	.	.	.	.	r	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arctostaphylos uva-ursi	0.108	0.069	2	0	4	6	.	.	.	.	.	.	.	.	.	.	2	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	3	.	.	1	+	.	.	.	.
Carex curvula s.str.	0.698	0.001	0	0	6	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	.	.	2	2	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.
Hieracium angustifolium	0.154	0.031	0	0	6	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	r	.	.	.	r	.	r	.	r	.	+
Leontodon helveticus	0.337	0.002	0	1	5	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	1	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	r	.	+
Achillea millefolium	0.098	0.088	4	1	0	5	.	+	.	.	.	r	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ajuga reptans	0.113	0.05	3	2	0	5	.	.	+	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Antennaria dioica	0.126	0.072	1	0	4	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	+	.	.	+	+	.	.	.	.
Helianthemum alpestre	0.094	0.071	3	0	2	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	2	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula lutea	0.145	0.025	0	0	5	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	r	.	+
Salix herbacea	0.368	0.001	0	3	2	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	1	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Saxifraga bryoides	0.064	0.515	0	0	5	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	r	.	.	.	r	.	+
Thymus praecox subsp. polytrichus	0.218	0.009	0	0	5	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	1	+	.	+	.	1	.	.	.	.

Plot name							M2844_1	M2844_2	M3110_1	M3110_2	M3126_1	M3126_2	M3127_1	M3127_2	M3128_1	M3128_2	M3138_1	M3138_2	M3139_1	M3139_2	M3140_1	M3140_2	M3141_1	M3141_2	M3150_1	M3150_2	M2976_1	M2976bis_2	M2980_1	M2980_2	M3109_1	M3109_2	M3132_1	M3132_2	M3592_1	M3592_2	M4121_1	M4121_2	R239_1	R239_2	R331_1	R331_2	R3901_1	R3901_2	R4003_1	R4003_2	R4005_1	R4005_2	R4224_1	R4224_2	R4225_1	R4225_2	R4472_1	R4472_2	R4482_1	R4482_2	R5066_1	R5066_2	R5145_1	R5145_2
Vaccinium vitis-idaea	0.121	0.056	1	0	4	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.
Veronica alpina	0.220	0.004	0	2	3	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	r	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Casual species																																																												
Achillea nana	0.082	0.141	0	0	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	+
Calluna vulgaris	0.307	0.004	0	0	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	.	.	r	.	.	.	.	.
Campanula rotundifolia	0.097	0.078	3	0	1	4	.	.	.	.	.	.	.	.	.	.	.	r	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Juniperus communis subsp. nana	0.218	0.009	4	0	0	4	.	.	.	.	r	+	r	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Minuartia sedoides	0.421	0.001	0	0	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	1	.	.	.
Primula farinosa	0.074	0.226	1	0	3	4	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	+	.	.
Pseudorchis albida	0.048	0.56	2	0	2	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Viola calcarata	0.090	0.114	0	0	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.
Arabis caerulea	0.169	0.009	0	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.
Carex capillaris	0.079	0.145	0	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	1	.	.	.
Cerastium cerastoides	0.248	0.002	0	3	0	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Erigeron neglectus	0.076	0.101	0	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	+	.	.	.	.
Gnaphalium supinum	0.262	0.006	0	3	0	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium bifidum aggr.	0.068	0.299	1	0	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Luzula multiflora	0.196	0.014	1	1	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pritzelago alpina s.str.	0.131	0.034	0	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhododendron ferrugineum	0.104	0.117	0	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r
Sempervivum tectorum subsp. alpinum	0.061	0.317	2	0	1	3	.	.	.	.	.	+	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Sibbaldia procumbens	0.216	0.013	0	3	0	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Solidago virgaurea subsp. minuta	0.308	0.002	2	0	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Taraxacum alpinum aggr.	0.468	0.001	0	3	0	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Thalictrum minus subsp. saxatile	0.072	0.179	2	0	1	3	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Vaccinium gaultherioides	0.183	0.013	0	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Veronica bellidioides	0.196	0.014	0	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Vicia sepium	0.101	0.113	2	1	0	3	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis rupestris	0.264	0.005	0	2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Allium victorialis	0.100	0.056	2	0	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Biscutella laevigata	0.026	0.782	1	0	1	2	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Brachypodium pinnatum	0.100	0.111	2	0	0	2	.	.	.	.	.	.	.	.	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanula cochleariifolia	0.043	0.471	1	0	1	2	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carum carvi	0.100	0.076	2	0	0	2	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Convallaria majalis	0.100	0.107	2	0	0	2	.	.	.	.	.	.	.	.	.	.	+	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Coronilla vaginalis	0.100	0.105	2	0	0	2	1	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Digitalis grandiflora	0.100	0.104	2	0	0	2	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Draba dubia	0.077	0.216	0	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Empetrum nigrum subsp. hermaphroditum	0.048	0.473	0	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Equisetum variegatum	0.167	0.024	0	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	+	.	.
Erigeron glabratus	0.077	0.2	0	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
Galium album	0.100	0.057	2	0	0	2	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gypsophila repens	0.100	0.05	2	0	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hedysarum hedysaroides	0.077	0.252	0	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium pilosella	0.234	0.003	1	0	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.
Juncus jacquinii	0.258	0.005	0	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.
Koeleria macrantha	0.100	0.113	2	0	0	2	.	.	.	.	+	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leucanthemopsis alpina	0.301	0.003	0	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mercurialis perennis	0.100	0.115	2	0	0	2	.	.	.	.	.	.	.	.	.	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Orchis mascula	0.100	0.125	2	0	0	2	.	.	.	.	.	.	.	.	.	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Oxytropis jacquinii	0.100	0.118	2	0	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Platanthera bifolia	0.100	0.06	2	0	0	2	r	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Primula auricula	0.100	0.057	2	0	0	2	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pseudolysimachion spicatum	0.100	0.12	2	0	0	2	.	.	.	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pyrola minor	0.045	0.556	0	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix appendiculata	0.100	0.062	2	0	0	2	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix foetida	0.129	0.041	0	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
Salix helvetica	0.172	0.013	0	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga androsacea	0.304	0.001	0	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stachys recta s.str.	0.100	0.065	2	0	0	2	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tragopogon pratensis s.l.	0.100	0.118	2	0	0	2	+	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium repens s.str.	0.104	0.07	1	1	0	2	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Viola rupestris	0.077	0.29	0	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.
Aconitum napellus aggr.	0.050	0.467	1	0	0	1	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis schraderiana	0.242	0.004	0	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla demissa aggr.	0.125	0.065	0	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Androsace chamaejasme	0.050	0.446	1	0	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arabis alpina s.str.	0.089	0.051	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arabis bellidifolia s.l.	0.038	1	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.
Arenaria multicaulis	0.050	0.455	1	0	0	1	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Asplenium ruta-muraria	0.050	0.459	1	0	0	1	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Astragalus frigidus	0.038	1	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex bicolor	0.338	0.001	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Carex caryophyllea	0.050	0.416	1	0	0	1	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex firma	0.038	1	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Carex nigra	0.127	0.075	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crepis conyzifolia	0.050	0.477	1	0	0	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dactylorhiza sambucina	0.050	0.479	1	0	0	1	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Plot name							M2844_1	M2844_2	M3110_1	M3110_2	M3126_1	M3126_2	M3127_1	M3127_2	M3128_1	M3128_2	M3138_1	M3138_2	M3139_1	M3139_2	M3140_1	M3140_2	M3141_1	M3141_2	M3150_1	M3150_2	M2976_1	M2976bis_2	M2980_1	M2980_2	M3109_1	M3109_2	M3132_1	M3132_2	M3592_1	M3592_2	M4121_1	M4121_2	R239_1	R239_2	R331_1	R331_2	R3901_1	R3901_2	R4003_1	R4003_2	R4005_1	R4005_2	R4224_1	R4224_2	R4225_1	R4225_2	R4472_1	R4472_2	R4482_1	R4482_2	R5066_1	R5066_2	R5145_1	R5145_2
Daphne mezereum	0.050	0.474	1	0	0	1	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Doronicum grandiflorum	0.089	0.044	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Draba siliquosa	0.038	1	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
Festuca halleri	0.220	0.008	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Fourraea alpina	0.050	0.48	1	0	0	1	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gagea fragifera	0.125	0.05	0	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Galium verum s.str.	0.050	0.462	1	0	0	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana acaulis	0.206	0.007	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana clusii	0.050	0.478	1	0	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana orbicularis	0.038	1	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana ramosa	0.550	0.001	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Geum montanum	0.594	0.001	0	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Globularia bisnagarica	0.050	0.469	1	0	0	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gnaphalium hoppeanum	0.038	1	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Gnaphalium norvegicum	0.064	0.313	0	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gnaphalium sylvaticum	0.125	0.052	0	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Heracleum sphondylium s.l.	0.050	0.457	1	0	0	1	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium alpinum	0.122	0.057	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Hieracium aurantiacum	0.050	0.476	1	0	0	1	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium lactucella	0.035	0.755	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.
Juncus trifidus	0.238	0.007	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Linaria alpina s.str.	0.038	1	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Loiseleuria procumbens	0.383	0.001	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.
Medicago lupulina	0.050	0.471	1	0	0	1	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Myosotis sylvatica	0.050	0.449	1	0	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Nardus stricta	0.692	0.001	0	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Orchis ustulata	0.050	0.457	1	0	0	1	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phyteuma spicatum	0.125	0.066	0	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Picea abies	0.032	0.891	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Picris hieracioides s.l.	0.050	0.491	1	0	0	1	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pinguicula alpina	0.038	1	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
Pinus cembra	0.038	1	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa minor	0.104	0.082	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa nemoralis	0.050	0.457	1	0	0	1	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla neumanniana	0.050	0.482	1	0	0	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus carinthiacus	0.050	0.456	1	0	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhamnus alpina	0.050	0.446	1	0	0	1	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rosa glauca	0.050	0.462	1	0	0	1	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rosa villosa	0.050	0.475	1	0	0	1	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rumex alpinus	0.125	0.071	0	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sedum album	0.050	0.451	1	0	0	1	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sedum dasyphyllum	0.050	0.468	1	0	0	1	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sedum rupestre aggr.	0.050	0.474	1	0	0	1	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sorbus mougeotii	0.050	0.45	1	0	0	1	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stachys alpina	0.050	0.464	1	0	0	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Thalictrum aquilegiifolium	0.050	0.483	1	0	0	1	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trisetum flavescens	0.050	0.484	1	0	0	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vaccinium myrtillus	0.160	0.02	0	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Viola biflora	0.088	0.176	0	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Appendix C4 - Plant species list of the inventories of *Nardion* and *Caricion curvulae* vegetation types, and corresponding cover classes of Braun-Blanquet (1964; see Table 4.1 for details). Within each vegetation type, plant species are classified into characteristic, companion and casual.

Plot name	ind.val	p-value	freq. (4)	freq. (5)	freq. tot.	G14_1	G14_2	G47_1	G47_2	G281_1	G281_2	G288_1	G288_2	G291_1	G291_2	G294_1	G294_2	G295_1	G295bis_2	G343_1	G343_2	G350_1	G350_2	G351_1	G351_2	G352_1	G352_2	G421_1	G421_2	G90_1	G90R_2	G92_1	G92_2	G334_1	G334_2	G335_1	G335_2	G337_1	G337_2	G338_1	G338_2	G339_1	G339_2	G340_1	G340_2	R4209_1	R4209_2	R4471_1	R4471_2	R5067_1	R5067_2
Species number						32	57	31	56	39	39	6	14	22	21	55	64	49	55	34	42	33	49	30	42	31	38	18	26	15	21	4	14	20	21	15	19	13	15	20	16	12	9	17	19	23	56	23	32	41	52
						Nardion strictae																								*Caricion curvulae*																					
Characteristic species of *Nardion strictae* (4)																																																			
Nardus stricta	0.692	0.001	24	7	31	3	2	3	2	4	3	5	2	2	2	1	1	2	2	4	+	4	3	2	1	3	3	2	3	2	2	.	.	1	+	.	+	.	.	.	.	.	.	.	.	1	2	.	.	.	.
Anthoxanthum odoratum aggr.	0.366	0.001	22	8	30	1	1	1	1	2	2	1	2	1	+	.	1	.	1	2	2	+	2	1	3	+	2	+	1	+	.	.	.	+	.	.	.	+	.	.	.	.	.	1	+	.	+	.	+	.	+
Festuca rubra aggr.	0.419	0.001	22	0	22	1	1	2	2	2	2	.	.	1	1	3	2	3	2	2	2	1	2	2	3	2	1	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanula barbata	0.811	0.001	20	1	21	1	1	1	1	1	2	.	.	.	.	1	+	1	+	1	2	1	2	+	+	1	1	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Campanula scheuchzeri	0.258	0.001	20	4	24	+	+	1	+	1	+	.	.	1	.	1	+	1	+	+	+	+	+	1	+	.	+	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	+
Euphrasia minima	0.462	0.001	20	6	26	1	+	1	1	1	+	.	+	1	+	+	+	+	+	+	+	+	.	1	+	1	+	.	.	.	r	.	.	.	.	.	.	.	+	.	r	.	.	.	.	.	+	.	+	.	+
Geum montanum	0.594	0.001	19	3	22	r	+	1	1	1	2	.	.	1	+	1	+	.	+	+	.	1	2	2	2	2	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	+	1
Potentilla aurea	0.375	0.001	19	6	25	.	.	1	2	1	1	.	.	1	+	1	1	1	+	+	+	+	+	1	+	1	1	.	1	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	1	1	2	.	+	3
Phyteuma hemisphaericum	0.460	0.001	18	14	32	1	+	1	+	.	+	.	.	+	+	1	.	1	+	+	+	+	+	+	.	.	+	1	+	r	r	.	.	1	+	1	+	+	+	.	.	.	.	.	r	+	+	r	+	.	r
Sempervivum montanum	0.236	0.008	16	10	26	r	.	1	+	.	+	.	.	.	.	+	+	.	r	+	+	r	+	+	+	.	+	+	+	.	r	.	.	r	+	1	r	.	.	.	.	.	.	.	.	1	+	+	.	2	+
Gentiana ramosa	0.550	0.001	14	0	14	r	+	.	+	1	+	.	.	+	.	1	+	1	+	.	.	.	+	r	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Selaginella selaginoides	0.192	0.024	13	2	15	.	r	1	r	.	.	.	.	.	.	.	+	1	+	r	+	r	r	r	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	+
Achillea erba-rotta subsp. moschata	0.500	0.001	12	0	12	.	r	.	+	.	.	.	.	.	.	+	+	.	.	+	.	r	+	1	+	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis schraderiana	0.242	0.004	12	0	12	.	.	1	+	1	+	.	2	.	+	.	.	.	.	r	+	+	.	.	+	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Coeloglossum viride	0.236	0.002	11	0	11	1	+	.	.	.	.	.	.	.	.	+	+	1	+	.	r	1	+	.	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium arvense subsp. strictum	0.222	0.007	10	0	10	r	+	.	+	.	.	.	.	.	.	+	+	1	+	.	.	.	r	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Solidago virgaurea subsp. minuta	0.308	0.002	10	0	10	.	+	.	.	.	r	.	.	.	.	.	+	1	+	.	+	.	r	.	+	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica fruticans	0.164	0.033	10	3	13	+	r	.	.	.	.	.	.	.	.	+	+	+	.	.	.	+	+	+	+	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	+
Calluna vulgaris	0.307	0.004	9	0	9	.	2	1	1	+	.	+	r	.	.	.	.	.	.	.	.	1	+	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Juncus trifidus	0.238	0.007	9	8	17	.	2	2	+	.	.	.	.	.	.	1	2	1	1	.	.	.	.	.	.	+	+	.	.	.	+	.	.	+	1	1	r	+	.	.	.	.	.	.	.	1	+	.	.	.	.
Pulsatilla vernalis	0.161	0.036	9	5	14	1	1	.	+	.	.	.	.	.	.	+	+	1	1	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	+	.	1	1
Thymus praecox subsp. polytrichus	0.218	0.009	9	0	9	+	+	.	+	.	.	.	.	.	.	+	+	.	+	.	.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium pratense subsp. nivale	0.375	0.001	9	0	9	.	+	.	.	.	.	.	.	.	.	1	1	.	+	.	+	.	+	r	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium pilosella	0.234	0.003	8	2	10	1	2	.	+	.	.	.	.	.	.	.	1	1	1	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	+	.	.	.	.
Luzula multiflora	0.196	0.014	8	1	9	.	+	1	r	.	+	.	.	.	.	1	r	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arnica montana	0.168	0.026	7	7	14	r	+	.	r	.	.	.	r	.	.	.	2	.	2	.	.	.	.	.	r	.	.	.	.	r	1	.	.	1	+	.	r	.	.	.	.	.	.	.	.	r	+	.	.	.	.
Botrychium lunaria	0.153	0.033	7	3	10	+	.	.	.	.	.	.	.	.	.	+	+	+	+	.	.	.	r	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	r	r
Bupleurum stellatum	0.292	0.001	7	0	7	.	+	.	+	.	r	.	.	.	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Juncus jacquinii	0.258	0.005	7	1	8	.	+	2	2	.	.	.	.	.	.	2	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
Luzula sudetica	0.292	0.001	7	0	7	.	.	.	.	.	+	.	+	.	.	.	.	+	.	1	+	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix helvetica	0.172	0.013	7	0	7	.	.	.	.	1	+	.	.	.	.	.	.	.	.	2	2	r	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana acaulis	0.206	0.007	6	2	8	.	+	.	+	.	+	.	.	.	.	.	+	1	+	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Juniperus communis subsp. nana	0.218	0.009	6	0	6	.	2	.	.	.	.	.	.	.	.	.	+	1	2	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leucanthemum vulgare aggr.	0.250	0.003	6	0	6	r	+	.	.	.	.	.	.	.	.	1	+	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Nigritella rhellicani	0.169	0.023	6	0	6	+	+	.	.	.	.	.	.	.	.	1	+	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa variegata	0.250	0.003	6	0	6	.	1	.	1	.	.	.	.	.	.	+	r	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phyteuma betonicifolium	0.208	0.002	5	0	5	.	+	.	.	.	.	.	.	.	.	1	+	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pulsatilla alpina subsp. apiifolia	0.208	0.002	5	0	5	.	.	.	+	.	.	.	.	.	.	1	1	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pedicularis tuberosa	0.131	0.046	4	1	5	.	.	.	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Potentilla grandiflora	0.167	0.016	4	0	4	.	2	.	.	.	.	.	.	.	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ajuga pyramidalis	0.125	0.027	3	0	3	.	r	.	.	.	.	.	.	.	.	.	r	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypochaeris uniflora	0.125	0.037	3	0	3	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Characteristic species of *Caricion curvulae* (5)																																																			
Carex curvula s.str.	0.698	0.001	2	22	24	.	.	.	.	.	.	.	.	4	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	2	1	2	4	3	3	3	2	2	1	+	+	+	+	1	2	1	2	2	2	2
Leontodon helveticus	0.337	0.002	17	21	38	.	.	1	1	1	1	.	1	2	3	.	.	.	.	1	1	1	+	1	1	+	+	+	1	1	1	.	+	2	+	2	+	1	2	+	1	+	+	+	1	1	1	1	2	+	+
Helictotrichon versicolor	0.310	0.001	16	17	33	1	1	1	+	.	+	.	.	1	1	1	+	1	1	.	.	.	+	.	.	+	+	2	1	+	1	.	+	1	+	1	1	+	2	+	+	.	.	.	.	1	1	1	+	+	1
Agrostis rupestris	0.264	0.005	10	14	24	2	.	1	.	1	+	.	.	1	.	.	.	.	.	2	+	.	+	.	+	.	.	+	.	.	.	.	2	1	+	1	+	.	+	.	+	.	+	.	+	1	1	+	+	.	+
Leucanthemopsis alpina	0.301	0.003	7	13	20	.	.	+	.	+	.	.	.	+	+	.	.	.	.	.	.	.	.	+	+	.	.	+	.	1	.	1	r	.	.	.	.	.	.	1	+	1	+	1	1	+	+	2	+	.	.
Minuartia sedoides	0.421	0.001	3	12	15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	3	2	2	2	1	+	1	+	+	+	+	+
Loiseleuria procumbens	0.383	0.001	3	10	13	.	.	1	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	3	3	3	3	3	2	.	.	.	.	.	.	.	.	+	1	.	.
Hieracium piliferum aggr.	0.222	0.002	5	8	13	.	.	.	.	1	.	+	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	1	.	+	.	.	1	+	1	+	+	+	.	.	+	.	.	.	.	.	.	.	.	.
Trifolium alpinum	0.211	0.011	11	8	19	.	1	.	+	.	+	.	.	2	+	+	.	2	2	.	.	.	.	.	+	.	.	+	+	r	1	.	.	2	2	.	2	.	.	.	.	.	.	.	.	4	3	.	.	.	r
Vaccinium gaultherioides	0.183	0.013	2	8	10	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	+	+	+	+	r	1	1	.	.	.	.	.	.	.	.	.	.	.	.
Veronica bellidioides	0.196	0.014	9	7	16	+	.	.	+	.	.	.	.	.	.	+	r	+	.	.	.	.	+	+	+	.	.	.	r	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	2	1	2	+	1	1
Festuca halleri	0.220	0.008	0	6	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	+	1	2	2
Hieracium angustifolium	0.154	0.031	4	6	10	.	+	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+
Poa laxa	0.273	0.007	0	6	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	+	+	1	1	.	.	.	.	.	.
Vaccinium myrtillus	0.160	0.02	3	6	9	.	.	.	1	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	+	.	.	.	+	.	+	.	+	.	.	.	.	.	.	.	r	.	.	.	.
Diphasiastrum alpinum	0.199	0.023	1	5	6	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	+	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
Luzula lutea	0.145	0.025	2	5	7	.	+	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	+	.	.	.	.	.	.	.	.	.	+	1	.	.	.
Sedum alpestre	0.154	0.026	1	5	6	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	r	.	.	+	.	.	+	.	+	.	.
Senecio incanus s.str.	0.136	0.02	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	2	+
Companion species																																																			
Carex sempervirens	0.519	0.001	20	6	26	2	1	2	3	1	2	.	.	+	+	1	2	3	2	+	+	2	+	.	+	2	1	.	+	r	+	.	.	1	+	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.

Plot name						G14_1	G14_2	G47_1	G47_2	G281_1	G281_2	G288_1	G288_2	G291_1	G291_2	G294_1	G294_2	G295_1	G295bis_2	G343_1	G343_2	G350_1	G350_2	G351_1	G351_2	G352_1	G352_2	G421_1	G421_2	G90_1	G90R_2	G92_1	G92_2	G334_1	G334_2	G335_1	G335_2	G337_1	G337_2	G338_1	G338_2	G339_1	G339_2	G340_1	G340_2	R4209_1	R4209_2	R4471_1	R4471_2	R5067_1	R5067_2
Homogyne alpina	0.115	0.445	13	12	25	.	.	1	+	1	1	.	+	+	+	.	.	+	.	.	+	.	+	.	.	+	+	+	.	1	1	.	+	.	.	.	.	1	+	.	+	.	.	.	+	.	+	+	+	r	+
Galium anisophyllon	0.264	0.003	19	2	21	1	+	.	+	1	+	.	.	.	.	1	+	1	+	+	+	+	+	+	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	+
Salix herbacea	0.368	0.001	6	13	19	.	.	1	+	1	+	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	r	.	1	.	.	.	.	+	2	1	+	1	2	+	1	.	+	+	+	.	.
Lotus corniculatus	0.414	0.001	17	1	18	+	+	1	1	1	+	.	.	.	.	+	+	1	+	.	+	+	1	.	2	+	1	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Ligusticum mutellina	0.576	0.001	11	7	18	.	.	+	+	.	+	1	+	1	+	.	r	1	.	.	.	.	.	.	.	.	.	+	+	1	1	.	1	+	.	.	.	+	.	2	.	.	.	.	.	.	.	+	.	.	.
Poa alpina	0.263	0.01	9	7	16	.	.	.	.	1	+	.	.	.	.	+	.	.	.	+	.	r	+	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	+	+	1	+	+
Gnaphalium supinum	0.262	0.006	4	11	15	.	.	+	.	+	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	2	.	.	.	.	.	.	+	+	+	+	1	1	.	+	+	+	.	.
Soldanella pusilla	0.246	0.004	7	6	13	.	.	1	+	.	.	.	.	.	+	.	+	+	+	.	.	.	.	.	.	.	.	r	.	.	+	1	1	.	.	.	.	.	+	.	.	.	.	+	2	.	.	.	.	.	.
Luzula spicata s.l.	0.186	0.018	10	3	13	+	.	.	+	+	+	.	.	+	.	+	.	.	.	.	.	.	+	.	r	+	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	.	r	.	.
Antennaria dioica	0.126	0.072	8	4	12	.	1	.	.	+	+	.	.	.	.	+	+	1	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	2	+	.	.	.	.
Ranunculus montanus aggr.	0.313	0.001	10	2	12	r	.	1	1	+	+	.	.	.	.	1	+	1	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	+
Myosotis alpestris	0.093	0.39	8	3	11	.	+	.	+	.	.	.	.	.	.	1	+	1	+	.	.	.	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	+
Silene exscapa	0.275	0.003	5	6	11	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	1	+	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	+	r	.	.	.	.	+	+
Trifolium badium	0.471	0.001	10	0	10	.	.	.	.	1	.	.	.	.	.	+	.	.	.	1	1	1	2	1	+	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Parnassia palustris	0.218	0.007	10	0	10	.	+	.	.	.	.	.	.	.	.	+	+	1	+	+	+	2	+	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis alpina	0.348	0.001	8	1	9	.	1	.	+	.	.	.	.	.	.	.	1	.	+	+	+	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Luzula alpinopilosa	0.190	0.033	2	6	8	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	+	.	1	2	.	.	.	+	.	.
Cirsium spinosissimum	0.463	0.001	8	0	8	.	.	.	+	1	.	.	.	.	.	.	.	.	.	+	.	r	r	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bartsia alpina	0.164	0.037	7	1	8	.	.	.	.	1	+	.	.	.	.	.	.	.	.	1	+	r	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
Polygonum viviparum	0.221	0.017	5	3	8	.	+	.	+	.	.	.	.	.	.	+	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+
Cardamine resedifolia	0.088	0.15	5	2	7	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	r	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.
Thesium alpinum	0.288	0.005	6	1	7	r	+	.	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Leontodon hispidus s.str.	0.609	0.001	6	1	7	.	.	.	.	.	.	.	.	.	.	2	1	1	+	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Sibbaldia procumbens	0.216	0.013	3	3	6	.	.	.	r	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	+
Veronica alpina	0.220	0.004	2	4	6	.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	+	.	.	.	r	.	.
Hieracium alpinum	0.122	0.057	2	4	6	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	.	+	.	.	.	.	.	.	.	.	.	.
Carlina acaulis subsp. caulescens	0.180	0.009	6	0	6	.	1	.	.	.	.	.	.	1	.	2	2	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene nutans s.str.	0.245	0.002	6	0	6	r	+	.	.	.	.	.	.	.	.	1	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phleum alpinum aggr.	0.495	0.001	5	1	6	.	.	.	1	1	.	.	.	.	.	1	+	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Erigeron uniflorus	0.221	0.003	4	2	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	+	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
Avenella flexuosa	0.094	0.063	2	3	5	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga bryoides	0.064	0.515	2	3	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	r	.	.	.	.	.	.	.	+	.	.
Gentiana nivalis	0.319	0.001	5	0	5	.	r	.	.	.	.	.	.	.	.	.	.	+	.	.	.	r	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Primula farinosa	0.074	0.226	4	0	4	r	+	.	.	.	.	.	.	.	.	+	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Primula hirsuta	0.061	0.285	2	2	4	.	+	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r	.	.
Gentiana punctata	0.082	0.111	1	3	4	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	r	.	.	.	.	.	.	+	.	.	.	.	.	.
Silene rupestris	0.047	0.509	2	2	4	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.
Vaccinium vitis-idaea	0.121	0.056	0	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla vulgaris aggr.	0.786	0.001	4	0	4	.	.	.	.	1	.	.	.	.	.	.	+	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crepis aurea	0.502	0.001	4	0	4	.	.	.	1	1	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca violacea aggr.	0.203	0.021	3	1	4	.	+	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Plantago alpina	0.658	0.001	0	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	2	.	.	+	1
Androsace obtusifolia	0.344	0.002	2	2	4	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.
Salix retusa	0.303	0.001	4	0	4	.	.	.	.	+	.	.	.	.	.	.	.	.	.	1	r	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Casual species																																																			
Rhododendron ferrugineum	0.104	0.117	3	0	3	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Viola biflora	0.088	0.176	3	0	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	r	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus kuepferi	0.090	0.086	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	+
Anthyllis vulneraria subsp. alpestris	0.493	0.001	2	1	3	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Gentiana bavarica	0.248	0.005	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	.	.	.	.	.	.	.
Antennaria carpatica	0.257	0.005	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	1	1
Ligusticum mutellinoides	0.463	0.001	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	+
Saxifraga exarata subsp. moschata	0.209	0.007	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	+	+
Alchemilla pentaphyllea	0.770	0.001	1	1	2	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
Carex foetida	0.912	0.001	2	0	2	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cardamine alpina	0.253	0.003	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	r	.	.
Cerastium pedunculatum	0.297	0.005	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.
Salix foetida	0.129	0.041	2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga seguieri	0.234	0.004	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	+	.	.	.	.	.	.	.
Pseudorchis albida	0.048	0.56	2	0	2	.	.	.	.	.	.	.	.	.	.	.	+	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Achillea nana	0.082	0.141	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+
Pyrola minor	0.045	0.556	2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Viola calcarata	0.090	0.114	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+
Gnaphalium norvegicum	0.064	0.313	2	0	2	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pinguicula leptoceras	0.083	0.176	2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Viola palustris	0.083	0.152	2	0	2	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana alpina	0.091	0.136	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	+	.	.	.	.
Huperzia selago	0.024	0.924	1	1	2	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Minuartia recurva	0.091	0.163	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.
Euphrasia hirtella	0.240	0.003	2	0	2	.	.	.	.	.	.	.	.	.	.	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Scabiosa lucida	0.619	0.001	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
Gentiana purpurea	0.265	0.002	2	0	2	.	.	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Soldanella alpina	0.707	0.001	1	1	2	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Trifolium thalii	0.842	0.001	2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veratrum album s.l.	0.114	0.047	2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Draba aizoides	0.302	0.001	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
Elyna myosuroides	0.793	0.001	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r
Festuca quadriflora	0.647	0.001	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
Gentiana brachyphylla	0.262	0.003	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+

Plot name						G14_1	G14_2	G47_1	G47_2	G281_1	G281_2	G288_1	G288_2	G291_1	G291_2	G294_1	G294_2	G295_1	G295bis_2	G343_1	G343_2	G350_1	G350_2	G351_1	G351_2	G352_1	G352_2	G421_1	G421_2	G90_1	G90R_2	G92_1	G92_2	G334_1	G334_2	G335_1	G335_2	G337_1	G337_2	G338_1	G338_2	G339_1	G339_2	G340_1	G340_2	R4209_1	R4209_2	R4471_1	R4471_2	R5067_1	R5067_2
Gentiana campestris s.str.	0.142	0.045	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+
Gentiana verna	0.427	0.001	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
Minuartia verna	0.399	0.001	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r
Salix serpillifolia	0.143	0.044	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	3
Sempervivum arachnoideum	0.150	0.016	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r
Doronicum clusii	0.131	0.029	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Saxifraga stellaris	0.483	0.001	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Biscutella laevigata	0.026	0.782	1	0	1	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex ornithopoda	0.072	0.278	1	0	1	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Empetrum nigrum subsp. hermaphroditum	0.048	0.473	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Picea abies	0.032	0.891	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla alpina	0.042	0.794	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Chamorchis alpina	0.042	0.819	1	0	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cystopteris fragilis	0.042	0.782	1	0	1	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium intybaceum	0.042	0.838	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium lactucella	0.035	0.755	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Peucedanum ostruthium	0.042	0.825	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phyteuma ovatum	0.042	0.822	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa chaixii	0.042	0.801	1	0	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polystichum lonchitis	0.042	0.809	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix breviserrata	0.042	0.799	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca acuminata	0.045	0.618	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.
Larix decidua	0.045	0.612	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
Pedicularis kerneri	0.045	0.652	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene suecica	0.045	0.623	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Arenaria biflora	0.072	0.265	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Carex nigra	0.127	0.075	1	0	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Epilobium nutans	0.052	0.32	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eriophorum angustifolium	0.110	0.054	1	0	1	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Geranium sylvaticum	0.345	0.001	1	0	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gymnadenia conopsea	0.739	0.001	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Helianthemum nummularium s.l.	0.762	0.001	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
Potentilla erecta	0.145	0.044	1	0	1	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhinanthus glacialis	0.171	0.006	1	0	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene vulgaris s.str.	0.263	0.003	1	0	1	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis capillaris	0.237	0.004	1	0	1	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dactylorhiza fuchsii	0.160	0.013	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Deschampsia cespitosa	0.520	0.001	1	0	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantago atrata s.str.	0.716	0.001	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
Rumex alpestris	0.581	0.001	1	0	1	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arenaria ciliata	0.162	0.018	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Aster bellidiastrum	0.160	0.041	1	0	1	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygala alpina	0.183	0.007	1	0	1	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga paniculata	0.463	0.001	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Silene acaulis	0.223	0.005	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Appendix C5 - Plant species list of the inventories of *Salicion herbaceae* and *Caricion bicolori-atrofuscae* vegetation types, and corresponding cover classes of Braun-Blanquet (1964; see Table 4.1 for details). Within each vegetation type, plant species are classified into characteristic, companion and casual.

Plot name						G336_1	G336_2	G341_1	G341_2	G404_1	G404_2	G405_1	G405_2	G417_1	G417_2	R264_1	R264R_2	R267_1	R267R_2	R3935_1	R3935_2	R4468_1	R4468_2	R3934_1	R3934_2	R3937_1	R3937_2	R4216_1	R4216_2	R4983_1	R4983_2	R5061_1	R5061_2	R5062_1	R5062_2	R5069_1	R5069_2	R5141_1	R5141_2
Species number						7	12	14	16	9	11	10	19	14	20	10	18	8	7	16	25	13	22	19	23	14	28	17	23	12	17	11	13	19	31	14	33	19	33
	ind.val	p-value	freq. (6)	freq. (7)	freq. tot.	*Salicion herbaceae*																		*Caricion bicolori-atrofuscae*															
Characteristic species of *Salicion herbaceae* (6)																																							
Carex foetida	0.912	0.001	16	0	16	+	2	.	r	4	2	r	1	4	3	2	+	4	4	.	+	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla pentaphyllea	0.770	0.001	15	2	17	.	.	2	2	2	1	3	3	1	1	4	3	2	.	+	1	4	3	.	.	.	+	.	.	.	.	.	.	.	r	.	.	.	.
Gnaphalium supinum	0.262	0.006	13	7	20	r	+	1	.	.	r	.	+	r	.	+	2	1	1	+	1	1	.	.	.	.	r	.	.	1	+	.	.	+	+	.	r	.	r
Luzula alpinopilosa	0.190	0.033	8	4	12	.	.	4	3	r	.	.	1	1	2	.	.	.	.	.	.	+	+	.	.	.	.	.	.	1	2	.	.	.	.	.	.	2	3
Sibbaldia procumbens	0.216	0.013	9	5	14	.	.	.	.	.	.	.	.	+	r	1	1	2	.	+	+	1	1	.	.	.	r	.	r	.	.	.	.	.	+	.	r	.	+
Soldanella pusilla	0.246	0.004	8	1	9	.	+	1	2	1	1	2	2	.	r	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.
Characteristic species of *Caricion bicolori-atrofuscae* (7)																																							
Salix herbacea	0.368	0.001	10	15	25	.	.	2	+	1	3	3	1	.	.	2	3	.	.	+	3	.	.	+	1	1	.	1	1	1	2	4	3	+	1	+	1	3	2
Taraxacum alpinum aggr.	0.468	0.001	5	12	17	.	.	1	.	.	.	.	.	.	.	.	+	.	.	+	+	.	r	+	1	+	+	1	+	+	+	.	.	2	1	.	1	.	+
Saxifraga stellaris	0.483	0.001	5	11	16	r	+	1	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	r	.	.	r	.	+	r	+	1	+	+	1	r	.	.
Cerastium cerastoides	0.248	0.002	11	9	20	r	+	.	.	+	r	1	.	.	.	.	+	.	+	+	+	1	+	+	.	.	+	.	.	1	+	+	+	+	+	+	.	.	.
Saxifraga oppositifolia	0.340	0.001	0	10	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	+	+	+	.	.	2	2	.	.	+	2	1	r
Carex parviflora	0.338	0.001	1	9	10	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	+	.	2	+	1	+	+	1	2	.	.	.	.	.	.
Veronica alpina	0.220	0.004	8	8	16	.	.	1	+	.	+	.	+	.	+	.	+	.	.	+	+	.	.	.	+	.	r	.	.	+	+	.	.	2	+	.	1	.	+
Oxyria digyna	0.412	0.001	1	6	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	+	+	+	+
Carex bicolor	0.338	0.001	0	6	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2	2	1	+	.	.	.	.	.	.	.	.	.	.
Cerastium pedunculatum	0.297	0.005	0	6	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	.	2	+	+	.	+	.
Juncus triglumis	0.353	0.001	0	6	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	2	+	2	+	.	.	.	.	.	.	.	.	.	.
Saxifraga androsacea	0.304	0.001	2	5	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	+	.	.	.	.	.	.	.	.	.	.	1	+	.	+	1	+	.	.
Cardamine alpina	0.253	0.003	2	4	6	.	.	.	.	.	.	.	.	.	r	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	+	.	.	+	+	.	.	.	.
Carex lachenalii	0.224	0.006	3	5	8	.	.	.	.	.	.	r	.	.	.	.	+	.	.	.	.	+	.	+	.	.	.	+	+	.	.	1	1	.	.	.	.	.	.
Ranunculus glacialis	0.294	0.004	0	5	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	2	1	.	.	.	+
Saxifraga seguieri	0.234	0.004	1	4	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	2	1
Arabis caerulea	0.169	0.009	1	3	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	1	+	.	.
Equisetum variegatum	0.167	0.024	0	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.	.	.
Salix foetida	0.129	0.041	0	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	1	.	.	.	.	.	.	.	.	+	.
Cerastium uniflorum	0.176	0.015	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	1
Doronicum clusii	0.131	0.029	1	3	4	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	2	1
Pritzelago alpina s.str.	0.131	0.034	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	1	1	.	.
Agrostis stolonifera	0.118	0.036	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.
Doronicum grandiflorum	0.089	0.044	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.
Juncus alpinoarticulatus	0.118	0.048	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Minuartia biflora	0.118	0.027	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	r	.	.	.	.	.	.
Companion species																																							
Poa alpina	0.263	0.01	12	14	26	.	+	2	+	.	.	r	.	+	.	.	+	1	2	1	1	+	+	+	+	+	2	+	.	.	+	+	+	1	2	+	+	+	+
Polygonum viviparum	0.221	0.017	3	12	15	.	.	.	.	.	.	.	.	.	.	2	+	.	.	.	+	.	.	1	1	1	2	+	1	.	.	2	2	.	+	.	r	2	+
Leontodon helveticus	0.337	0.002	7	6	13	.	r	.	2	.	.	.	1	r	+	.	.	.	+	.	.	.	1	.	1	.	+	.	.	.	r	.	.	1	+	.	.	.	2
Sagina saginoides	0.406	0.001	4	9	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	+	r	+	+	+	+	.	.	.	.	+	.	1	+	1	r	.	.
Gentiana bavarica	0.248	0.005	2	9	11	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	+	+	.	+	.	+	2	1	.	.	1	+	.	.	.	+
Leucanthemopsis alpina	0.301	0.003	7	4	11	r	r	1	r	.	.	.	r	.	+	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	+	.	.	1	+
Nardus stricta	0.692	0.001	10	0	10	.	r	.	.	+	2	2	2	r	+	.	1	.	.	.	+	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantago alpina	0.658	0.001	4	6	10	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	1	+	+	+	+	+	+	1	2	.	.	.	.	.	.	.	.	.	.
Campanula scheuchzeri	0.258	0.001	1	8	9	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	r	.	r	.	.	+	.	+	+	.	+	+	+
Homogyne alpina	0.115	0.445	7	2	9	.	.	1	2	.	.	r	1	.	+	.	.	.	.	.	+	.	1	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	+
Cirsium spinosissimum	0.463	0.001	4	4	8	.	.	.	+	.	.	.	.	+	1	.	.	.	.	.	+	.	.	+	+	r	+	.	.	.	.	.	.	.	.	.	.	.	.
Festuca violacea aggr.	0.203	0.021	2	5	7	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	+	.	1	2	1
Alchemilla vulgaris aggr.	0.786	0.001	4	2	6	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	.	+	+	+	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex nigra	0.127	0.075	3	3	6	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	+	3	3	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Ligusticum mutellina	0.576	0.001	6	0	6	.	.	.	2	+	+	.	2	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phleum alpinum aggr.	0.495	0.001	6	0	6	.	.	1	.	r	+	r	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anthoxanthum odoratum aggr.	0.366	0.001	5	0	5	.	.	.	1	.	.	.	+	+	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Euphrasia minima	0.462	0.001	1	4	5	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	+	.	+	.	.	.	+
Geum montanum	0.594	0.001	4	1	5	.	.	.	.	.	.	.	r	+	1	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Agrostis schraderiana	0.242	0.004	3	1	4	.	.	.	.	.	.	.	+	1	2	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bartsia alpina	0.164	0.037	1	3	4	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	+	.	.	+	.
Carex curvula s.str.	0.698	0.001	4	0	4	r	+	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Helictotrichon versicolor	0.310	0.001	4	0	4	.	.	.	.	.	r	.	1	.	.	.	+	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene exscapa	0.275	0.003	1	3	4	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	1	+
Agrostis rupestris	0.264	0.005	3	0	3	.	+	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Epilobium anagallidifolium	0.101	0.141	1	2	3	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Ligusticum mutellinoides	0.463	0.001	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	+
Myosotis alpestris	0.093	0.39	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	1	+
Potentilla aurea	0.375	0.001	3	0	3	.	.	.	.	.	.	.	.	r	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga bryoides	0.064	0.515	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	1
Silene acaulis	0.223	0.005	0	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1	.	.	.	.	.	.	.	+	.	.
Casual species																																							
Androsace alpina	0.118	0.052	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	.	.	.
Androsace obtusifolia	0.344	0.002	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+
Arabis alpina s.str.	0.089	0.051	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r
Arenaria biflora	0.072	0.265	2	0	2	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arenaria ciliata	0.162	0.018	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
Carex atrata aggr.	0.357	0.002	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Carex capillaris	0.079	0.145	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	.	.	.	.	.	.	.	.	.	.
Deschampsia cespitosa	0.520	0.001	1	1	2	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Erigeron uniflorus	0.221	0.003	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	r
Eriophorum angustifolium	0.110	0.054	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Festuca halleri	0.220	0.008	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Luzula spicata s.l.	0.186	0.018	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Minuartia verna	0.399	0.001	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r
Poa minor	0.104	0.082	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	+	.	.
Poa supina	0.304	0.001	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Pritzelago alpina subsp. brevicaulis	0.053	0.413	2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus alpestris	0.149	0.01	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	2	.	.
Ranunculus kuepferi	0.090	0.086	2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus montanus aggr.	0.313	0.001	2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix helvetica	0.172	0.013	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	r	.	.	.	.	.	.	.	.	.	.
Saxifraga aizoides	0.133	0.029	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sedum alpestre	0.154	0.026	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	r
Selaginella selaginoides	0.192	0.024	0	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	r	.	.	.	.	.	.	.	.	.	.
Agrostis alpina	0.348	0.001	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arabis subcoriacea	0.059	0.339	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Aster bellidiastrum	0.160	0.041	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
Cardamine resedifolia	0.088	0.15	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r
Carex flava	0.059	0.337	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex frigida	0.059	0.341	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium arvense subsp. strictum	0.222	0.007	1	0	1	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Epilobium nutans	0.052	0.32	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Erigeron neglectus	0.076	0.101	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Eriophorum scheuchzeri	0.059	0.31	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Gentiana punctata	0.082	0.111	1	0	1	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana verna	0.427	0.001	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Leontodon hispidus s.str.	0.609	0.001	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula multiflora	0.196	0.014	1	0	1	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Minuartia sedoides	0.421	0.001	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Phyteuma hemisphaericum	0.460	0.001	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Salix reticulata	0.519	0.001	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.

Plot name						G336_1	G336_2	G341_1	G341_2	G404_1	G404_2	G405_1	G405_2	G417_1	G417_2	R264_1	R264R_2	R267_1	R267R_2	R3935_1	R3935_2	R4468_1	R4468_2	R3934_1	R3934_2	R3937_1	R3937_2	R4216_1	R4216_2	R4983_1	R4983_2	R5061_1	R5061_2	R5062_1	R5062_2	R5069_1	R5069_2	R5141_1	R5141_2
Salix retusa	0.303	0.001	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Trifolium alpinum	0.211	0.011	1	0	1	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium badium	0.471	0.001	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica bellidioides	0.196	0.014	0	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+

Appendix C6 - Plant species list of the recent inventories discarded from the Vegetation study (Appendix C2), and corresponding cover classes of Braun-Blanquet (1964; see Table 4.1 for details). (r) : species occurring in the historical inventories that were just outside the plot area in the recent inventory.

Plot name	**M2716**	**M2976**	**M2965-6**	**M3167**	**M3167R**	**G38**	**G39**	**G90**	**G283**	**G286**	**G401**	**G403**	**R264**	**R267**	**R3900**	**R3912**	**R3913**	**R4217**	**R4469**	**R4470**	**R5140**	**R5144**
Species number	52	43	45	46	14	13	6	22	33	24	28	22	35	24	35	40	36	29	32	42	24	48
Species name																						
Achillea atrata	r	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Achillea erba-rotta subsp. moschata	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Achillea nana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+
Adenostyles alliariae	2	.	.	2	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis alpina	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Agrostis rupestris	.	+	.	.	.	.	.	.	(r)	.	+	.	.	1	.	.	.	1	+	+	.	.
Agrostis schraderiana	.	2	.	.	.	1	.	.	+	.	1	1	.	.	.	.	.	.	.	.	.	1
Agrostis stolonifera	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Ajuga pyramidalis	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Ajuga reptans	.	.	.	r	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla conjuncta aggr.	+	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla fissa	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla pentaphyllea	.	.	.	.	.	3	1	.	.	.	.	3	4	+	.	2	2	.	.	.	.	.
Alchemilla vulgaris aggr.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Allium schoenoprasum	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Androsace alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Androsace obtusifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	r	+	.	.	.	.	.
Antennaria carpatica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
Anthoxanthum alpinum	+	.	.	.	.	.	.	.	2	1	+	+	.	.	.	.	.	.	.	.	.	+
Anthyllis vulneraria ssp. alpestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Anthyllis vulneraria subsp. alpestris	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aposeris foetida	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arabis alpina	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arabis caerulea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	+	.	.
Arenaria ciliata	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r
Arnica montana	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aster alpinus	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aster bellidiastrum	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Athyrium filix-femina	.	.	.	.	.	.	.	.	(r)	.	.	.	.	.	.	.	.	.	.	.	.	.
Bartsia alpina	+	1	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	(r)	+	+
Briza media	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calamagrostis varia	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calluna vulgaris	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanula barbata	.	.	.	.	.	.	.	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.
Campanula scheuchzeri	+	+	.	+	+	.	.	.	+	+	+	.	+	+	r	.	.	.	r	1	+	+
Cardamine alpina	+	.	.	+	.	.	.	.	.	.	.	.	+	.	+	+	r	.	.	.	.	.
Cardamine resedifolia	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.
Carduus defloratus	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex atrata s.l.	+	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex bicolor	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	+	1	.	.	.	.
Carex brunnescens	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
Carex capillaris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Carex cf parviflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Carex curvula	.	.	.	.	.	.	.	2	.	+	+	r	.	+	.	+	+	.	1	.	2	.
Carex ferruginea	+	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex flacca	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex foetida	.	.	.	.	.	1	.	.	.	.	.	.	+	1	.	.	.	+	.	.	.	.
Carex lachenalii	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.
Carex nigra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	+	.	.	.	.
Carex ornithopodioides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Carex parviflora	.	.	.	.	.	.	.	.	.	.	.	.	+	.	2	.	(r)	1	.	+	.	.
Carex sempervirens	+	+	3	1	.	.	.	+	2	3	2	+	.	.	.	.	.	.	.	.	.	.
Carlina acaulis subsp. caulescens	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Centaurea montana	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium arvense ssp. strictum	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Cerastium cerastoides	.	.	.	.	.	r	.	.	.	.	.	.	+	.	1	r	.	.	.	.	.	.
Cirsium spinosissimum	.	.	.	.	.	.	.	.	1	.	.	.	+	.	+	.	.	.	.	1	.	.
Cirsium spinossisimum	2	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Coeloglossum viride	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
Crepis aurea	1	2	.	+	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
Daphne mezereum	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Deschampsia cespitosa	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Doronicum clusii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Doronicum grandiflorum	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Draba aizoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Dryas octopetala	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Elyna myosuroides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	+	.	2
Empetrum nigrum	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Epilobium alsinifolium	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Epilobium anagallidifolium	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.
Epilobium nutans	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
Equisetum variegatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.
Erigeron uniflorus	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	+	+	.	.
Eriophorum angustifolium	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
Eriophorum scheuchzeri	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Euphorbia cyparissias	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Euphrasia hirtella	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Euphrasia minima	+	+	.	+	.	.	.	+	+	+	+	r	.	r	.	r	1	+	+	+	r	.
Euphrasia salisburgensis	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca diffusa	+	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca halleri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	+	+	.
Festuca laevigata s.l.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca melanopsis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Festuca nigrescens	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca quadriflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+
Festuca rubra aggr.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Festuca violacea aggr.	1	.	.	2	+	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	+	2
Festuca violacea s.str.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Galium anisophyllon	1	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana acaulis	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana bavarica	+	.	.	+	.	.	.	.	.	.	.	.	+	.	+	r	+	+	.	+	.	.
Gentiana campestris	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
Gentiana cf campestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Gentiana cf punctata	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana clusii	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana nivalis	+	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	+	.	+	.	.
Gentiana purpurea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	(r)	.	.	.	.	.
Gentiana tenella	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Gentiana verna	.	.	+	.	.	.	.	.	.	.	.	r	+	1	+	+	.	.	.	.	.	+
Geum montanum	.	.	.	.	.	.	.	.	1	2	r	+	1	r	.	r	2	.	2	.	.	.
Globularia cordifolia	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Globularia nudicaulis	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Plot name	M2716	M2976	M2965-6	M3167	M3167R	G38	G39	G90	G283	G286	G401	G403	R264	R267	R3900	R3912	R3913	R4217	R4469	R4470	R5140	R5144
Gnaphalium supinum	.	+	.	.	.	(r)	.	.	.	.	+	+	+	1	+	1	2	+	+	.	.	.
Gymnadenia conopsea	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gymnadenia odoratissima	.	.	(r)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gypsophila repens	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hedysarum hedysaroides	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Helianthemum nummularium subsp. grandiflorum	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Helictotrichon versicolor	.	.	.	.	.	(r)	.	1	r	1	+	1	.	.	.	.	.	.	.	.	.	.
Helictotricon versicolor	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	2	1	.	1	.	1	1
Hieracium alpinum	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium angustifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.
Hieracium bifidum aggr.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Hieracium murorum aggr.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium piliferum	.	.	.	.	.	.	.	+	.	r	.	.	.	.	.	.	.	.	+	.	.	.
Hieracium pilosum	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hippocrepis comosa	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Homogyne alpina	+	+	.	r	.	.	.	2	+	+	+	1	1	.	.	+	+	.	.	+	.	+
Huperzia selago	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
Juncus filiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.
Juncus jacquinii	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.
Juncus trifidus	.	.	.	.	.	.	.	+	.	.	r	.	.	.	.	.	.	.	.	.	.	.
Juncus triglumis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Juniperus communis subsp. nana	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Juniperus nana	.	.	.	.	.	.	.	(r)	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Larix decidua	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Leontodon helveticus	.	+	.	.	.	.	.	1	+	1	1	+	1	3	r	1	1	r	1	+	+	.
Leontodon hispidus	1	2	.	+	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	1
Leucanthemopsis alpina	.	.	.	.	.	.	.	.	.	.	r	.	+	2	+	+	+	.	.	r	+	.
Leucanthemum adustum	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ligusticum mutellina	+	+	.	.	.	1	.	1	.	+	+	2	.	.	.	.	.	.	.	.	.	.
Ligusticum mutellinoides	.	.	.	.	.	.	.	.	.	.	.	.	+	r	1	+	+	.	.	+	+	+
Linaria alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	(r)	.	.
Linum catharticum	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lloydia serotina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Loiseleuria procumbens	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	3	.
Lotus corniculatus	.	.	+	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	r	.	.	.
Luzula alpinopilosa	1	+	.	2	.	1	+	.	.	.	+	.	.	.	.	+	+	.	.	.	1	.
Luzula lutea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Luzula multiflora	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
Luzula spicata	.	.	.	.	.	.	.	.	.	.	.	.	r	+	.	.	.	.	+	r	.	.
Minuartia sedoides	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	+	.	+	.
Minuartia verna	.	.	.	r	r	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	r	.
Myosotis alpestris	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	.	.	.
Nardus stricta	.	.	.	.	.	2	1	3	2	3	1	2	1	.	.	.	.	.	2	.	.	.
Nigritella rhellicani	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Onobrychis montana	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Oxyria digyna	.	.	.	.	(r)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Parnassia palustris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Pedicularis ascendens	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pedicularis verticillata	r	.	.	+	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	+
Petasites paradoxus	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Peucedanum ostruthium	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phleum alpinum subsp. rhaeticum	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phleum hirsutum	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phleum rhaeticum	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Phyteuma betonicifolium	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
Phyteuma hemisphaericum	.	.	.	.	.	.	.	r	.	+	+	.	.	.	.	.	.	.	.	.	.	.
Phyteuma orbiculare	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phyteuma spicatum	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Picea abies	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	(r)
Pinguicula alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Pinus cembra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Plantago alpina	1	1	.	.	.	.	.	.	.	.	.	.	+	1	.	+	+	+	2	1	.	.
Plantago atrata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Poa alpina	+	.	.	1	1	.	.	.	+	.	+	.	+	1	2	1	+	+	+	+	.	+
Polygala alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r
Polygala chamaebuxus	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygonum viviparum	+	+	+	+	.	.	.	.	.	.	.	.	1	.	+	1	+	+	.	+	+	+
Polystichum lonchitis	.	.	.	.	.	.	.	.	(r)	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla aurea	.	+	.	.	.	.	.	.	2	1	.	.	+	.	.	1	r	.	2	.	.	.
Primula farinosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Primula veris	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pritzelago alpina	.	.	.	+	1	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Pritzelago alpina brevicaulis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Prunella grandiflora	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pulsatilla alpina s.str.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pyrola minor	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r
Ranunculus alpestris	2	+	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus glacialis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	+	.	.
Ranunculus kuepferi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	3	.	1	.	.	.
Ranunculus montanus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.
Ranunculus montanus aggr.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus tuberosus	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhododendron ferrugineum	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Sagina saginoides	.	.	.	r	.	.	.	.	.	.	.	.	+	+	.	+	+	.	.	.	.	.
Salix foetida	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	2
Salix helvetica	.	.	.	.	.	.	.	.	(r)	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix herbacea	+	+	.	2	.	1	3	.	.	.	2	1	2	r	+	3	3	3	.	.	1	.
Salix reticulata	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	2
Salix retusa	+	1	.	2	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	1
Saxifraga aizoides	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	r
Saxifraga androsacea	r	.	.	+	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Saxifraga bryoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
Saxifraga exarata subsp. moschata	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga oppositifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	+	+	+
Saxifraga oppositifolia s.str.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga paniculata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Saxifraga seguieri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	r	.	.	.	.	.
Saxifraga stellaris	.	.	.	+	.	.	.	.	.	.	+	.	.	.	r	+	+	.	.	.	.	.
Scabiosa lucida	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sedum alpestre	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Sedum atratum	+	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Selaginella selaginoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	r	.	.	.	+
Selaginella selaginoides	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sempervivum montanum	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	1	.	.	r
Senecio incanus s.str.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	+	.	.	.
Serratula tinctoria subsp. monticola	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sesleria caerulea	+	+	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Sibbaldia procumbens	.	+	.	.	.	.	.	.	.	.	.	.	1	+	+	+	.	+	r	.	.	.
Silene acaulis	.	.	.	+	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	+
Silene exscapa	.	.	.	.	.	.	.	.	.	.	+	.	.	1	.	+	+	.	+	1	+	.
Silene rupestris	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
Silene suecica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Soldanella alpina	2	1	.	+	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.
Soldanella pusilla	.	.	.	.	.	1	+	+	.	.	1	1	.	.	.	.	(r)	.	.	r	.	.
Taraxacum alpinum	.	.	.	+	.	.	.	.	.	.	.	.	1	.	.	+	.	.	.	.	.	.
Taraxacum alpinum aggr.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	+	.	+	.	.
Taraxacum cf schroterianum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Thesium alpinum	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Thymus praecox subsp. polytrichus	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Thymus pulegioides	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tofieldia calyculata	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium alpinum	.	.	.	.	.	.	.	1	.	.	.	.	r	.	.	.	.	.	.	.	.	.
Trifolium badium	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.	+

Plot name	**M2716**	**M2976**	**M2965-6**	**M3167**	**M3167R**	**G38**	**G39**	**G90**	**G283**	**G286**	**G401**	**G403**	**R264**	**R267**	**R3900**	**R3912**	**R3913**	**R4217**	**R4469**	**R4470**	**R5140**	**R5144**
Trifolium medium	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium pratense subsp. nivale	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trollius europaeus	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vaccinium gaultherioides	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	2	1
Vaccinium myrtillus	.	+	.	.	.	.	.	+	1	r	+	r	.	.	.	.	.	.	.	.	.	.
Vaccinium uliginosum	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica alpina	+	r	.	+	+	+	.	.	.	.	.	+	+	+	1	+	+	.	.	+	.	+
Veronica aphylla	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Veronica bellidioides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
Viola biflora	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Viola calcarata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	(r)	.	r	+	.	.

D. Soil profile descriptions

A graphic soil profile description is given for 20 soil profiles, among the 46 described. These 20 profiles have been selected as representative of the main soil types encountered.

Soil nomenclature follows Baize and Girard (2009) and IUSS Working Group (2015). Nomenclature of humus forms follows Jabiol et al. (2013).

LEGEND

Ψ Bryophytes

⋔ Lichens

⌣ OLv horizon

▦ OF horizon

▩ OH horizon

▨ A horizon

⟋ OM-rich horizon (except A)

⟨ ⟨ Roots < 2mm / > 2mm

— Sharp transition

┄ Diffuse transition

⊕ Siliceous skeleton weakly weathered

⊕ Siliceous skeleton weathered

⊜ Calcareous skeleton weakly weathered

⊜ Calcareous skeleton weathered

∘ Pebbles

═ Clay

═ Silt

≡ Sand

r Fe 2+

‖ Fe 3+

REMARKS

GPS coordinates : CH 1903 system

Texture: Laser granulometer

pH: pH water measured in the laboratory

The skeleton of Morteys soil profiles was not recorded in the field

S*: surface horizon that consists of tissues of living bryophytes intermixed to a minor extent with litter (Green et al. 1993).

M2716 BRUNISOL DYSTRIQUE hemiorganique, sur colluvionnement calcaire, à MESOMULL

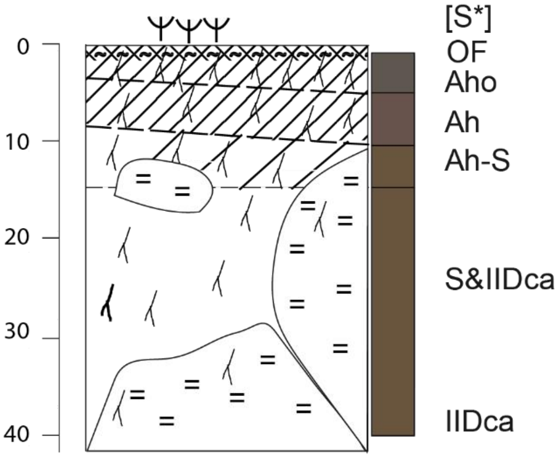
Dystric Cambisol

Station settings

Location: Morteys, Rochers des Tours
Coordinates: 578907 / 153414
Elevation: 1966 m
Description date: 3.09.2013
Vegetation type: Calcareous snowbed (*Arabidion caeruleae*)
Lithology / Surficial deposit: Limestone colluvium

Topography: depression
Aspect: 320°
Slope: 30°

Profile description



Depth (cm)	Horizon	Characteristics
0.5-0	S*	
0-0.5	OF	
0.5-3/6	Aho	Structure: micro granular / Texture: silty clay loam / Roots: many / pH: 5.5 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 3/1
3/6-8/10	Ah	Structure: micro granular / Texture: silty clay loam / Roots: common, 2-5 mm: very few / pH: 5.5 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 3/2
8/10-14	Ah-S	Structure: micro granular - blocky subangular / Texture: silty clay loam / Roots: common, > 5 mm: very few / pH: 6.5 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 3/3
14 - 32/41	S&IIDca	Structure: blocky subangular / Texture: silty clay loam / Roots: few / pH: 6.1 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 3/3
32/41 +	IIDca	

M2980 BRUNISOL DYSTRIQUE rédoxique, à OLIGOMULL

Dystric Cambisol

Station settings

Location: Morteys, Morteys Dessous

Coordinates: 578735 / 153453

Elevation: 1945 m

Description date: 24.07.2013

Vegetation type: Subalpine pasture (*Poion alpinae*)

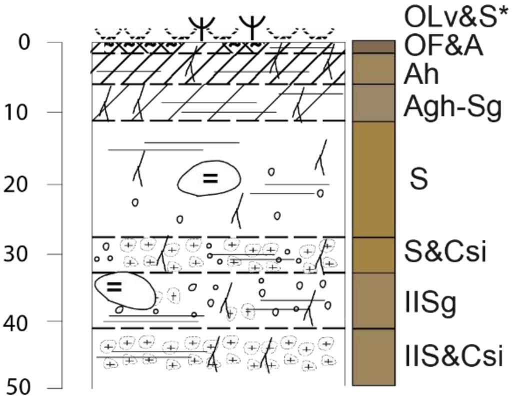
Lithology / Surficial deposit: Compact limestone

Topography: depression

Aspect: 340°

Slope: 10°

Profile description



Depth (cm)	Horizon	Characteristics
0.5-0	OLv&S*	
0-1	OF&A	Structure: -- / Texture: silty loam / Roots 0-2 mm: common / pH: 5 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 4/3
1-6	Ah	Structure: micro granular / Texture: silty clay loam / Roots 0-2 mm: very few / pH: 5 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/4
6-11	Agh-Sg	Structure: micro granular - blocky subangular / Texture: silty clay loam / Roots 0-2 mm: very few / pH: 4.8 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/3
11-28	S	Structure: blocky subangular / Texture: silty clay loam / Roots 0-2 mm: few / pH: 5.6 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/6
28-33	S&Csi	Structure: blocky subangular / Texture: silty clay loam / Roots 0-2 mm: few / pH: 5.7 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/6
33-41	IISg	Structure: blocky subangular / Texture: silty clay loam / Roots 0-2 mm: few / pH: 6.3 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/4
41-50+	IIS&Csi	Structure: blocky subangular / Texture: silty clay loam / Roots 0-2 mm: -- / pH: 7.2 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/4

M3126 CALCISOL leptique bathycarbonaté, hémiorganique, à OLIGOMULL (Rhizic)

Eutric Cambisol

Station settings

Location: Morteys, Brenleire Dessus

Coordinates: 580896 / 155961

Elevation: 1716 m

Description date: 4.07.2013

Vegetation type: Calcareous grassland (*Seslerion caeruleae*)

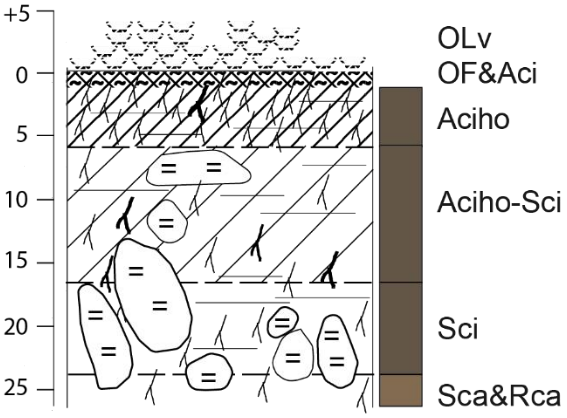
Lithology / Surficial deposit: Compact limestone

Topography: slope

Aspect: 108°

Slope: 48°

Profile description



Depth (cm)	Horizon	Characteristics
4-0	OLv	
0-2	OF&Aci	Structure: meso granular / Texture: silty clay loam / Roots 0-2 mm: many, 2-5 mm: common / pH: 6.2 / Test HCl: 0/4 / Color wet sample (Munsell): --
2-6	Aciho	Structure: meso granular / Texture: silty clay loam / Roots 0-2 mm: many, 2-5 mm: common / pH: 6.2 / Test HCl: 1/4 / Color wet sample (Munsell): 10YR 3/2
6-16	Aciho-Sci	Structure: meso granular - blocky subangular / Texture: silty clay / Roots 0-2 mm: many / pH: 6.8 / Test HCl: 1/4 / Color wet sample (Munsell): 10YR 3/2
16-24	Sci	Structure: blocky subangular / Texture: -- / Roots 0-2 mm: common / pH: -- / Test HCl: -- / Color wet sample (Munsell): 10YR 3/2. Sample not collected.
24-25 +	Sca&Rca	Structure: blocky subangular / Texture: -- / Roots 0-2 mm: common / pH: -- / Test HCl: -- / Color wet sample (Munsell): 10YR 4/3. Sample not collected.

M3138 CALCISOL bathycarbonaté leptique, à DYSMULL (Hyperhumic, Rhizic)

Calcaric Cambisol

Station settings

Location: Morteys, Les Bimis

Coordinates: 579959 / 153138

Elevation: 1711 m

Description date: 28.08.2015

Vegetation type: Calcareous grassland (*Seslerion caeruleae*)

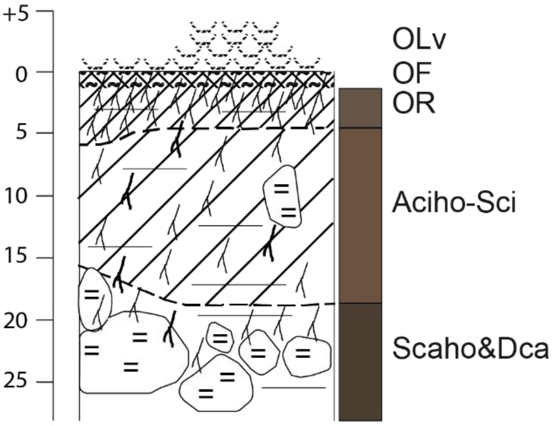
Lithology / Surficial deposit: Detritic limestone

Topography: slope

Aspect: 142°

Slope: 33°

Profile description



Depth (cm)	Horizon	Characteristics
5/2-0	OLv	
0-2	OF	
2-5/6	OR	Skeleton 2-20 mm: 10% / Structure: meso granular / Texture: silty loam / Roots 0-2 mm: many, 2-5 mm: common / pH: 6.6 / Test HCl: 0/4 / Color wet sample (Munsell): 7.5YR 3/2
5/6-16/19	Aciho-Sci	Skeleton 5-20 cm: 20% / Structure: meso granular - blocky subangular / Texture: silty loam / Roots 0-2 mm: common, > 5 mm: very few / pH: 6.6 / Test HCl: 0/4 / Color wet sample (Munsell): 7.5YR 3/3
16/19-26+	Scaho& Dca	Skeleton 5-20 cm: 70%, > 20 cm: 10% / Structure: blocky subangular / Texture: silty clay loam / Roots 0-2 mm: common, 2-5 mm: few / pH: 7 / Test HCl: 2/4 / Color wet sample (Munsell): 10YR 2/2

M3140 CALCOSOL leptique, hémiorganique, issu de colluvionnement calcaire, à charge calcaire, à OLIGOMULL (Rhizic, Skeletic)

Calcaric Cambisol

Station settings

Location: Morteys, Dent des Bimis

Coordinates: 579691 / 153559

Elevation: 1997 m

Description date: 15.07.2013

Vegetation type: Calcareous grassland (*Seslerion caeruleae*)

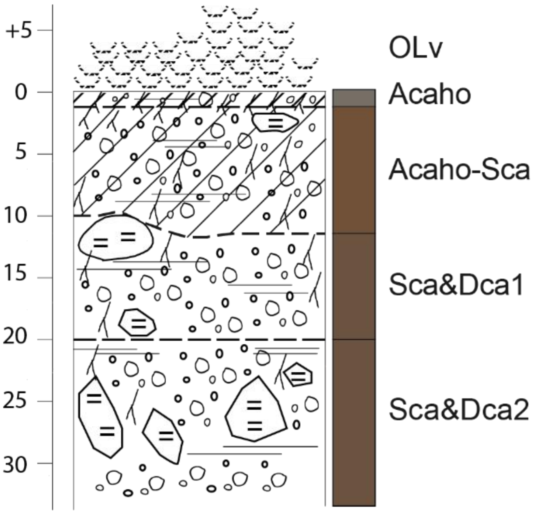
Lithology / Surficial deposit: Detritic limestone colluvium

Topography: slope

Aspect: 136°

Slope: 35°

Profile description



Depth (cm)	Horizon	Characteristics
7-0	OLv	
0-1	Acaho	Structure: meso granular / Texture: silty clay loam / Roots 0-2 mm: many / pH: 7.4 / Test HCl: 4/4 / Color wet sample (Munsell): 2.5YR 4/1
1-10/13	Acaho-Sca	Structure: meso granular - blocky subangular / Texture: silty clay loam / Roots 0-2 mm: common / pH: 7.5 / Test HCl: 4/4 / Color wet sample (Munsell): 7.5YR 3/4
10/13-20	Sca&Dca1	Structure: blocky subangular / Texture: -- / Roots 0-2 mm: common / pH: -- / Test HCl: 4/4 / Color wet sample (Munsell): 7.5YR 3/3. Sample not collected.
20-32+	Sca& Dca2	Structure: blocky subangular / Texture: -- / Roots 0-2 mm: very few / pH: -- / Test HCl: 4/4 / Color wet sample (Munsell): 7.5YR 3/3. Sample not collected.

M4121 LITHOSOL holorganique, à Hyperlithic PARAHUMUS (Rhizic)

Rendzic Leptosol Hyperhumic

Station settings

Location: Morteys, Selles des Morteys

Coordinates: 578145 / 154108

Elevation: 2180 m

Description date: 25.07.2013

Vegetation type: Calcareous snowbed (*Arabidion caeruleae*)

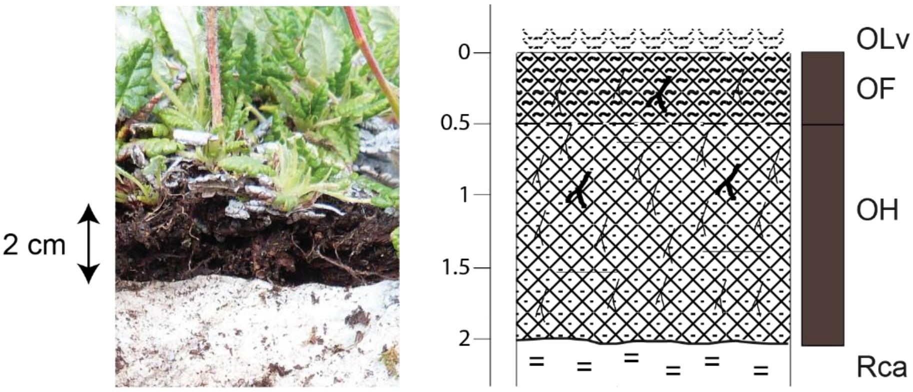
Lithology / Surficial deposit: Compact limestone

Topography: slope

Aspect: 330°

Slope: 50°

Profile description



Depth (cm)	Horizon	Characteristics
0.2-0	OLv	
0-0.5	OF	
0.5-2	OH	Structure: -- / Texture: silty loam / Roots: many / pH: -- / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 2/2
2+	Rca	Test HCl: 4/4

G336 PODZOSOL MEUBLE leptique, développé dans un paléo Podzosol Meuble, à HEMIMODER (Bryoic)

Leptic Entic Podzol

Station settings

Location: Grimsel, Jostsee

Coordinates: 667218 / 155531

Elevation: 2497 m

Description date: 15.08.2013

Vegetation type: Typical snowbed (*Salicion herbaceae*)

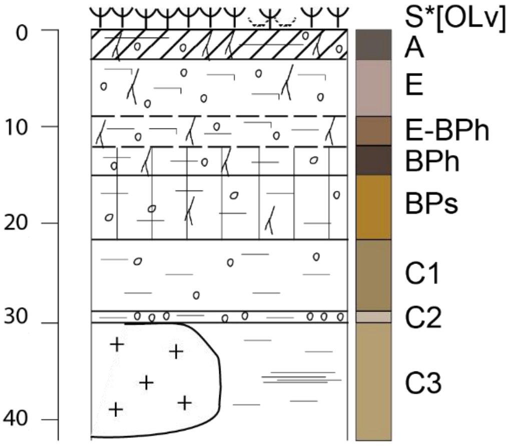
Lithology / Surficial deposit: Aar-Granite

Topography: depression

Aspect: 0°

Slope: 0°

Profile description



Depth (cm)	Horizon	Characteristics
	S*[OLv]	
0-3	A	Skeleton 2-20 mm: -- / Structure: single grain / Texture: silty loam / Roots 0-2 mm: common / pH: 4.1 / Test HCl: 0/4 / Color wet sample (Munsell): 7.5YR 3/1
3-9	E	Skeleton 2-20 mm: present / Structure: single grain / Texture: sandy loam / Roots 0-2 mm: common / pH: 4.4 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5YR 6/2
9-12	E-BPh	Skeleton 2-20 mm: present / Structure: single grain / Texture: sandy loam / Roots 0-2 mm: common / pH: 4.3 / Test HCl: 0/4 / Color wet sample (Munsell): 7.5YR 4/4
12-15	BPh	Skeleton 2-20 mm: present / Structure: single grain / Texture: sandy loam / Roots 0-2 mm: common / pH: 4.8 / Test HCl: 0/4 / Color wet sample (Munsell): 5YR 2.5/2
15 - 22	BPs	Skeleton 2-20 mm: present / Structure: single grain / Texture: sandy loam / Roots 0-2 mm: -- / pH: 5 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 5/8
22-28	C1	Skeleton 2-20 mm: present / Structure: -- / Texture: sandy loam / Roots 0-2 mm: -- / pH: 5 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/4
28-30	C2	Skeleton 2-20 mm: present / Structure: -- / Texture: loamy sand / Roots 0-2 mm: -- / pH: 5 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 7/2
30 - 46+	C3	Skeleton 2-20 mm: present + silty pouch / Structure: -- / Texture: sandy loam / Roots 0-2 mm: -- / pH: 5.2 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 6/4

G403 RANKOSOL alpin, graveleux, leptique, podzolisé, hémiorganique, à HEMIMODER

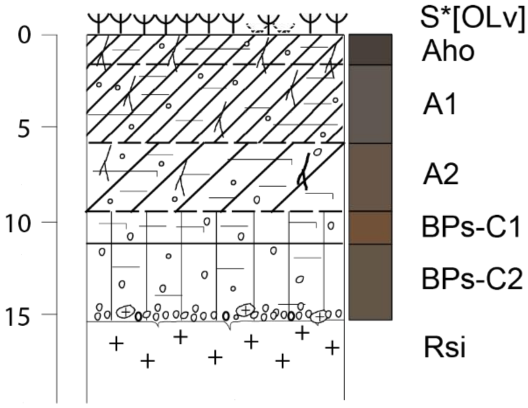
Umbric Leptosol

Station settings

Location: Grimsel, Oberaarsee
Coordinates: 663076 / 155424
Elevation: 2313 m
Description date: 27.08.2013
Vegetation type: Typical snowbed (*Salicion herbaceae*)
Lithology / Surficial deposit: Acidic moraine

Topography: depression
Aspect: 0°
Slope: 20°

Profile description



Depth (cm)	Horizon	Characteristics
1-0	S*[OLv]	
0-2	Aho	Skeleton 2-20 mm: present / Structure: single grain / Texture: silty loam / Roots 0-2 mm: common / pH: 4.6 / Test HCl: 0/4 / Color wet sample (Munsell): 7.5YR 2.5/1
2-6	A1	Skeleton 2-20 mm: present / Structure: single grain / Texture: silty loam / Roots 0-2 mm: common / pH: 4.7 / Test HCl: 0/4 / Color wet sample (Munsell): 7.5YR 3/1
6-9.5	A2	Skeleton 2-20 mm: present / Structure: single grain / Texture: silty loam / Roots 0-2 mm: common / pH: 5 / Test HCl: 0/4 / Color wet sample (Munsell): 7.5YR 3/2
9.5-11.5	BPs-C1	Skeleton 2-20 mm: present / Structure: single grain / Texture: sandy loam / Roots 0-2 mm: common / pH: 4.9 / Test HCl: 0/4 / Color wet sample (Munsell): 7.5YR 3/4
15.5 +	BPs-C2	Skeleton 2-20 mm: present / Structure: -- / Texture: -- / Roots 0-2 mm: present / pH: 5 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 3/2

R264R REDOXISOL à horizon réduit de surface, à EUANMOOR

Gleyic Stagnosol

Station settings

Location: Réchy, Gouille de Potoc | **Topography:** depression

Coordinates: 604728 / 114805 | **Aspect:** 0°

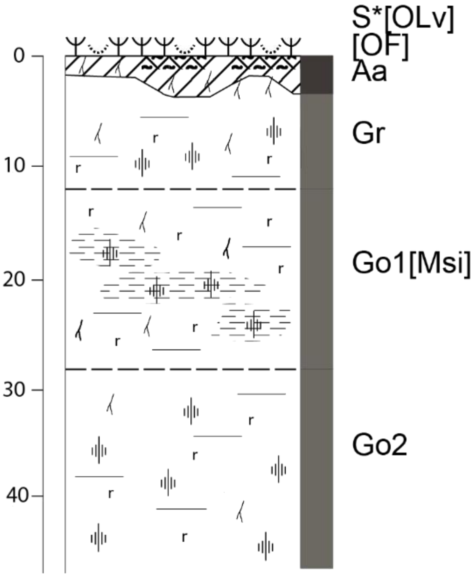
Elevation: 2489 m | **Slope:** 0°

Description date: 15.07.2015

Vegetation type: Typical snowbed (*Salicion herbaceae*)

Lithology / Surficial deposit: Mixed moraine

Profile description



Depth (cm)	Horizon	Characteristics
1.5-0	S*[OLv]	
0-1	[OF]	
1-2/4	Aa	Skeleton: -- / Structure: meso-granular / Texture: silty loam / Roots 0-2 mm: common / pH: 4.6 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 2/1
2/4-12	Gr	Skeleton: -- / Structure: blocky subangular / Texture: silty loam / Roots 0-2 mm: very few / pH: 5 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 4/1
12-28	Go1[Msi]	Skeleton: -- / Structure: single grain & blocky subangular / Texture: silty loam / Roots 0-2 mm & 2-5 mm: very few / pH (Go1): 5 & pH (Msi): 5.3/ Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 4/1 (Go1) & 7.5YR 2.5/1 (Msi)
28-45+	Go2	Skeleton: -- / Structure: blocky subangular / Texture: silty loam / Roots 0-2 mm: very few / pH : 4.9 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 4/1

R267R PODZOSOL OCRIQUE leptique, à HEMIMODER (Rhizic)

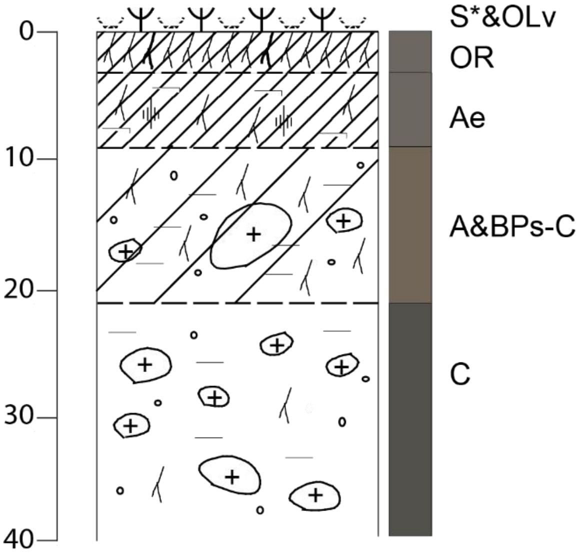
Entic Podzol

Station settings

Location: Réchy, La Maya
Coordinates: 604629 / 113420
Elevation: 2685 m
Description date: 16.07.2015
Vegetation type: Typical snowbed (*Salicion herbaceae*)
Lithology / Surficial deposit: Quartzite

Topography: depression
Aspect: 272°
Slope: 5°

Profile description



Depth (cm)	Horizon	Characteristics
2-0	S*&OLv	
0-3	OR	Skeleton 2-20 mm: 5% / Structure: micro-granular / Texture: silty loam / Roots 0-2 mm: many; 2-5 mm: very few / pH: 4.4 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 4/1
3-9	Ae	Skeleton: 2-20 mm: 5% / Structure: micro-granular / Texture: silty loam / Roots 0-2 mm: few / pH: 4.3 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 4/1
9-21	A&BPs-C	Skeleton: 2-20 mm: 10%; 2-5 cm: 10%; 5-20 cm: 25% / Structure: micro-granular - single grain / Texture: silty loam / Roots 0-2 mm: common / pH: 4.4 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 4/2
21-30+	C	Skeleton: 2-20 mm: 10%; 2-5 cm: 20%; 5-20 cm: 20% / Structure: single grain / Texture: silty loam / Roots 0-2 mm: very few / pH: 4.4 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/1

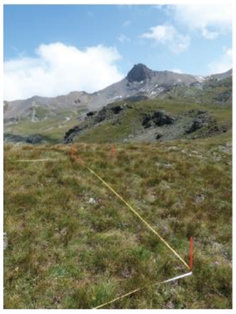
R3901 BRUNISOL EUTRIQUE hémiorganique, leptique, juvénile, développé dans un Régosol cryoturbé issu de loess et de quartzites, sur calschistes et quartzites, à DYSMULL

Endocalcaric Eutric Cambisol (Humic)

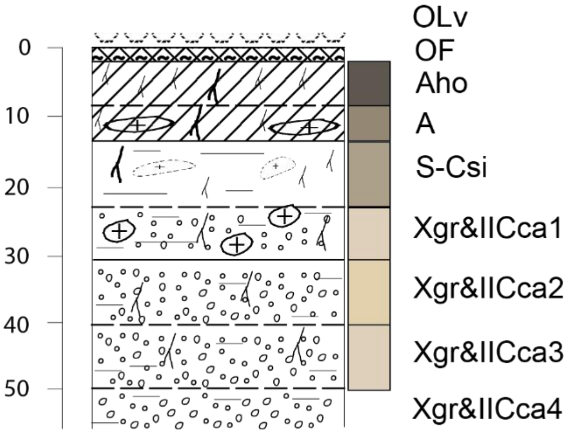
Station settings

Location: Réchy, Pas de Lovégno
Coordinates: 603963 / 113870
Elevation: 2697 m
Description date: 22.08.2014
Vegetation type: Windy ridge (*Elynion myosuroides*)
Lithology / Surficial deposit: Marble and phyllitic calcschist

Topography: ridge
Aspect: 251°
Slope: 6°



Profile description



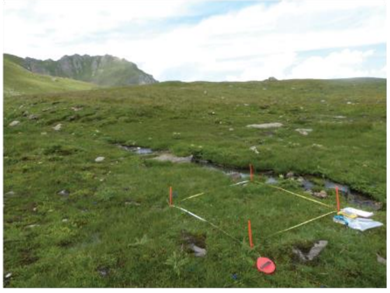
Depth (cm)	Horizon	Characteristics
1-0	OLv	
0-1	OF	
1-8	Aho	Skeleton 2-20 mm: 5% / Structure: micro granular / Texture: silty loam / Roots 0-2 mm: many, 2-5 mm: very few / pH: 5.4 / Test HCl: 0/4 / Color dry sample (Munsell): 2,5Y 3/1
8-13	A	Skeleton 2-20 mm: 15%, weathered / Structure: micro granular / Texture: silty loam / Roots 0-2 mm: common, 2-5 mm: very few / pH: 6.2 / Test HCl: 0/4 / Color dry sample (Munsell): 2,5Y 5/2
13-22.5	S-Csi	Skeleton 2-20 mm: 30%, weathered, schists / Structure: single grain - blocky subangular / Texture: silty loam / Roots 0-2 mm: few, > 5 mm: very few / pH: 7.1 / Test HCl: 0/4 / Color dry sample (Munsell): 2,5Y 6/2
22.5 - 30.5	Xgr&IICca1	Skeleton 2-20 mm: 40%, 5-20 cm: 20% / Structure: -- / Texture: silty loam / Roots 0-2 mm: very few / pH: 8 / Test HCl: 4/4 & 0/4 (quartz grains) / Color dry sample (Munsell): 2,5Y 8/2 (whiter line at the bottom of the horizon)
30.5-40.5	Xgr&IICca2	Skeleton 2-20 mm: 60%, weathered / Structure: -- / Texture: silty loam / Roots 0-2 mm: very few / pH: 8.1 / Test HCl: 4/4 & 0/4 (quartz grains) / Color dry sample (Munsell): 2,5Y 8/3
40.5-50	Xgr&IICca3	Skeleton 2-20 mm: 70%, weathered / Structure: -- / Texture: silty loam / Roots 0-2 mm: very few / pH: 8.2 / Test HCl: 4/4 & 0/4 (quartz grains) / Color dry sample (Munsell): 2,5Y 8/2
50+	Xgr&IICca4	

R3934 REDUCTISOL TYPIQUE, à EUANMOOR (Bryoic)

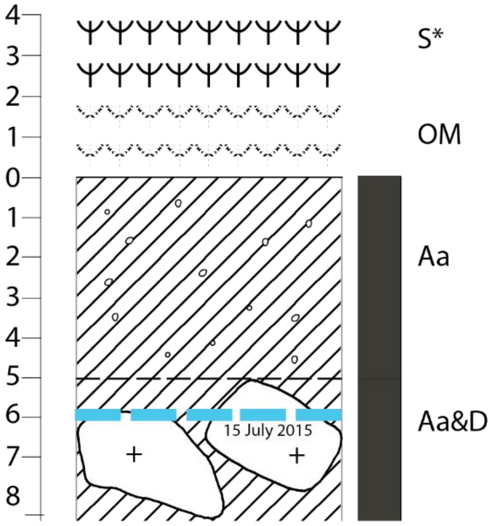
Gleysol

Station settings

Location: Réchy, Gouille de Potoc
Topography: depression
Coordinates: 604710 / 115093
Aspect: 116°
Elevation: 2468 m
Slope: 5°
Description date: 15.07.2015
Vegetation type: Wet snowbed (*Caricion bicolori-atrofuscae*)
Lithology / Surficial deposit: Mixed moraine



Profile description



Depth (cm)	Horizon	Characteristics
4-2	S*	
2-0	OM	Senescent mosses > 75% volume
0-5	Aa	Skeleton 2-20 mm: 10% / Structure: massive / Texture: silt / Roots 0-2 mm: few; 2-5 mm: few / pH: 6.1 / Test HCl: 0/4 / Color wet sample (Munsell): 5Y 2.5/1
5-8+	Aa&D	Skeleton: >20 cm: 80% / Structure: -- / Texture: -- / Roots: -- / pH: -- / Test HCl: -- / Color wet sample (Munsell): --

Remarks

1. Reductisols generally require a G horizon. In this case, as the soil description was made just after the snowmelt, when the flow of the nearby brook was at its maximum, I assume the G horizon is still under water.

2. Aa horizons could be Histic horizons (H) instead. This could be verified by measuring the ash proportion of the sample (by calcination at 600°C). In the case of histic horizon the ash content should be lower than 50%. In this case, the soil reference would be REDUCTISOL TYPIQUE épihistique / Histic Gleysol.

R3935 REDUCTISOL TYPIQUE, à EUANMOOR - MESOMULL

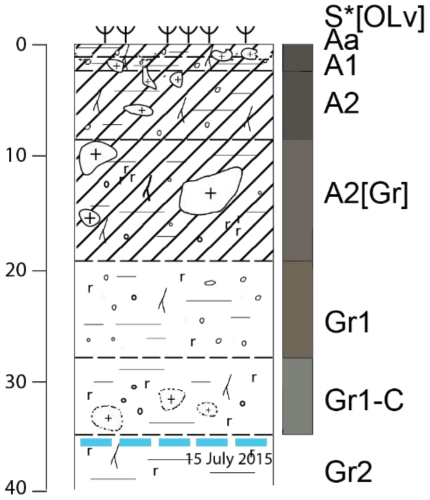
Gleysol

Station settings

Location: Réchy, Gouille de Potoc
Coordinates: 604647 / 115072
Elevation: 2468 m
Description date: 15.07.2015
Vegetation type: Typical snowbed (*Salicion herbaceae*)
Lithology / Surficial deposit: Mixed moraine

Topography: depression
Aspect: 1°
Slope: 10°

Profile description



Depth (cm)	Horizon	Characteristics
1-0	S*[OLv]	
0-1	Aa	Skeleton 2-20 mm: 10% / Structure: massive / Texture: silty loam / Roots 0-2 mm: few; 2-5 mm: very few / pH: 5.1 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 3/1
1-2	A1	Skeleton: -- / Structure: -- / Texture: silty loam / Roots 0-2 mm: few; 2-5 mm: very few / pH: -- / Test HCl: 0/4 / Color wet sample (Munsell): --
2-8	A2	Skeleton: 2-20 mm: 10%; 2-5 cm: 40%; weakly weathered / Structure: meso-granular / Texture: silty loam / Roots 0-2 mm: few / pH: 5.9 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 3/1
8-17	A2[Gr]	Skeleton: 2-20 mm: 10%; 2-5 cm: 20%; 5-20 cm: 10% / Structure: meso-granular - blocky subangular / Texture: silty loam / Roots 0-2 mm: few; 2-5 mm: very few / pH: 5.9 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 4/1
17-26	Gr1	Skeleton: 2-20 mm: 30%; 2-5 cm: 10%; 5-20 cm: 20%; weakly weathered / Structure: blocky subangular / Texture: silty loam / Roots 0-2 mm: very few / pH: 6 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 4/2
26-36	Gr1-C	Skeleton 2-20 mm: 10%; 2-5 cm: 10%; 5-20 cm: 30%; strongly weathered / Structure: blocky subangular - massive / Texture: silty loam / Roots 0-2 mm: very few / pH: 6.2 / Test HCl: 0/4 / Color wet sample (Munsell): GLEY14/10Y1/5
36+	Gr2	Skeleton: -- / Structure: -- / Texture: -- / Roots: -- / pH: -- / Test HCl: -- / Color wet sample (Munsell): --

R4209 PODZOSOL OCRIQUE, à HEMIMODER (Rhizic)

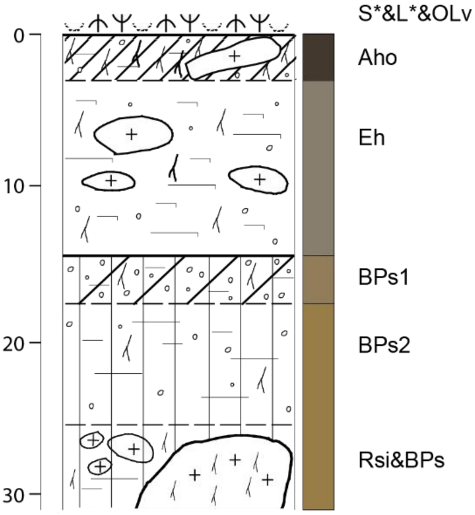
Leptic Entic Podzol

Station settings

Location: Réchy, Pas de Lovégno
Coordinates: 603487 / 113884
Elevation: 2581 m
Description date: 14.07.2015
Vegetation type: Siliceous alpine grassland (*Caricion curvulae*)
Lithology / Surficial deposit: Gneiss, chlorite, amphibolite, prasinite

Topography: slope
Aspect: 207°
Slope: 14°

Profile description



Depth (cm)	Horizon	Characteristics
0.5/1-0	S*&L*&[OLv]	
0-3	Aho	Skeleton 2-20 mm: 10%; 5-20 cm: 10% / Structure: micro-granular / Texture: silty loam / Roots 0-2 mm: common; 2-5 mm: very few / pH: 4.2 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 2/2
3-15	Eh	Skeleton 2-20 mm: 7%; 2-5 cm: 15%; >20 cm: 25% / Structure: single grain / Texture: silty loam / Roots 0-2 mm: few; 2-5 mm: very few / pH: 4.4 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/2
15-18	BPs1	Skeleton: 2-20 mm: 25% / Structure: single grain - blocky subangular / Texture: silty loam / Roots 0-2 mm: -- / pH: 4.6 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/4
18-24.5	BPs2	Skeleton: 2-20 mm: 10%; 5-20 cm: 15% / Structure: single grain - blocky subangular / Texture: silty loam / Roots 0-2 mm: very few / pH: 4.7 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/6
24.5 - 31.5+	Rsi&BPs	Skeleton: 5-20 cm: 20%; >20 cm: 60%; weakly weathered / Structure: single grain - blocky subangular / Texture: silty loam / Roots 0-2 mm: few / pH: 5 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/6

R4217 REDUCTISOL TYPIQUE graveleux, leptique, à EUANMOOR

Gleysol

Station settings

Location: Réchy, Lac du Louché

Coordinates: 604949 / 113947

Elevation: 2568 m

Description date: 16.07.2015

Vegetation type: Wet snowbeds (*Caricion bicolori-atrofuscae*)

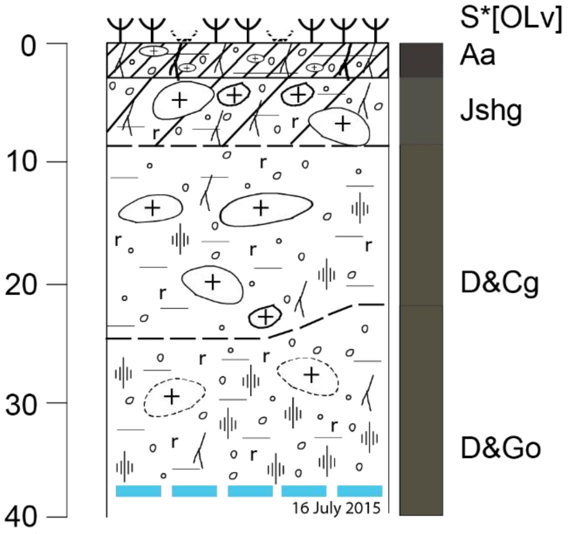
Lithology / Surficial deposit: Quartzite-rich alluvial deposits

Topography: depression

Aspect: 0°

Slope: 0°

Profile description



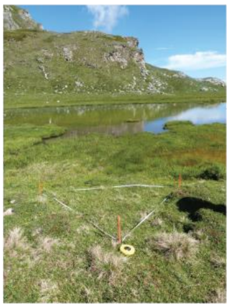
Depth (cm)	Horizon	Characteristics
0.5-0	S*[OLv]	
0-2	Aa	Skeleton 2-20 mm: 15% / Structure: massive / Texture: silty loam / Roots 0-2 mm: few; 2-5 mm: very few / pH: 6.0 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 2/1
2-9	Jshg	Skeleton 2-20 mm: 15%; 2-5 cm: 25%; 5-20 cm: 35% / Structure: micro-granular - single grain / Texture: sandy loam / Roots 0-2 mm: few / pH: 6.7 / Test HCl: 0/4 / Color wet sample (Munsell): 5Y3/1
9-23/26	D&Cg	Skeleton: 2-20 mm: 25%; 2-5 cm: 20%; 5-20 cm: 40% / Structure: single grain / Texture: sandy loam / Roots 0-2 mm: very few / pH: 6.8 / Test HCl: 0/4 / Color wet sample (Munsell): 5Y3/2
23/26-36+	D&Go	Skeleton: 2-20 mm: 25%; 2-5 cm: 30%; 5-20 cm: 40% / Structure: single grain / Texture: silty loam / Roots 0-2 mm: very few / pH: 6.3 / Test HCl: 0/4 / Color wet sample (Munsell): 5Y3/2 + 2.5Y4/4

R4468 REDOXISOL sur REDUCTISOL STAGNIQUE, à HEMIMODER

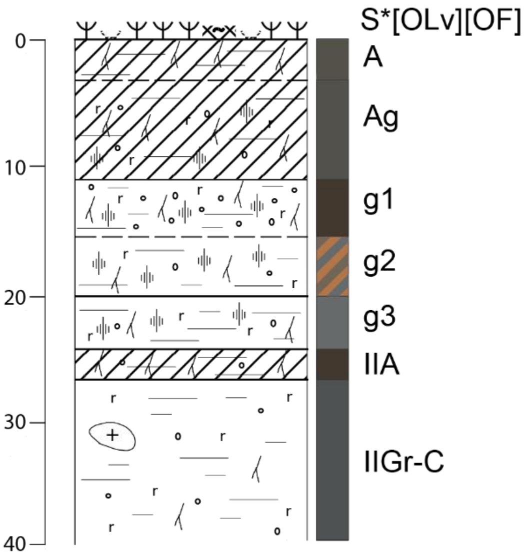
Stagnosol on Gleysol

Station settings

Location: Réchy, Guille de la Fâche
Topography: depression
Coordinates: 604733 / 115800
Aspect: 342°
Elevation: 2440 m
Slope: 3°
Description date: 13.07.2015
Vegetation type: Typical snowbeds (*Salicion herbaceae*)
Lithology / Surficial deposit: Mixed moraine



Profile description



Depth (cm)	Horizon	Characteristics
1-0	S*[OLv][OF]	
0-3.5	A	Skeleton: -- / Structure: micro-granular / Texture: silty loam / Roots: few / pH: 4.5 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 2/2
3.5-10.5	Ag	Skeleton: -- / Structure:micro-granular / Texture: silty loam / Roots few / pH: 4.8 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/2
10.5-15.5	g1	Skeleton: 2-20 mm: 40%; weakly weathered / Structure: single grain - micro-granular / Texture: silty loam / Roots: few / pH: 5.3 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/4
15.5-20	g2	Skeleton: 2-20 mm: 10% / Structure: blocky subangular / Texture: silty loam / Roots: very few / pH: 5.4 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/6
20-23.5	g3	Skeleton: 2-20 mm: 10%; weakly weathered / Structure: blocky subangular / Texture: silty loam / Roots: very few / pH: 5.3 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/6
23.5-26.5	IIA	Skeleton: 2-20 mm: 10% / Structure: micro-granular / Texture: silty loam / Roots: few / pH: 5.1 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/6
26.5 - 34.5+	IIGr-C	Skeleton: 2-20 cm: 10%; 5-20 cm: 20%; weakly weathered / Structure: single grain / Texture: silty loam / Roots: very few / pH: 5.4 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/6

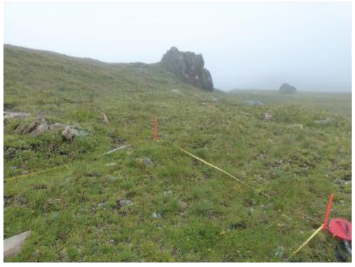
R4469 PODZOSOL OCRIQUE hémiorganique, à HEMIMODER

Entic Podzol

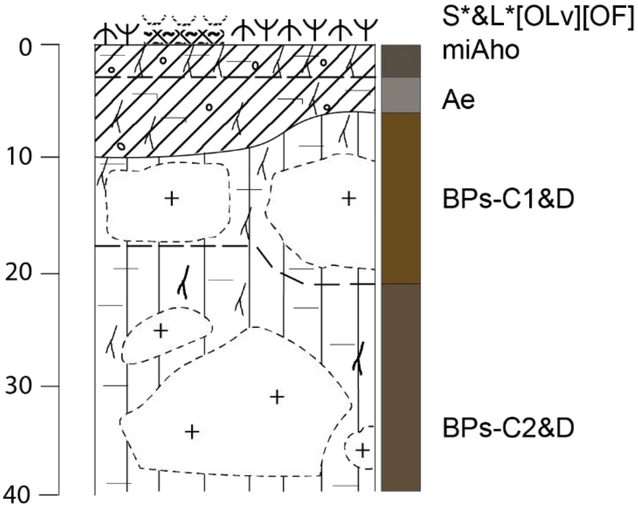
Station settings

Location: Réchy, Lac du Louché
Coordinates: 604607 / 114009
Elevation: 2578 m
Description date: 16.07.2015
Vegetation type: Siliceous alpine grassland (*Caricion curvulae*)
Lithology / Surficial deposit: Mixed moraine

Topography: slope
Aspect: 182°
Slope: 18°



Profile description



Depth (cm)	Horizon	Characteristics
1-0	S*&L*[OLv][OF]	
0-2	miAho	Skeleton 2-20 mm: 10% / Structure: micro-granular / Texture: silty loam / Roots 0-2 mm: common / pH: 4.1 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 3/2
2-8/10	Ae	Skeleton 2-20 mm: 10% / Structure: micro-granular / Texture: silty loam / Roots 0-2 mm: very few / pH: 4.0 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 5/1
8/10-17/22	BPs-C1&D	Skeleton: >20 cm: 60% highly weathered / Structure: micro-granular / Texture: silty loam / Roots 0-2 mm: very few / pH: 5.0 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 3/6
17/22-43+	BPs-C2&D	Skeleton: 5-20 cm: 25%; >20 cm: 45% highly weathered / Structure: single grain - blocky subangular / Texture: silty loam / Roots 0-2 mm: few; 2-5 mm: few / pH: 6.1 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 3/3

R4471 PODZOSOL OCRIQUE leptique, pierreux, à HEMIMODER

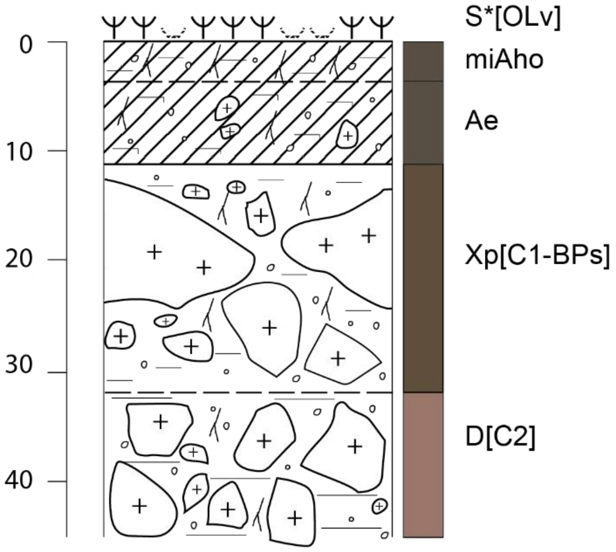
Leptic Entic Podzol

Station settings

Location: Réchy, Pas de Lovégno
Coordinates: 604033 / 113848
Elevation: 2682 m
Description date: 14.07.2015
Vegetation type: Siliceous alpine grassland (*Caricion curvulae*)
Lithology / Surficial deposit: Quartzite, metaconglomerate

Topography: slope
Aspect: 64°
Slope: 22°

Profile description

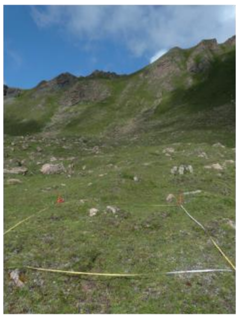


Depth (cm)	Horizon	Characteristics
0.5-0	S*[OLv]	
0-3	miAho	Skeleton 2-20 mm: 20% / Structure: micro-granular / Texture: silty loam / Roots 0-2 mm: few / pH: 4.2 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 3/2
3-11	Ae	Skeleton 2-20 mm: 20%; 2-5 cm: 10%; 5-20 cm: 20% / Structure: micro-granular / Texture: silty loam / Roots 0-2 mm: very few / pH: 4.1 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/2
11-32	Xp[C1-BPs]	Skeleton: 2-20 mm: 20%; 2-5 cm: 10%; 5-20 cm: 60%, highly weathered / Structure: single grain / Texture: silty loam / Roots 0-2 mm: few / pH: 4.3 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 3/3
32-52+	D[C2]	Skeleton: 2-20 mm: 10%; 2-5 cm: 10%; 5-20 cm: 50%; >20 cm: 20% / Structure: blocky subangular / Texture: silty loam / Roots 0-2 mm: very few / pH: 4.3 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 5/4

R5067 PODZOSOL OCRIQUE leptique, à DYSMODER (Rhizic)

Leptic Entic Podzol

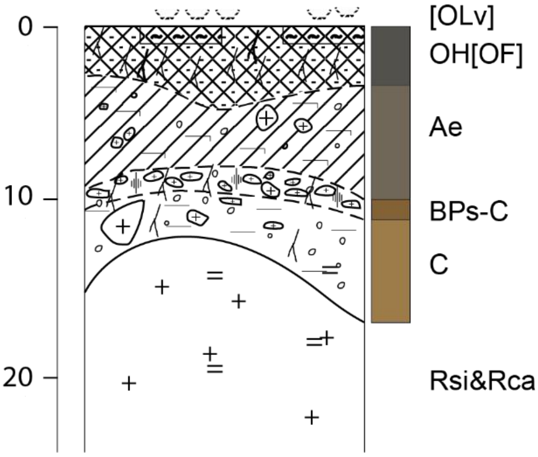
Station settings



Location: Réchy, Cirque de Brechette
Coordinates: 604333 / 115949
Elevation: 2528 m
Description date: 13.07.2015
Vegetation type: Siliceous alpine grassland (*Caricion curvulae*)
Lithology / Surficial deposit: Mixed moraine

Topography: slope
Aspect: 20°
Slope: 8°

Profile description



Depth (cm)	Horizon	Characteristics
1-0	[OLv]	
0-1.5/4	OH[OF]	Skeleton: -- / Structure: micro-granular / Texture: silty loam / Roots 0-2 mm: many; 2-5 mm: very few / pH: 4.8 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 3/1
1.5/4-6.5/8.5	Ae	Skeleton 2-20 mm: 15%; 2-5 cm: 10% / Structure: single grain / Texture: silty loam / Roots 0-2 mm: very few / pH: 4.6 / Test HCl: 0/4 / Color wet sample (Munsell): 2.5Y 4/2
6.5/8.5-10/11.5	BPs-C	Skeleton: 2-20 mm: 50%, highly weathered / Structure: single grain / Texture: silty loam / Roots 0-2 mm: few / pH: 4.9 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 4/6
10/11.5-14.5/20.5	C	Skeleton: 2-20 mm: 20%; 2-5 cm: 20%, weathered / Structure: single grain / Texture: silty loam / Roots 0-2 mm: very few / pH: 5.2 / Test HCl: 0/4 / Color wet sample (Munsell): 10YR 5/6
14.5/20.5 +	Rsi&Rca	highly weathered

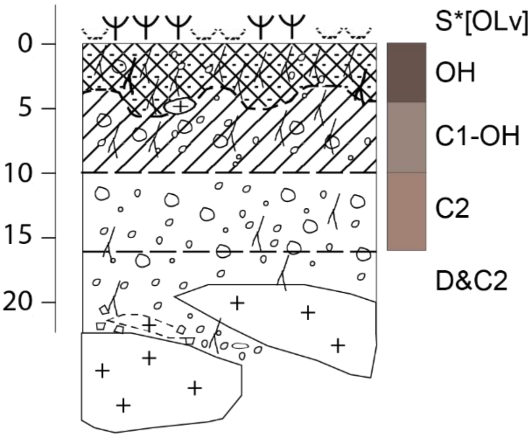
R5141 REGOSOL humique, issu de colluvionnement, à HEMIMOR (Rhizic) Skeletic Leptosol (Colluvic)

Station settings

Location: Réchy, Lac du Louché
Coordinates: 605116 / 114197
Elevation: 2567 m
Description date: 20.08.2014
Vegetation type: Wet snowbed (*Caricion bicolori-atrofuscae*)
Lithology / Surficial deposit: Gneiss and micaschist colluvium

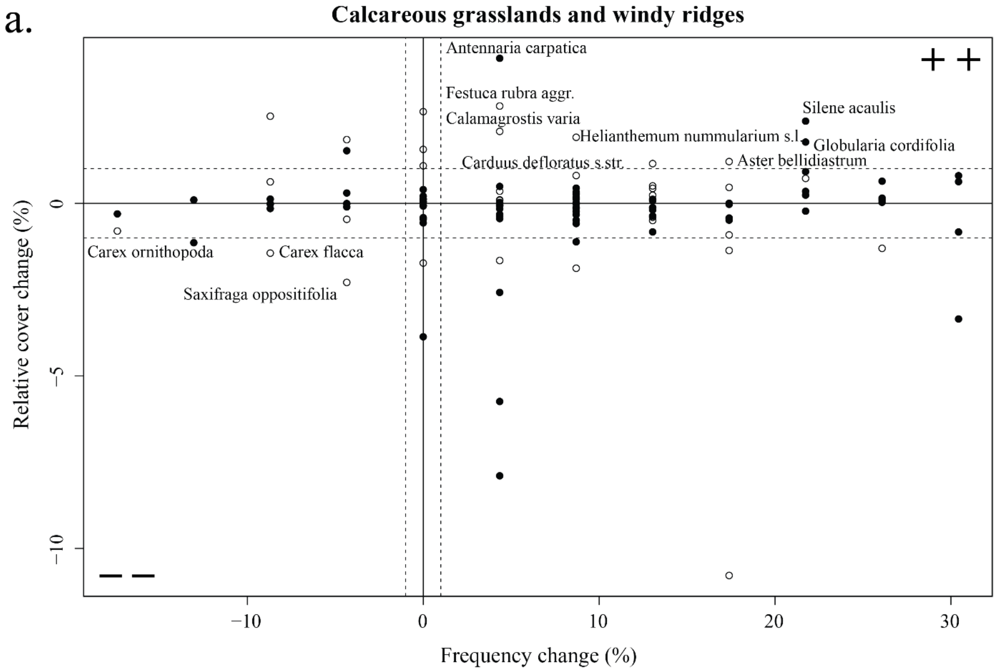
Topography: slope
Aspect: 340°
Slope: 2°

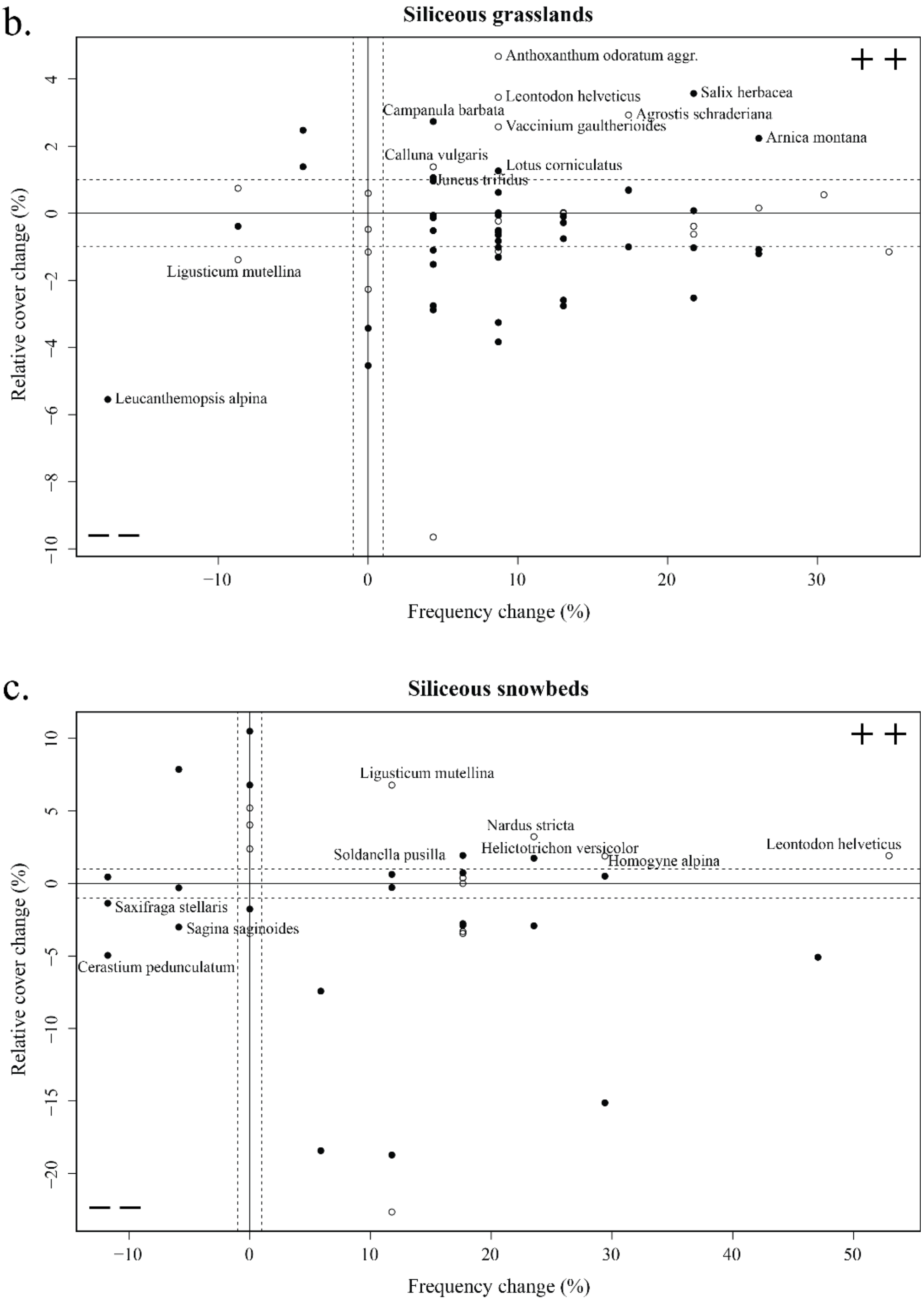
Profile description



Depth (cm)	Horizon	Characteristics
1-0	S*[OLv]	
0-4/5.5	OH	Skeleton 2-20 mm: 5% / Structure: massive / Texture: silty loam / Roots 0-2 mm: many; 2-5 mm: few / pH: 5.5 / Test HCl: 0/4 / Color dry sample (Munsell): 2.5Y 3/2
4/5.5-10	C1-OH	Skeleton 2-20 mm: 45%; 2-5 cm: 10%, slightly weathered / Structure: single grain / Texture: silty loam / Roots 0-2 mm: common / pH: 4.1 / Test HCl: 0/4 / Color dry sample (Munsell): 2.5Y 5/2
10-16.5	C2	Skeleton: 2-20 mm: 70%, slightly weathered / Structure: single grain / Texture: silty loam / Roots 0-2 mm: few / pH: 4.3 / Test HCl: 0/4 / Color dry sample (Munsell): 2.5Y 5/3
16.5-21	D&C2	

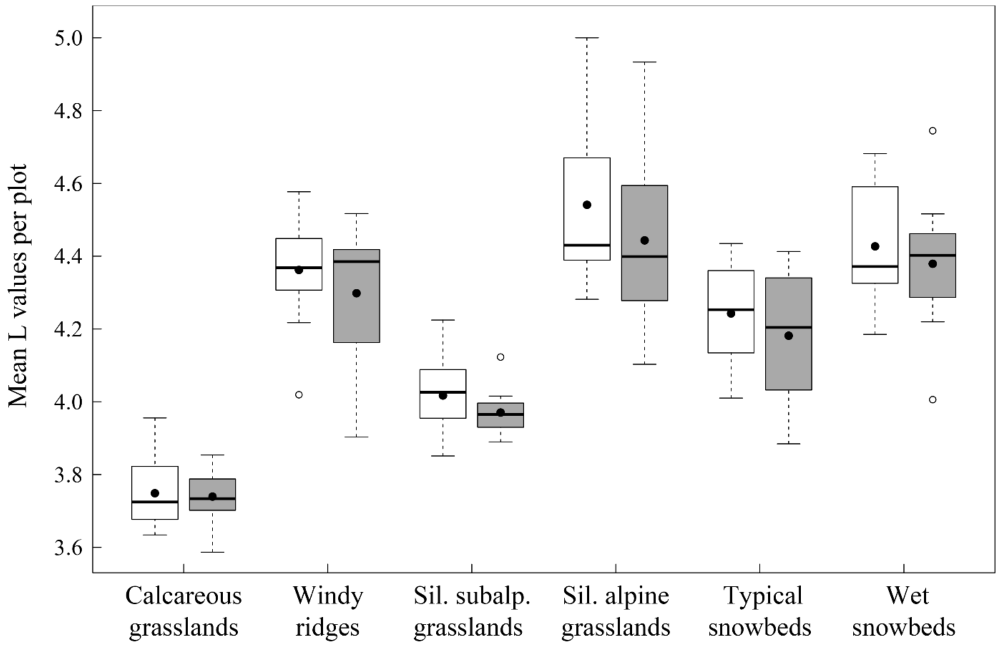
E. Supplementary material related to Chapter 4



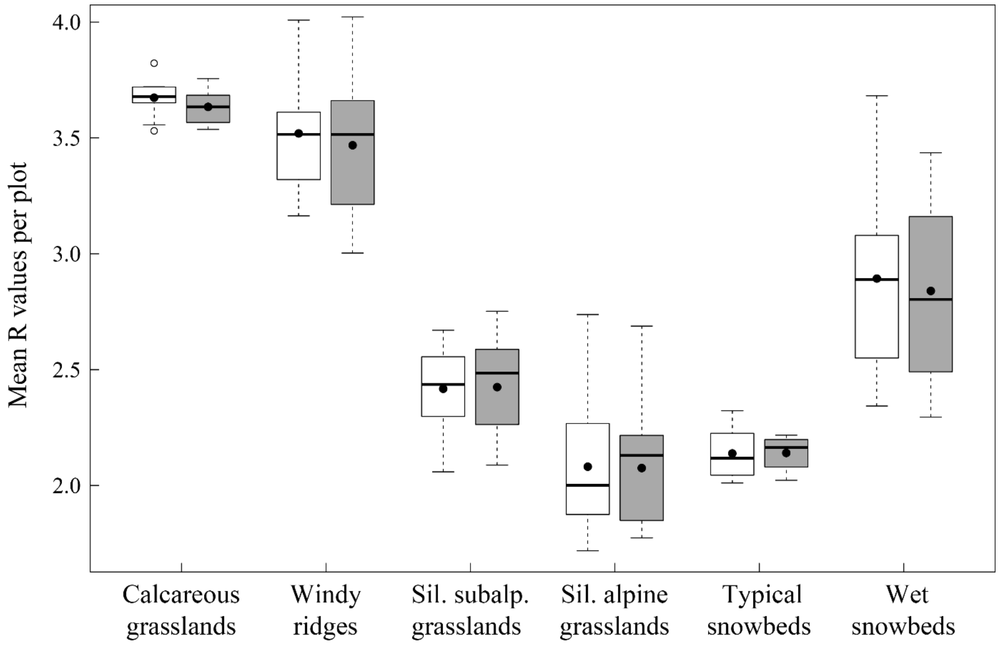


Appendix E1 - Relative change in cover vs. relative change in frequency of the species occurring in at least 20% of the historical or recent records (frequent species). The relative cover and frequency of the frequent species are calculated separately for (a) calcareous grasslands and windy ridges (*Seslerion* and *Elynion*), (b) subalpine and alpine siliceous grasslands (*Nardion* and *Caricion curvulae*), and (c) typical and wet snowbeds (*Salicion herbaceae* and *Caricion bicolori-atrofuscae*). Dotted lines represent an arbitrary thereshold of ±1% in cover and frequency changes. Only the plant species above and below this threshold are taken into account in order to focus on the main changes.

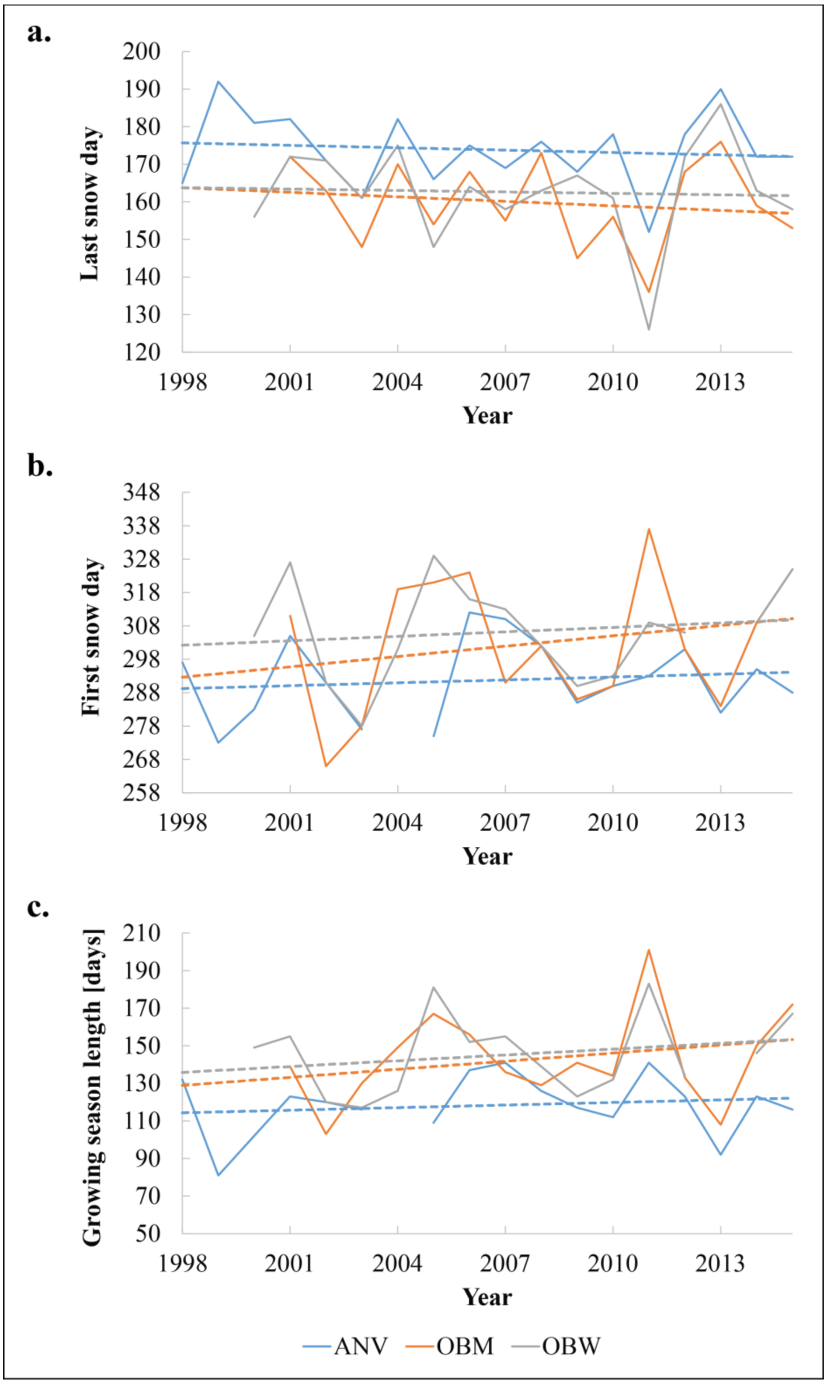
Plant species have been splitted into generalist and specialist ones based on Delarze and Gonseth (2008). This publication assigns to each Swiss plant species one or more natural habitats, from which the species is typical of. We defined a plant species as a specialist when only one habitat type was associated to it (filled circles), otherwise it is a generalist (hollow circles). Species names are provided only for winning (++) and losing (--) species.



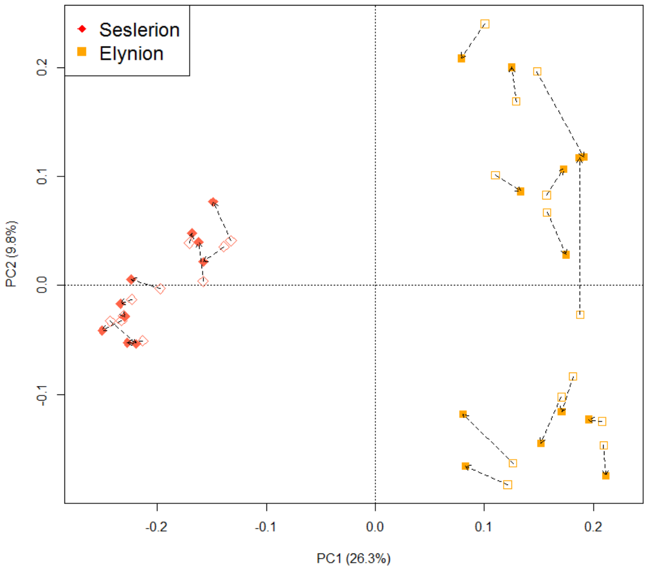
Appendix E2 - Cover-weighted means of indicator values (Landolt et al., 2010) for light (L) in historical (white boxes) and recent (grey boxes) inventories for each plant community. "Sil.": Siliceous; "subalp.": subalpine. Black dots represent the mean values, the black line is the median and boxes are limited by 1st and 3rd quartiles. None of the change is significant with a pairwise Wilcoxon-Mann-Whitney test.



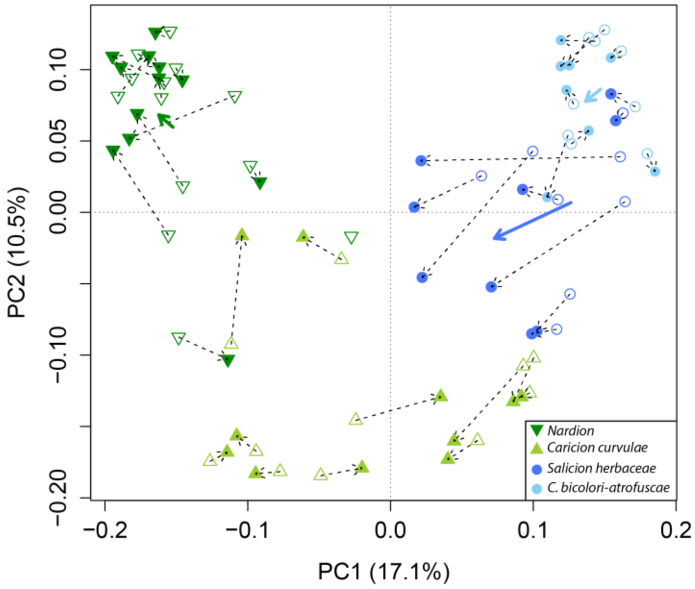
Appendix E3 - Cover-weighted means of indicator values (Landolt et al., 2010) for soil pH (R) in historical (white boxes) and recent (grey boxes) inventories for each plant community. Symbols and abbreviations are the same as in Appendix E2.



Appendix E4 - Recent variation of the last snow day (a), first snow day (b) and growing season length (c) on Anniviers meteorological station (ANV, 2630 m a.s.l.; period 1998-2015), on the Oberwald one (OBW, 2430 m a.s.l.; period 2000-2015) and on the Ober Meiel (OBM, 2110 m a.s.l.; period 2001-2015), respectively close to the study sites of Rechy, Grimsel and Morteys. All the stations belong to the WSL Institute for Snow and Avalanche Research SLF (SLF-Messdaten © 2016). Days are calculated from the 1st of January. The "last snow day" is defined as the last day of the winter season with snow cover, the "first snow day" as the first day of the fall season with snow cover and followed by at least one week of continuous snow cover. The growing season length is the difference between the "first snow day" and the "last snow day". The time series of these three parameters was tested for each station separately with ANOVA, and for all the stations combined with ANCOVA. No significant changes of the "last snow day", "first snow day" and "growing season length" were detected over these 15-18 years.



Appendix E5 - Principal Component Analysis based on species composition and cover of the calcareous plant communities: calcareous grasslands (*Seslerion*), windy ridges (*Elynion*) The first axis represents 26.3 % and the second 9.8% of the total variance, respectively. Couples of historical (hollow symbols) and recent (full symbols) records are connected with dotted arrows. Shift of centroids are not represented as they are negligible.



Appendix E6 - Principal Component Analysis based on species composition and cover of the siliceous plant communities: subalpine siliceous grasslands (*Nardion*), alpine siliceous grasslands (*Caricion curvulae*), typical snowbeds (*Salicion herbaceae*), wet snowbeds (*Caricion bicolori-atrofuscae*). The first axis represents 17.1 % and the second 10.5% of the variance, respectively. Couples of historical (hollow symbols) and recent (full symbols) records are connected with dotted arrows. Shift of centroids are represented by thick arrows, except for *Caricion curvulae* with a negligible shift.

F. Supplementary material related to Chapter 5

Appendix F1 - Chemical and physical characteristics of the investigated soil horizons grouped by soil profile: name of the horizon according to Baize and Girard (2009) and Jabiol et al. (2013); its translation in FAO nomenclature (FAO, 2006); depth; root abundance according to FAO (2006 p. 60) and subdivided by root diameter when the information was recorded; horizon structure according to (FAO, 2006 p. 45), HCl reaction from 0 (non-calcareous) to 4 (extremely-calcareous) according to FAO (2006, p. 38); pH; proportions of Sand (0.063-2 mm); Silt (0.002-0.063 mm); Clay (< 0.002 mm); organic Carbon; total Nitrogen; C/N ratio. Missing values are indicated by "-". In the column of horizon names: "[ ]" = discontinuous horizon; "&" = presence of different horizons in the same layer, each keeping its properties; "-" = the layer is a transition between two horizons with intermediate properties; "S*" = moss layer, both living and dead; "L*"= lichen layer, both living and dead.

Profile	Soil horizon (Baize & Girard, 2009 & Jabiol et al. 2013)	Soil horizon (FAO 2006)	Depth [cm]	Root abundance			Structure	HCl react.	pH (H_2O)	Sand [%]	Silt [%]	Clay [%]	Corg [%]	Ntot [%]	C/N
				0-2mm	2-5mm	>5mm									
M2716	OF&S*	Oe	0-0.5		-		-	-	-	38	47	15	24.7	1.5	16.6
	Aho	Ah	0.5-3/6		many		granular (micro)	0/4	5.5	9	59	32	9.5	0.8	12.0
	Ah	Ah	3/6-8/10		common		granular (micro)	0/4	5.5	7	57	35	6.7	0.7	10.3
	Ah-S	Ah-B	8/10-14		common		granular / blocky subangular	0/4	6.5	5	60	35	5.6	0.6	9.8
	S	Bw	14-32/41		very few		blocky subangular	0/4	6.1	7	56	36	1.4	0.1	10.2
	IIDca	IIBw	32/41+		few		-	-	-	-	-	-	-	-	-
M2844	OLv	Oi	0.5/0		-		-	-	-	-	-	-	29.3	1.1	25.6
	Aciho	Ah	0/5.5		many		granular	0/4	6.4	10	52	37	10.0	0.9	11.3
	Acih-Sci	Ah-B	5.5/15.5		common		granular/blocky subangular	0/4	6.8	11	50	39	6.4	0.6	10.7
	Sca	Bw	12189		few		-	-	-	-	-	-	-	-	-
	Sca&Dca	Bw	33+		very few		-	-	-	-	-	-	-	-	-
M2965-6	OLv	Oi	5-0	-	-	-	-	-	-	-	-	-	32.8	0.6	53.2
	Acaho	A	0-1/4	-	-	-	-	4/4	7.3	29	49	22	9.7	0.7	13.2
	Sca	Bw	1/4-24/28	-	-	-	-	4/4	7.5	22	49	29	3.8	0.4	9.3
	Dca-Sca	Bw	24/28-34+	-	-	-	-	4/4	7.7	22	49	29	2.2	0.3	7.1
M2976	OLv	Oi	1-0	-	-	-	-	-	-	-	-	-	38.9	1.2	31.8
	OH	Oa	0-0/3	-	-	-	-	1/4	5.4	22	63	15	29.6	1.5	19.8
	Aciho	Ah	0/3-6/8	-	-	-	-	1/4	5.4	11	52	37	12.9	0.9	13.8
	Acih-Sci	Ah-B	6/8-17/18	-	-	-	-	1/4	5.3	6	54	40	7.5	0.6	12.4
	Sci	Bw	17/18-32	-	-	-	-	1/4	4.9	7	58	35	2.8	0.3	9.6
	Sci&Rca-IICsi	Bw&R-IIC	32-43	-	-	-	-	0/4	5.3	8	55	37	2.0	0.2	8.9
	Rca	R	43+	-	-	-	-	-	-	-	-	-	-	-	-
M2980	OLv&S*	Oi	0.5-0		-		-	-	-	-	-	-	-	-	-
	OF&A	A&Oe	0-1		common		-	0/4	5.0	26	58	16	28.2	1.7	16.9
	Ah	Ah	1-6		very few		granular (micro)	0/4	5.0	7	59	34	6.3	0.6	10.9
	Agh-Sg	Ah-Bg	6-11		very few		granular (micro) / blocky subangular	0/4	4.8	4	62	34	5.2	0.5	10.7
	S	Bw	11-28		few		blocky subangular	0/4	5.6	3	58	38	2.5	0.2	10.2
	S&Csi	Bw&C	28-33		few		blocky subangular	0/4	5.7	7	60	34	1.5	0.1	10.4
	IISg	IIBg	33-41		few		blocky subangular	0/4	6.3	5	60	35	1.1	0.1	9.1
	IIS&Csi	IIBw&C	41-50+		-		blocky subangular	0/4&0/4	7.2	5	60	35	1.1	0.1	9.1
M3109	[OLv]	[Oi]	1.5/2-0		-		-	-	-	-	-	-	37.1	1.4	26.9
	A&OF	A&Oe	0-2/3		common		-	0/4	5.7	12	50	38	10.1	0.8	12.2
	Ah-S	Ah-B	2/3-4/5		-		-	0/4	5.7	8	50	41	8.5	0.7	11.6

Profile	Soil horizon (Baize & Girard, 2009 & Jabiol et al. 2013)	Soil horizon (FAO 2006)	Depth [cm]	Root abundance			Structure	HCl react.	pH (H_2O)	Sand [%]	Silt [%]	Clay [%]	Corg [%]	Ntot [%]	C/N
				0-2mm	2-5mm	>5mm									
	S&IIDca	Bw	4/5-8/14		-		-	0/4	6.4	6	51	43	4.8	0.5	10.2
	S&Csi&IIDca	Bw-C	8/14-8/19		-		-	4/4&1/4	6.5	7	51	41	3.3	0.4	9.4
	S&Csi&IIDca	Bw-C	8/19-39+		-		-	0/4&1/4	5.6	9	50	40	4.7	0.4	10.6
M3126	OLv	Oi	4-0		-		-	-	-	-	-	-	50.3	0.7	71.6
	OF&Aci	A&Oe	0-2		many		granular (meso)	0/4	6.2	15	48	37	16.3	1.2	14.2
	Aciho	Ah	2-6		many		granular	1/4	6.2	17	46	37	12.1	1.0	12.7
	Aciho-Sci	Ah-B	6-16		many		granular / blocky subangular	1/4	6.8	7	47	46	10.9	0.9	12.3
	Sci	Bw	16-24		many		-	-	-	-	-	-	-	-	-
	Sca&Rca	Bw&R	24-25+		many		-	-	-	-	-	-	-	-	-
M3127	[OLv][S*]	[Oi]	1/4-0	-	-	-	-	-	-	-	-	-	37.2	1.0	36.6
	OF-Aci	A-Oe	0-4	many	-	-	granular (meso)	0/4	6.7	6	52	42	18.1	1.2	15.4
	Aciho-Sci	Ah-B	4-14/15	many	-	-	granular (meso) / blocky subangular	0/4	6.2	4	49	47	10.7	0.8	12.9
	Scih&Rca	Bw&R	14/15-24/30	many	-	very few	blocky subangular	0/4	6.9	5	49	46	9.7	0.7	13.2
M3128	OLv-S*	Oi	3/6-0	-	-	-	-	-	-	-	-	-	35.3	0.8	43.6
	OR	A	0-5/8	many	-	-	granular (meso)	0/4	6.5	10	54	36	19.6	1.1	18.6
	Aciho-Sci	Ah-B	5/8-18/21	common	very few	-	granular / blocky subangular	0/4	6.6	21	47	33	12.3	0.7	17.1
	Sciho1&Rca	Bw&R	18/21-40	few	-	very few	blocky subangular	0/4	6.8	23	46	31	10.7	0.6	16.5
	Sciho2&Rca	Bw&R	40-44+	few	-	very few	blocky subangular	0/4	7.1	21	48	31	9.5	0.6	16.5
M3132	[OLv]&[S*]	[Oi]	0.5-0		-		-	-	-	-	-	-	-	-	-
	Aho	Ah	0-1.5/3		common		-	0/4	5.0	9	53	38	13.2	1.0	13.8
	S1	Bw	1.5/3-10/18		very few		-	0/4	4.3	9	53	39	4.6	0.5	9.6
	S2	Bw	10/18-23		few		blocky subangular	0/4	4.3	8	52	40	1.5	0.2	8.3
	Sg1	Bg	23-45		-		blocky subangular	0/4	-	10	52	38	1.0	0.1	7.8
	Sg2	Bg	45-68+		-		-	0/4	5.7	10	49	41	0.9	0.1	7.8
M3138	OLv	Oi	2/5-0	-	-	-	-	-	-	-	-	-	37.9	0.7	51.9
	OF	Oe	0-2	-	-	-	-	0/4	6.6	-	-	-	36.1	1.5	24.4
	OR	A	2-5/6	many	common	-	granular (meso)	0/4	6.6	15	62	23	22.4	1.4	16.5
	Aciho-Sci	Ah-B	5/6-16/19	common	-	very few	granular (meso) / blocky subangular	0/4	6.6	15	58	27	13.9	1.0	13.7
	Scaho&Dca	Bw	16/19-26	common	few	-	blocky subangular	2/4	7.0	14	58	29	12.7	0.9	13.9
M3139	OLv	Oi	3/5-0	-	-	-	-	-	-	-	-	-	35.8	0.8	42.5
	Aci&OF	A&Oe	0-3/6	many	-	few	granular (meso)	0/4	6.1	23	51	26	12.6	0.7	18.2
	Scih1	Bw	3/6-7/16	common	-	-	blocky subangular	0/4	5.5	18	53	29	6.0	0.4	14.6
	Scih2	Bw	7/16-24	common	-	-	blocky subangular	0/4	6.3	19	52	29	6.2	0.4	15.6
	Scih2&Rca	Bw	24-27+	common	-	-	blocky subangular	1/4	6.9	21	51	28	6.4	0.4	15.0
M3140	OLv	Oi	7-0		-		-	-	-	-	-	-	37.1	0.8	46.1
	Acaho	Ah	0-1		many		granular	4/4	7.4	13	50	37	10.6	1.0	10.8
	Acaho-Sca	Ah-B	1-10/13		common		granular / blocky subangular	4/4	7.5	11	52	37	9.4	0.9	10.4
	Sca-Dca1	Bw	10/13-20		common		-	-	-	-	-	-	-	-	-
	Sca&Dca2	Bw	20-32+		very few		-	-	-	-	-	-	-	-	-
M3141	OLv	Oi	0/7-0		-		-	-	-	-	-	-	35.0	0.7	51.4
	A&OF	A&Oe	0-2/6		many		granular	0/4	5.4	30	48	22	8.6	0.5	16.7
	S	Bw	2/6-16/23		-		blocky subangular	0/4	5.3	29	45	26	5.0	0.4	14.0
	S&IIDca	Bw	16/23+		-		-	-	-	-	-	-	-	-	-
M3150	OLv	Oi	3/5-0		-		-	-	-	-	-	-	39.3	1.1	35.5
	OF	Oe	0-5/8		many		-	0/4	6.2	24	62	14	27.7	1.3	21.0
	Aciho	A	5/8-10/13		many		granular (meso)	2/4	6.2	16	47	38	18.4	1.1	16.0
	Aciho-Sci&Rca[Rsi]	Ah-Bw&R	10/13-20+		-		blocky subangular	0/4	6.9	9	42	48	12.0	0.9	13.9
M3167/a	[OLv]S*	[Oi]	0.5/2-0	-	-	-	-	-	-	-	-	-	37.6	2.0	18.8
	Acih	Ah	0-7/10	-	-	-	granular (micro)	0/4	6.6	23	54	23	7.8	0.8	9.5
	Aca-Sca	AB	7/10-7.5/10.5	-	-	-	granular / blocky subangular	-	-	-	-	-	-	-	-

Profile	Soil horizon (Baize & Girard, 2009 & Jabiol et al. 2013)	Soil horizon (FAO 2006)	Depth [cm]	Root abundance			Structure	HCl react.	pH (H_2O)	Sand [%]	Silt [%]	Clay [%]	Corg [%]	Ntot [%]	C/N
				0-2mm	2-5mm	>5mm									
	Dca	Bw	7.5/10.5-10.5+	-	-	-	-	-	-	-	-	-	-	-	-
M3167/b	Aho	Ah	0.5/9	-	-	-	granular (micro)	0/4	-	24	59	17	19.3	1.7	11.5
M3592	[OF]	[Oe]	0-0/5		-		-	-	-	40	45	15	25.2	1.6	15.9
	OF-Aciho	A-Oe	0/5-0/1		common		granular (meso)	0/4	6.1	33	45	22	19.3	1.3	14.8
	Aciho	A	0/1-2/23		common		granular (meso)	1/4	7.1	21	48	32	11.5	1.0	11.2
	Acih-Sci	AB	2/23-2/13		common		blocky subangular	1/4	7.2	17	45	38	5.7	0.5	10.6
	Scih	Bw	2/13-13/30		very few		blocky subangular	1/4	7.1	21	44	35	6.9	0.6	11.2
	Sci	Bw	13/30-13/35		few		blocky subangular	1/4	7.3	8	48	45	3.4	0.3	10.9
	Dca	B	13/35-35+		-		-	-	-	-	-	-	-	-	-
M4121	OLv	Oi	0.2-0	-	-	-	-	-	-	-	-	-	45.6	1.1	40.7
	OF	Oe	0-0.5	-	-	-	-	-	-	51	46	2	43.5	1.6	26.6
	OH	Oa	0.5-2	-	-	-	-	0/4	-	45	51	4	39.4	2.0	19.5
	Rca	R	2+	-	-	-	-	-	-	-	-	-	-	-	-
G47	OLv	Oi	0/2-0		-		-	-	-	-	-	-	37.0	0.7	50.9
	OF	Oe	0-2		many		single grain	0/4	4.7	-	-	-	26.2	1.1	24.2
	miAho	Ah	2-5		many		single grain	0/4	4.7	24	69	7	15.2	0.8	19.9
	Ae	AE	5-14		common		single grain	0/4	4.6	56	40	5	2.2	0.2	14.0
	D [BPs-C]	Bs-C	14-33		many		-	0/4	-	-	-	-	-	-	-
	D	Bs-C	33-42+		common		-	0/4	-	-	-	-	-	-	-
G90	OLv	Oi	2-0		-		-	-	-	-	-	-	40.4	0.9	45.1
	OF	Oe	0-1		none		-	0/4	4.7	-	-	-	40.1	1.6	24.7
	OH	Oa	1-3/4.5		common		granular (micro)	0/4	4.7	-	-	-	36.5	1.5	24.4
	sgAeho - D	AE	3/4.5-8		many		single grain	0/4	4.7	46	49	5	11.1	0.6	17.7
	BPs-BPh	Bs-Bh	8-13.5		common		granular (micro)	0/4	4.7	38	58	4	5.2	0.2	21.7
	BPs-D1	Bs	13.5-42		many		granular (micro)	0/4	5.2	44	53	3	2.5	0.1	24.9
	BPs-D2	Bs	42+		none		-	0/4	-	-	-	-	-	-	-
G92	S*[OLv]	[Oi]	0.5-0		-		-	-	-	-	-	-	-	-	-
	Ae	AE	0-8.5		many		single grain	0/4	4.1	26	70	4	8.6	0.5	17.5
	C-BPs1	Bs	8.5-15.5		many		single grain	0/4	4.7	47	50	3	1.4	0.1	21.5
	C-BPs2	Bs	15.5-23.5		common		single grain	0/4	5.1	65	32	3	1.1	0.1	20.6
	C-BPs3	Bs	23.5-26.5		common		-	0/4	-	-	-	-	-	-	-
	C	C	26.5-28.5		common		-	0/4	-	-	-	-	-	-	-
	R	R	28.5+		-		-	0/4	-	-	-	-	-	-	-
G291	OLv	Oi	1/2-0		-		-	-	-	-	-	-	37.5	0.8	47.3
	OF	Oe	0-3		many		-	0/4	4.1	-	-	-	38.4	1.9	20.7
	OH1	Oa	3-8		many		-	0/4	4.1	13	80	7	30.0	2.1	14.4
	OH2	Oa	8-14		many		-	0/4	3.1	12	79	9	27.1	1.6	17.0
	BPs-BPh	Bs-Bh	14-22		common		-	0/4	4.7	32	61	7	8.9	0.5	18.8
	Dsi-Csi	C	22-25		-		single grain	0/4	4.8	33	64	4	2.5	0.1	24.8
	IIA	IIA	25-33/35		common		-	0/4	4.9	44	52	4	3.3	0.1	27.3
	IIBPs-C1	IIBs-C	33/35-35/47		common		-	0/4	-	-	-	-	-	-	-
	IIBPs-C2	IIBs-C	35/47-47		common		-	0/4	-	-	-	-	-	-	-
	IIBPs-C3	IIB-C	47-51+		common		-	0/4	-	-	-	-	-	-	-
G334	OF [OH]	Oe [Oa]	0-3/7		many		-	-	-	-	-	-	37.8	0.8	44.8
	OH	Oa	3/7-10		many		single grain	0/4	2.5	31	62	6	28.8	1.2	24.0
	E	E	10-18		common		single grain	0/4	4.1	64	33	2	2.0	0.1	14.3
	BPh	Bh	18-24		common		single grain	0/4	4.5	47	50	3	3.9	0.2	20.8
	BPs 1	Bs	24-46		common		single grain	0/4	4.7	49	48	3	2.6	0.1	22.4
	BPs 2	Bs	46-52+		common		single grain	0/4	4.8	47	51	2	1.4	0.1	21.2

Profile	Soil horizon (Baize & Girard, 2009 & Jabiol et al. 2013)	Soil horizon (FAO 2006)	Depth [cm]	Root abundance			Structure	HCl react.	pH (H_2O)	Sand [%]	Silt [%]	Clay [%]	Corg [%]	Ntot [%]	C/N
				0-2mm	2-5mm	>5mm									
G336	A	A	0-3	common			single grain	0/4	4.1	40	54	6	8.2	0.6	12.7
	E	E	3-9	common			single grain	0/4	4.4	51	47	3	0.6	0.1	11.4
	E-BPh	E-Bh	9-12	common			single grain	0/4	4.3	65	33	2	1.0	0.1	17.7
	BPh	Bh	12-15	common			single grain	0/4	4.8	54	43	3	2.8	0.1	26.7
	BPs	Bs	15-22	none			single grain	0/4	5.0	67	31	2	-	-	-
	C1	C	22-28	none			single grain	0/4	5.0	64	34	2	-	-	-
	C2	C	28-30	none			single grain	0/4	5.0	73	26	1	-	-	-
	C3	C	30-46+	none			single grain	0/4	5.2	68	30	2	-	-	-
G339	S*	O		-			-	-	-	-	-	-	-	-	-
	A1	A	0-2	common			single grain	0/4	3.9	36	59	5	5.6	0.3	19.1
	sgA2	A	2-10	common			single grain	0/4	4.4	55	41	4	1.5	0.1	15.5
	A-C	A-C	10-15/23	common			single grain	0/4	4.6	62	35	4	2.0	0.1	17.3
	Rsi	R	15/23-23	-			-	0/4	-	-	-	-	-	-	-
G340	S*[OLv]	Oi	2-0	-			-	-	-	-	-	-	-	-	-
	Aho	Ah	0-1	common			granular (micro)	0/4	4.3	44	53	3	8.6	0.5	17.7
	A1	A	1-8	common			granular (micro)	0/4	4.4	53	44	3	2.7	0.2	15.8
	A2	A	8-18	common			granular (micro)	0/4	4.4	52	45	3	2.4	0.1	16.9
	A3	A	18-25	common			granular (micro)	0/4	2.4	57	40	3	1.8	0.1	18.1
	C-BPs	C-Bs	25-27	common			single grain	0/4	2.5	52	46	2	1.2	0.1	19.8
	Rsi	R	27+	-			-	0/4	-	-	-	-	-	-	-
G350	OLv	Oi	1-0	-			-	-	-	-	-	-	40.2	0.9	44.1
	OH	Oa	0-4	many			granular (micro)	0/4	5.2	-	-	-	31.2	1.7	18.1
	Ae	AE	4-7	many			single grain	0/4	3.0	49	47	4	3.5	0.2	14.1
	BPs1	Bs	7-20	many			single grain	0/4	4.9	47	49	4	1.5	-	-
	BPs2	Bs	20-24	common			-	0/4	-	-	-	-	-	-	-
	C	C	24-32	common			-	0/4	-	-	-	-	-	-	-
	Rsi	R	32+	-			-	0/4	-	-	-	-	-	-	-
G403	S*-OLv	Oi	1-0	-			-	-	-	-	-	-	-	-	-
	Aho	Ah	0-2	common			single grain	0/4	4.6	28	67	5	17.0	1.0	17.3
	A1	A	2-6	common			single grain	0/4	4.7	40	56	4	4.2	0.3	13.7
	A2	A	6-9.5	common			single grain	0/4	5.0	45	52	4	1.9	0.1	14.0
	BPs-C1	Bs-C	9.5-11.5	common			single grain	0/4	4.9	56	42	3	1.4	0.1	14.8
	BPs-C2	Bs-C	11.5-15.5	common			-	0/4	-	-	-	-	-	-	-
	Rsi	R	15.5+	-			-	0/4	-	-	-	-	-	-	-
G421	OLv	Oi	3-0	-			-	-	-	-	-	-	38.9	1.3	30.9
	OF	Oe	0-3	many			-	-	-	-	-	-	31.5	1.6	19.3
	Aho	Ah	3-7	many			granular (micro)	0/4	3.8	30	64	6	13.2	0.9	14.3
	A-E	AE	7-7/11	many			single grain	0/4	4.2	34	59	7	4.9	0.4	13.1
	BPS2	Bs	7/11-18	many			-	0/4	-	-	-	-	-	-	-
	BPS2*	Bs	18-34	many			-	0/4	-	-	-	-	-	-	-
	X	-	34-43/52	many			-	0/4	-	-	-	-	-	-	-
	M	C	43/52-52	common			-	0/4	-	-	-	-	-	-	-
R264R	S*[OLv]	[Oi]	1.5-0	-	-	-	-	-	-	-	-	-	45.2	1.5	30.7
	[OF]	[Oe]	0-1	-	-	-	-	-	-	-	-	-	37.6	1.7	22.7
	Aa	A	1-2/4	common	-	-	granular (meso)	0/4	4.6	18	79	2	15.5	1.0	15.4
	Gr	Br	2/4-12	very few	-	-	blocky subangular	0/4	5.0	26	73	2	1.4	0.1	9.8
	Msi	C	12-28	very few	very few	-	single grain / blocky subangular	0/4	5.3	33	66	1	0.4	0.1	6.7
	Go1	Br	12-28	-	-	-	single grain / blocky subangular	0/4	5.0	31	67	1	0.6	0.1	6.9
	Go2	Br	28-45+	very few	-	-	blocky subangular	0/4	4.9	28	71	1	0.8	0.1	7.4

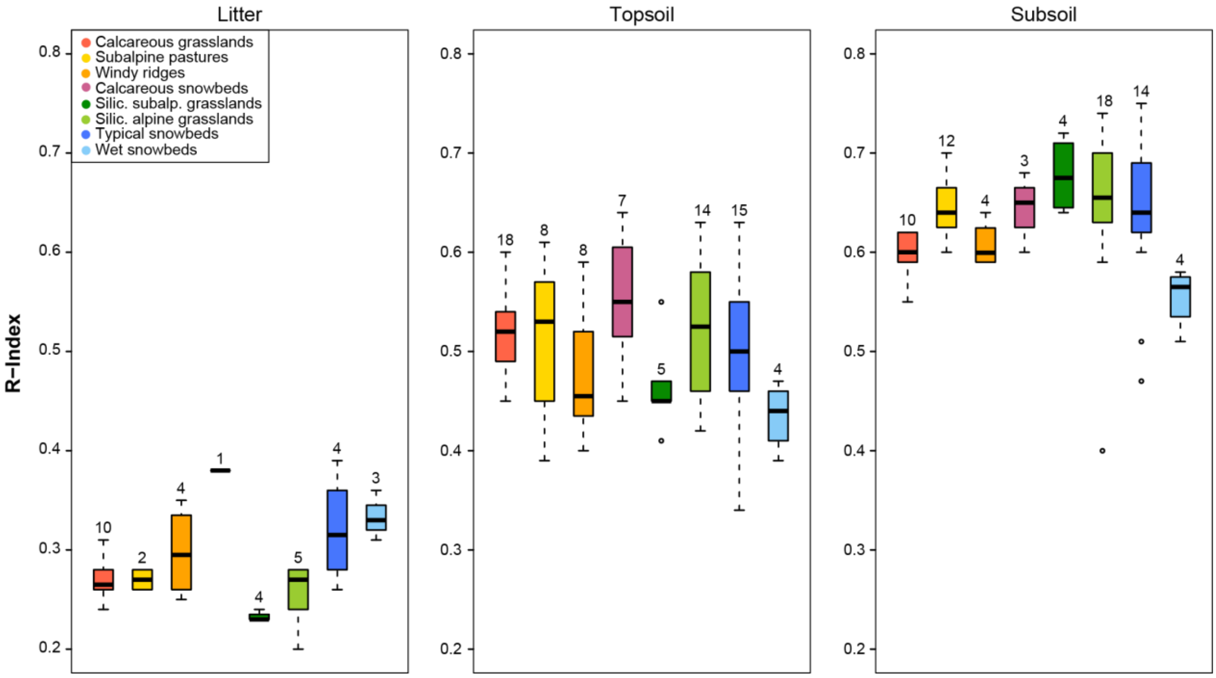
Profile	Soil horizon (Baize & Girard, 2009 & Jabiol et al. 2013)	Soil horizon (FAO 2006)	Depth [cm]	Root abundance			Structure	HCl react.	pH (H_2O)	Sand [%]	Silt [%]	Clay [%]	Corg [%]	Ntot [%]	C/N
				0-2mm	2-5mm	>5mm									
R267R	S*&OLv	Oi	2-0	-	-	-	-	-	-	-	-	-	43.3	1.7	24.9
	OR	A	0-3	many	very few	-	granular (micro)	0/4	4.4	22	74	4	15.3	0.9	17.7
	Ae	AE	3-9	few	-	-	granular (micro)	0/4	4.3	20	76	4	4.3	0.3	13.5
	A&BPs-C	A&Bs-C	9-21	common	-	-	granular (micro) / single grain	0/4	4.4	28	69	3	2.0	0.2	10.7
	C	C	21-30+	very few	-	-	single grain	0/4	4.4	22	75	3	0.5	-	-
R3901	OLv	Oi	1-0	-	-	-	-	-	-	-	-	-	42.2	1.1	38.8
	OF	Oe	0-1	-	-	-	-	-	-	-	-	-	39.7	1.3	30.6
	Aho	Ah	1-8	many	very few	-	granular (micro)	0/4	5.4	20	76	4	12.1	0.8	15.0
	A	A	8-13	common	very few	-	granular (micro)	0/4	6.2	26	72	2	1.6	0.2	8.8
	S-Csi	Bw-C	13-22.5	few	-	very few	single grain / blocky subangular	0/4	7.1	24	73	3	0.6	0.1	8.7
	Xgr&IICca1	C	22.5-30.5	very few	-	-	no	4/4 & quartz grains 0/4	8.0	26	70	4	-	-	-
	Xgr&IICca2	C	30.5-40.5	-	-	-	no	-	-	-	-	-	-	-	-
	Xgr&IICca3	C	40.5-50	very few	-	-	no	4/4 & quartz grain 0/4	8.1	43	53	3	-	-	-
	Xgr&IICca4	C	50+	very few	-	-	no	4/4 & quartz grain 0/4	8.2	35	61	4	-	-	-
R3913	S*[OLv]-A	[Oi]-A	1-0	-	-	-	-	-	-	-	-	-	10.0	0.6	16.6
	A1	A	0-3.5	few	-	-	granular (micro)	0/4	5.4	18	79	4	3.9	0.3	12.8
	A2	A	3.5-9.8	common	very few	-	granular (micro) / massive	0/4	5.5	28	70	2	1.5	0.1	12.4
	C1	C	9.8-14.5	very few	very few	-	single grain	0/4	5.6	34	65	1	-	-	-
	C2	C	14.5-24	very few	-	-	single grain	0/4	5.7	32	67	1	-	-	-
	C3[A3]	C[A]	24-30	very few	-	-	single grain	0/4	5.8	29	70	1	-	-	-
	II A	IIA	30-33	very few	-	-	granular (micro)	0/4	5.9	28	70	2	-	-	-
	II C	IIC	33-41+	very few	-	-	single grain	0/4	5.9	32	67	1	-	-	-
R3934	S*	-	4-2	-	-	-	-	-	-	-	-	-	-	-	-
	OM	Oi	2-0	-	-	-	-	-	-	-	-	-	48.0	1.1	42.1
	Aa	A	0-5	few	few	-	massive	0/4	6.1	16	80	4	9.0	0.4	21.9
	Aa&D	A	5-8+	-	-	-	-	0/4	-	-	-	-	-	-	-
R3935	S*[OLv]	[Oi]	1-0	-	-	-	-	-	-	-	-	-	59.0	2.2	26.3
	Aa	A	0-1	few	very few	-	massive	0/4	5.1	20	76	3	13.1	0.6	23.1
	A1	A	1-2	few	very few	-	-	0/4	-	18	79	3	5.6	0.3	16.3
	A2	A	2-8	few	-	-	granular (meso)	0/4	5.9	26	71	3	2.4	0.2	13.6
	A2[Gr]	A[Br]	8-17	few	very few	-	granular (meso) / blocky subangular	0/4	5.9	23	74	3	2.0	0.2	12.8
	Gr1	Br	17-26	very few	-	-	blocky subangular	0/4	6.0	26	72	3	-	-	-
	Gr1-C	Br-C	26-36	very few	-	-	blocky subangular / massive	0/4	6.2	18	78	3	-	-	-
	Gr2	Br(W)	36+	-	-	-	-	0/4	-	-	-	-	-	-	-
R4003	S*[OLv][OF]	[Oi][Oe]	2-0	-			-	-	-	-	-	-	44.2	1.8	25.0
	Aciho	Ah	0-2/5	many			granular (micro)	1/4	6.8	25	71	4	15.6	1.4	11.3
	Aca	A	2/5-3/6	many			granular (micro)	2/4	7.4	23	74	4	3.6	0.4	10.0
	Sca-Cca	Bw-C	3/6-28/8	many			blocky subangular	4/4	7.8	20	76	4	1.0	-	-
	Xpca&Cca	C	28/8-40	common			single grain	4/4	7.9	22	74	4	1.1	-	-
	IICsi&Dsi	IIC	40+	none			-	-	-	-	-	-	-	-	-
R4209	S*&L*&OLv	Oi	0.5/1-0	-	-	-	-	-	-	-	-	-	47.8	0.6	75.8
	Aho	Ah	0-3	common	very few	-	granular (micro)	0/4	4.2	17	75	7	16.2	0.7	22.1
	Eh	Eh	3-15	few	very few	-	single grain	0/4	4.4	21	75	4	2.2	0.2	13.6
	BPs1	Bs	15-18	-	-	-	single grain / blocky subangular	0/4	4.6	23	72	5	2.0	0.1	17.4
	BPs2	Bs	18-24.5	very few	-	-	single grain / blocky subangular	0/4	4.7	17	78	5	1.2	-	-

Profile	Soil horizon (Baize & Girard, 2009 & Jabiol et al. 2013)	Soil horizon (FAO 2006)	Depth [cm]	Root abundance			Structure	HCl react.	pH (H_2O)	Sand [%]	Silt [%]	Clay [%]	Corg [%]	Ntot [%]	C/N
				0-2mm	2-5mm	>5mm									
	Rsi&BPs	Bs&R	24.5-31.5+	few	-	-	single grain / blocky subangular	0/4	5.0	13	81	6	1.4	-	-
R4217	S*[OLv]	Oi	0.5-0	-	-	-	-	-	-	-	-	-	50.0	1.2	43.4
	Aa	A	0-2	few	very few	-	massive	0/4	6.0	29	68	3	12.5	0.6	22.6
	Jshg	Bg	2-9	few	-	-	granular (micro) / single grain	0/4	6.7	49	50	2	0.5	0.0	13.2
	D&Cg	Cg	9-23/26	very few	-	-	single grain	0/4	6.8	48	50	2	-	0.0	0.0
	D&Go	Br(W)	23/26-36+	very few	-	-	single grain	0/4	6.3	42	56	2	-	-	-
R4468	S*[OLv][OF]	[Oi][Oe]	1-0	-			-	-	-	-	-	-	42.7	1.1	39.0
	Ag1	Ag	0-3.5	few			granular (micro)	0/4	4.5	22	75	3	5.0	0.4	13.5
	Ag2	Ag	3.5-10.5	few			granular (micro)	0/4	4.8	25	72	3	2.8	0.2	12.1
	g1	Bg	10.5-15.5	few			granular (micro) / single grain	0/4	5.3	25	73	3	0.7	0.1	7.6
	g2	Bg	15.5-20	very few			blocky subangular	0/4	5.4	21	76	3	0.7	0.1	6.9
	g3	Bg	20-23.5	very few			blocky subangular	0/4	5.3	24	73	3	1.5	0.2	9.5
	II A	IIA	23.5-26.5	few			granular (micro)	0/4	5.1	25	73	2	6.4	0.4	15.6
	IIGr-C	IIBr-C	26.5-34.5+	very few			single grain	-	5.4	34	64	2	-	-	-
R4469	S*&L*[OLv][OF]	[Oi][Oe]	1-0	-	-	-	-	-	-	-	-	-	41.3	1.0	40.9
	miAho	Ah	0-2	common	-	-	granular (micro)	0/4	4.1	24	70	5	16.1	1.0	16.8
	Ae	AE	2-8/10	very few	-	-	granular (micro)	0/4	4.0	24	71	4	4.7	0.3	14.3
	BPs-C1&D	Bs-C	8/10-17/22	very few	-	-	granular (micro)	0/4	5.0	47	52	1	1.5	-	-
	BPs-C2&D	Bs-C	17/22-43+	few	few	-	single grain / blocky subangular	0/4	6.1	34	64	2	0.8	0.1	6.3
R4471	S*[OLv]	[Oi]	0.5-0	-	-	-	-	-	-	-	-	-	35.2	1.0	34.9
	miAho	Ah	0-3	few	-	-	granular (micro)	0/4	4.2	32	63	4	15.2	0.9	17.1
	Ae	AE	3-11	very few	-	-	granular (micro)	0/4	4.1	32	65	4	4.1	0.3	15.2
	D-C1 around roots	C	11-	-	-	-	-	0	4.3	37	59	3	1.9	-	-
	Xp[C1-BP]	Bs	0-32	few	-	-	single grain	0/4	4.3	35	63	3	1.1	-	-
	D[C2]	C	32-52+	very few	-	-	blocky subangular	0/4	4.3	23	75	2	-	-	-
R4482	OLv	Oi	2/4-0	-			-	-	-	-	-	-	40.4	1.2	33.7
	Aci	A	0-9	common			granular (micro)	0/4	6.4	24	72	4	6.6	0.7	10.1
	Aci-Sci	AB	9-18	common			granular (micro) / blocky subangular	1/4	6.8	25	72	3	2.1	0.3	7.0
	Xpca&Cca	C	18-52+	common			single grain	4/4	7.5	18	80	2	1.2	-	-
R5061	S*[OLv]	[Oi]	1-0	-	-	-	-	-	-	-	-	-	40.5	1.3	30.7
	Aa	A	0-1/7	many	-	-	massive	0/4	5.3	21	77	3	18.2	1.0	18.2
	A&D&Gr1	A&Br	1/7-6/9	many	-	-	massive	0/4	5.7	19	78	3	4.3	0.3	13.2
	Gr1	Br	6/9-19	few	-	-	single grain	0/4	6.0	41	57	2	0.5	-	-
	Gr2	Br	19-25	very few	-	-	single grain	0/4	6.3	46	52	2	-	-	-
	Gr3	W	25-32+	-	-	-	-	-	-	-	-	-	-	-	-
R5067	[OLv]	[Oi]	1-0	-	-	-	-	-	-	-	-	-	49.9	1.1	46.5
	[OF]	[Oe]	0-0.5	-	-	-	-	-	-	-	-	-	-	-	-
	OH	Oa	0.5-1.5/4	many	very few	-	granular (micro)	0/4	4.8	16	74	10	21.4	1.1	19.3
	Ae	AE	1.5/4-6.5/8.5	very few	-	-	single grain	0/4	4.6	25	71	5	4.2	0.3	13.7
	BPs-C	Bs-C	6.5/8.5-10/11.5	few	-	-	single grain	0/4	4.9	26	70	4	2.6	-	-
	C	C	10/11.5-14.5/20.5	very few	-	-	single grain	0/4	5.2	35	61	3	1.8	-	-
	Rsi&Rca	R	14.5/20.5+	-	-	-	-	0/4	-	-	-	-	-	-	-
R5141	S*[OLv]	[Oi]	1-0	-	-	-	-	-	-	-	-	-	39.7	1.9	20.8
	OH	Oa	0-4/5.5	many	few	-	massive	0/4	5.5	36	61	3	25.7	1.2	21.0
	C1-OH	C-Oa	4/5.5-10	common	-	-	single grain	0/4	4.1	34	64	2	2.4	-	-
	C2	C	10-16.5	few	-	-	single grain	0/4	4.3	37	61	2	1.5	-	-
	D[C2]	C	16.5-21	-	-	-	-	-	-	-	-	-	-	-	-
R5145	OLv[OF]	Oi[Oe]	1-0	-			-	-	-	-	-	-	39.9	1.4	28.7

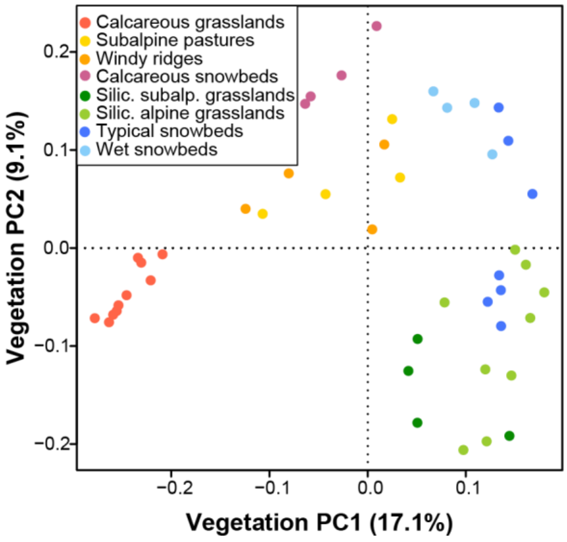
Profile	Soil horizon (Baize & Girard, 2009 & Jabiol et al. 2013)	Soil horizon (FAO 2006)	Depth [cm]	Root abundance			Structure	HCl react.	pH (H_2O)	Sand [%]	Silt [%]	Clay [%]	Corg [%]	Ntot [%]	C/N
				0-2mm	2-5mm	>5mm									
	Aho	Ah	0-3/6		many		granular (micro)	0/4	6.0	10	87	3	14.8	0.8	18.6
	A	A	3/6-6		many		granular (micro)	0/4	5.7	16	82	2	5.4	0.3	18.9
	A&D1	A	6-11		many		granular/single grain/blocky subangular	0/4	5.8	21	77	2	2.0	-	-
	A&D2	A	11-20		common		granular/single grain	0/4	5.8	24	73	2	1.4	-	-
	C&Dca	C	20-30+		common		blocky subangular	0/4 & stones 2/4	6.2	20	78	1	-	-	-

Appendix F2 - Observation of soil macrofauna in two soil profiles in the Morteys site: **(a and b)** Profile M3109, Dystric Brunisol, Oligomull, 1900 m; **(c)** profile M3139, Eutric Cambisol, Oligomull (Hyperhumic, Rhizic), 1774 m.

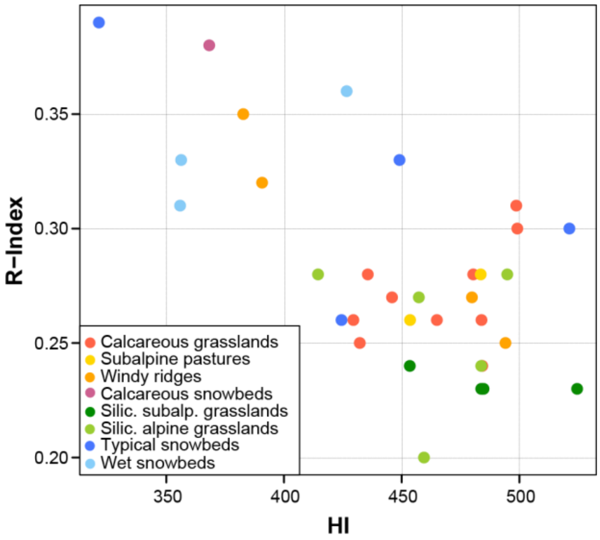
G. Supplementary material related to Chapter 6



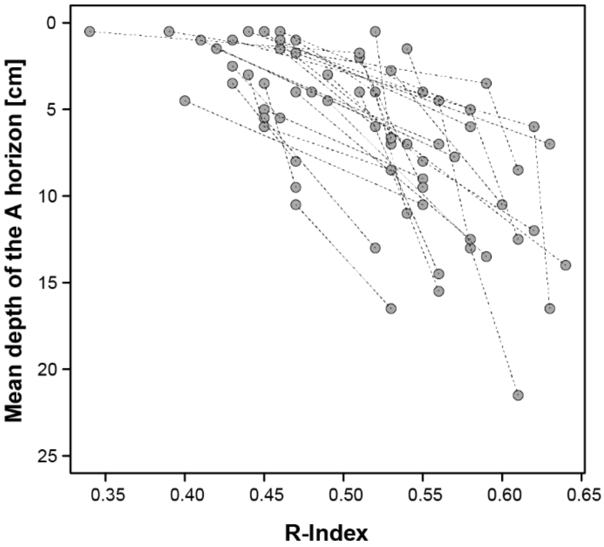
Appendix G1 - Box plot of R-Index for litter, topsoil, and subsoil mineral layers among the eight plant communities. The bold horizontal line in the boxes corresponds to the median, the whisker bars indicate data range within 5 and 95th percentiles and the numbers above plots refer to the number of samples. Colours represent the eight plant communities. “Silic.”: siliceous. “subalp.”: subalpine.



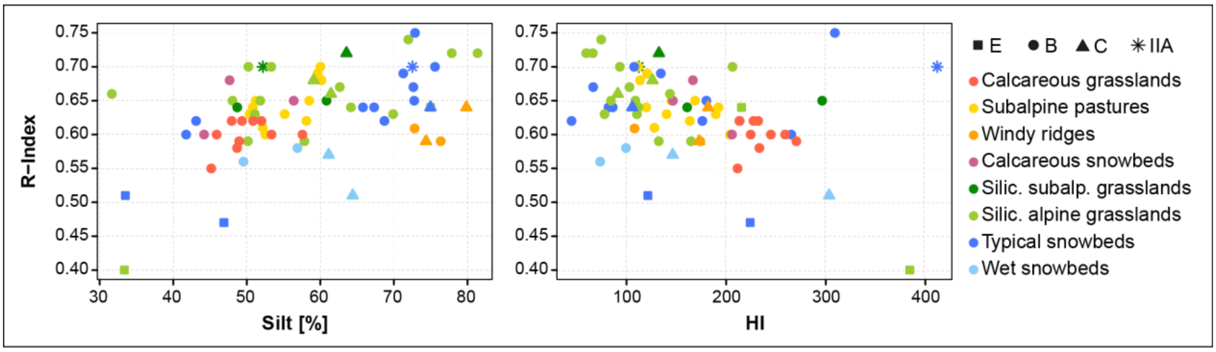
Appendix G2 - Principal Component Analysis (PCA) based on plant species composition and cover. Each point represents a plant inventory associated to a soil profile. The first axis represents 17.1% and the second 9.1% of the total variance in the dataset. Colours represent the eight plant communities. Same colours and abbreviations as in Appendix G1.



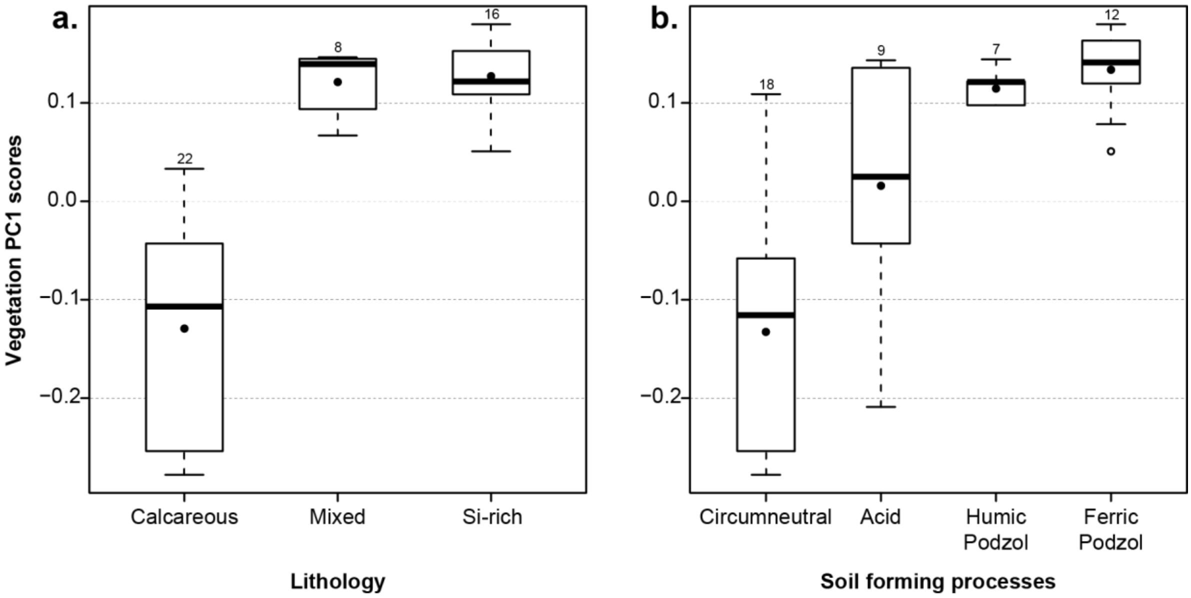
Appendix G3 - Thermal stability (R-Index) of the litter layer plotted against the Hydrogen Index (HI). Same colours and abbreviations as in Appendix G1.



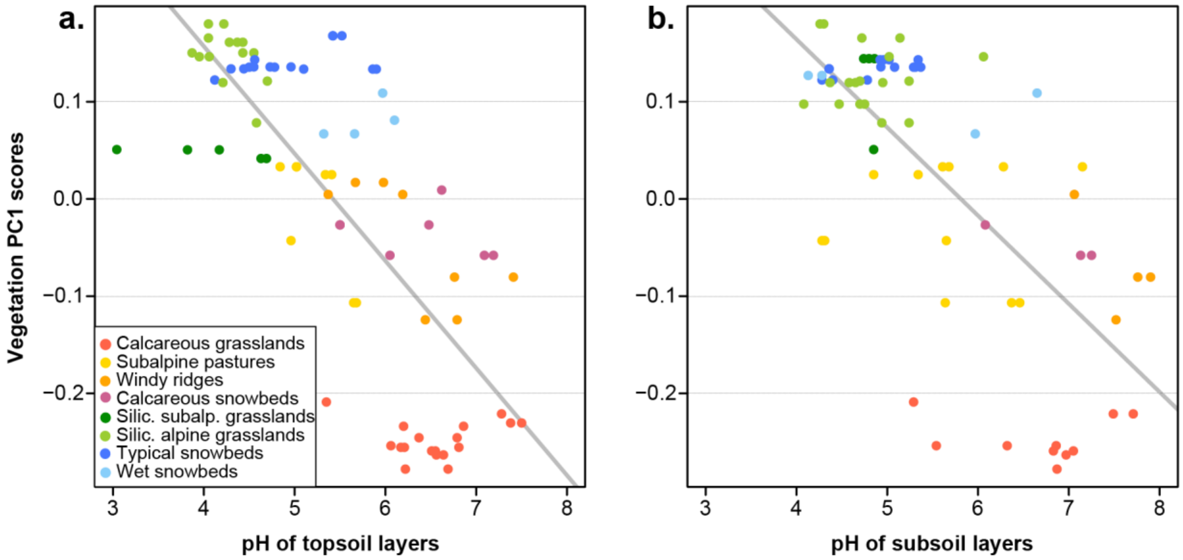
Appendix G4 - R-Index of mineral topsoil layers as a function of their depth. Lines join A horizons of the same soil profile. Only soil profiles presenting more than one A horizon are represented (*n*=28).



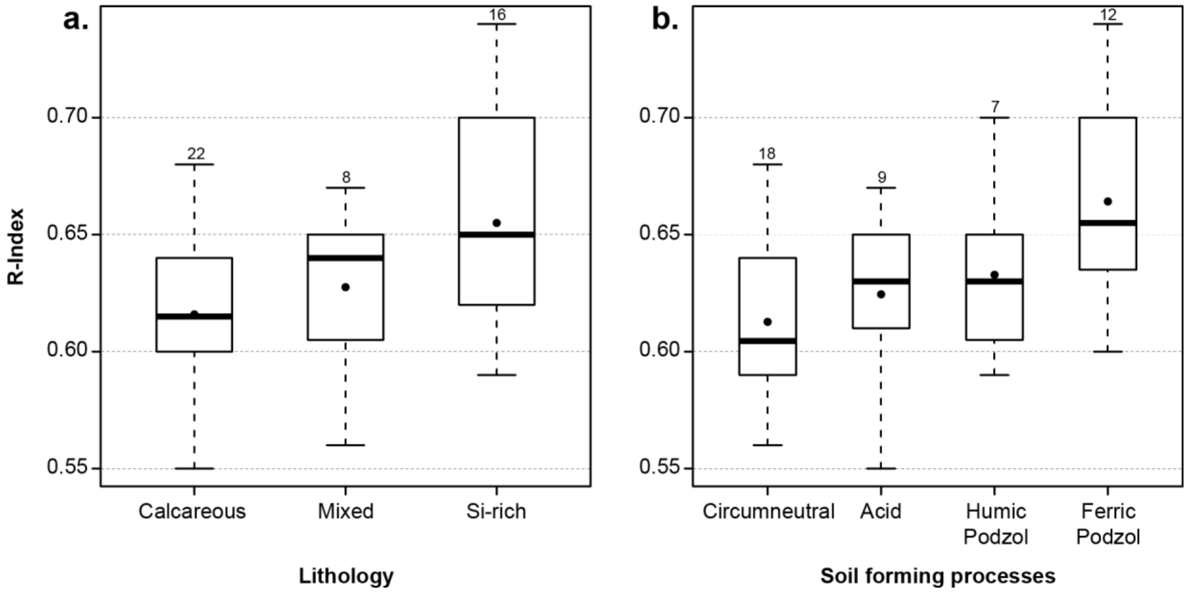
Appendix G5 - R-Index values plotted against silt % **(a)** and HI **(b)**, respectively the third and fourth most important predictors of OM thermal stability in the subsoil. Symbols represent the horizon categories. Same colours and abbreviations as in Appendix G1.



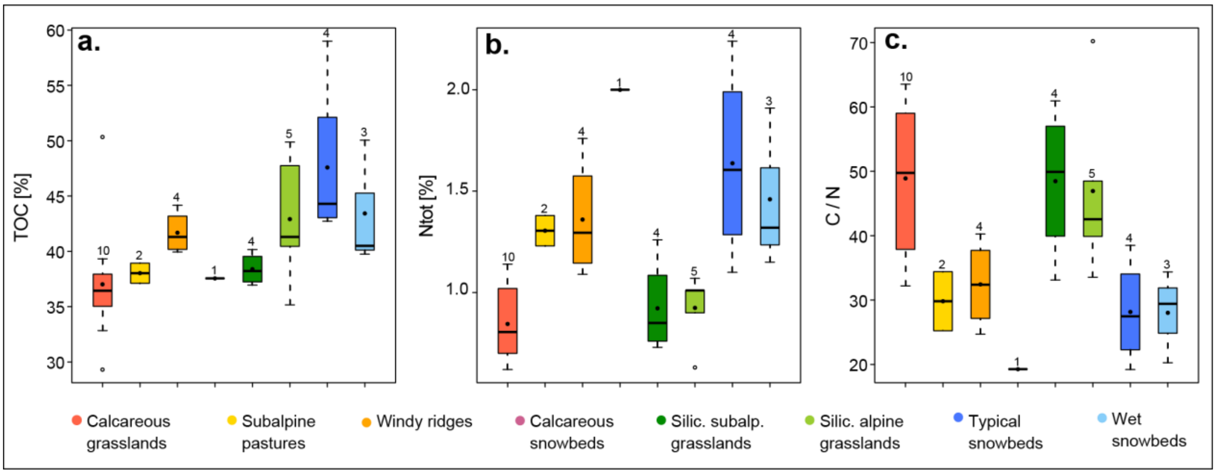
Appendix G6 - Relationship between scores from the first principal component of vegetation composition and **(a)** the lithology of soil's parent material, **(b)** the dominant soil-forming process. For lithologies, the "Calcareous" category refers to limestones, calcareous sandstones, marbles, and surficial deposits (screes and moraines) derived almost exclusively from these materials. The "Mixed" category contains surficial deposits of mixed origin (sedimentary, metamorphic, and igneous components). The "Si-rich" category contains granite, gneiss, quartzite, and surficial deposits derived almost exclusively from these materials. Regarding the soil-forming processes, the "Circumneutral" category refers to weakly differentiated solums (Cambisols, Leptosols, Regosols, Gleysols, Stagnosols) with a subsoil of pH > 6, while the "Acid" category refers to weakly differentiated solums with a subsoil at pH < 5.6. "Humic Podzols" and "Ferric Podzols" refer to acid solums with illuvial subsoil horizons enriched in organic compounds and/or sesquioxides. Black dots represent the mean values, the black line is the median, and boxes are limited by 1st and 3rd quartiles. Numbers of observations are indicated above boxplots.



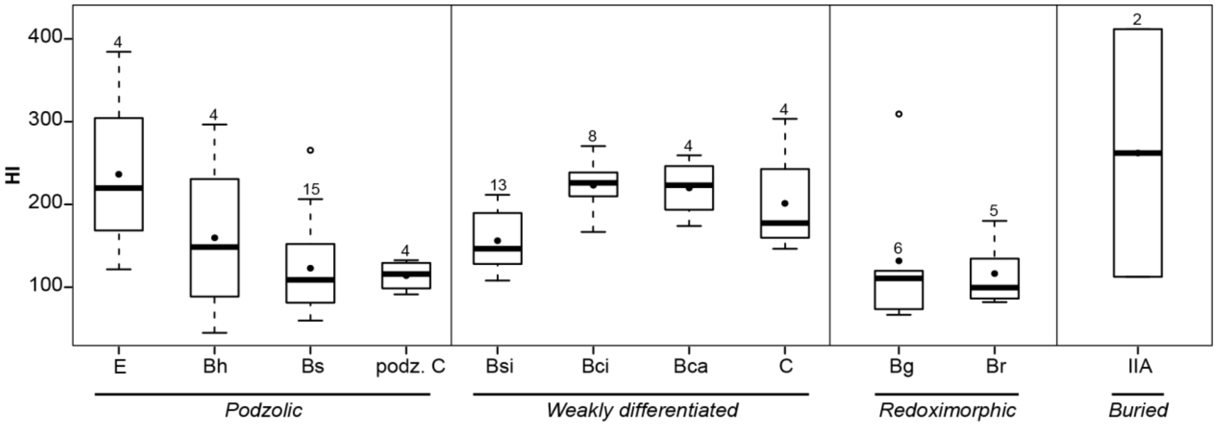
Appendix G7 - Relationship between scores from the first principal component of vegetation composition and **(a)** pH of topsoil layers (Pearson's r= -0.75, -0.84< r < -0.64) and **(b)** pH of subsoil layers (r= -0.70, -0.80 < r < -0.56) with their respective regression lines. Same colours and abbreviations as in Appendix G1.



Appendix G8 - Relationship between the R-index and **(a)** the lithology of soil's parent material, **(b)** the dominant soil-forming process. Same symbols and legend as in Appendix G6.



Appendix G9 - Relationship between the vegetation type and **(a)** the total organic C concentrations (TOC), **(b)** total Nitrogen concentration (Ntot) and **(c)** their ratio (C/N) of the litter samples. Same symbols as in F6. Same colours and abbreviations as in Appendix G1.



Appendix G10 - Relationship between the Hydrogen Index (HI) and the type of mineral subsoil layers. The first four horizon types represent the podzolic soil sequence, including: “E”(eluvial horizon); “Bh” (illuvial accumulation of organic matter), average pH = 4.7; “Bs”(illuvial accumulation of sesquioxides), average pH = 4.9; “podzolic C” (horizon weakly affected by pedogenic processes underlying a podzolic profile). The next four horizon types are found in weakly-developed solums such as Cambisols, Leptosols, and Regosols and include: “Bsi” (siliceous, low Ca saturation), average pH=5.7; “Bci” (absence of Ca-carbonate but high Ca saturation), average pH = 6.7; “Bca” (presence of calcium (Ca) carbonate), average pH = 7.5; “C” (horizon weakly affected by pedogenic processes). The next two horizon types are found in soils with expressed redoximorphic features and include “Bg” (stagnic conditions) and “Br” (strong reducing conditions) horizons. The last class “IIA”refers to buried A horizons (FAO, 2006). Same symbols as in Appendix G6.

H. Published article

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Snowbeds are more affected than other subalpine–alpine plant communities by climate change in the Swiss Alps

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Keywords
Colonization, cover changes, diversity, ecological indicator values, grasslands, homogenization, resurvey study, semipermanent plot, snowmelt, Switzerland.

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Funding Information
No funding information provided.

Received: 10 February 2016; Revised: 23 June 2016; Accepted: 30 June 2016

***Ecology and Evolution* 2016; 6(19): 6969–6982**

doi: 10.1002/ece3.2354

Abstract

While the upward shift of plant species has been observed on many alpine and nival summits, the reaction of the subalpine and lower alpine plant communities to the current warming and lower snow precipitation has been little investigated so far. To this aim, 63 old, exhaustive plant inventories, distributed along a subalpine–alpine elevation gradient of the Swiss Alps and covering different plant community types (acidic and calcareous grasslands; windy ridges; snowbeds), were revisited after 25–50 years. Old and recent inventories were compared in terms of species diversity with Simpson diversity and Bray–Curtis dissimilarity indices, and in terms of community composition with principal component analysis. Changes in ecological conditions were inferred from the ecological indicator values. The alpha-diversity increased in every plant community, likely because of the arrival of new species. As observed on mountain summits, the new species led to a homogenization of community compositions. The grasslands were quite stable in terms of species composition, whatever the bedrock type. Indeed, the newly arrived species were part of the typical species pool of the colonized community. In contrast, snowbed communities showed pronounced vegetation changes and a clear shift toward dryer conditions and shorter snow cover, evidenced by their colonization by species from surrounding grasslands. Longer growing seasons allow alpine grassland species, which are taller and hence more competitive, to colonize the snowbeds. This study showed that subalpine–alpine plant communities reacted differently to the ongoing climate changes. Lower snow/rain ratio and longer growing seasons seem to have a higher impact than warming, at least on plant communities dependent on long snow cover. Consequently, they are the most vulnerable to climate change and their persistence in the near future is seriously threatened. Subalpine and alpine grasslands are more stable, and, until now, they do not seem to be affected by a warmer climate.

Introduction

During the end of the 20th century (1975–2004), the mean annual temperature in Switzerland increased by 0.57°C per decade with a stronger trend in spring and summer seasons (Rebetez and Reinhard 2008). After a gradual increase until the early 1980s, snow precipitation in Switzerland significantly decreased (Laternser and Schneebeli 2003) with a particularly pronounced trend at lower elevations (501–800 m a.s.l., Serquet et al. 2013). Snowfall decreased above 1700 m as well, but only at the beginning and at the end of the winter season (Serquet et al. 2013). At such elevations, winter temperatures are generally much lower than the melting point, and, even with warmer conditions, there is little potential for a decrease in snowfall days (Serquet et al. 2011). By contrast, the combination of higher temperatures and lower snowfalls during the spring season results in a lower snow cover (IPCC, 2014), earlier melt-out dates, and longer growing seasons for plants (Dye 2002). Future scenarios predict the continuation of this trend through the 21st century and indicate that vegetation of high latitudes and elevations is the most threatened (ACIA, 2005; IPCC, 2014).

Impacts of the recent climate change on alpine vegetation have been largely recorded by many long-term studies on European upper alpine and nival summits. Authors observed an increase in species richness during the last century (see Stöckli et al. 2011 for a review), already noticeable on a shorter timescale (2001–2008; Pauli et al. 2012). The newly arrived species are subalpine and lower alpine species (Vittoz et al. 2008a; Engler et al. 2011) and now, because of longer growing seasons, they are able to grow at higher elevations. Space on the summits is not a constraint to colonization as it is widely available. However, the upward shift of plant species led not only to higher species number, but also to a homogenization of plant composition across Alpine Swiss summits (Jurasinski and Kreyling 2007). Similarly, vegetation of the high northern latitudes has been changing over the past few decades and a general increase in biomass and proliferation of shrub species are responsible for the tundra "greening" (see Epstein et al. 2013 for a review).

Many more uncertainties exist about the effects of climate warming at lower elevations. A shift of tree line northwards and to higher elevations is the most often observed change on European mountain ranges (see Garamvoelgyi and Hufnagel 2013 for a review). In the Swiss Alps, the forest limit moved upward with a mean decadal increment of 28 m between 1985 and 1997 (Gehrig-Fasel et al. 2007). However, between tree line and the upper alpine–nival belt, there is a wide range of plant communities whose responses to altered temperatures and precipitations have been poorly investigated so far. This is unfortunate, as identifying the most threatened plant communities is very important to establish proper conservation measures. Some previous long-term surveys focused on changes of specific plant community, such as alpine siliceous grasslands (Dupré et al. 2010; Windmaißer and Reisch 2013), calcareous grasslands (Kudernatsch et al. 2005; Vittoz et al. 2009), or snowbed communities (Carbognani et al. 2014; Pickering et al. 2014; Sandvik and Odland 2014). However, only a couple of studies located in the Scottish highlands (Britton et al. 2009; Ross et al. 2012) and one in the Italian Alps (Cannone and Pignatti 2014) looked at long-term vegetation changes in a variety of alpine plant communities.

At these elevations, the effects of climate and land-use changes are difficult to disentangle. Indeed, seasonal grazing has been decreasing and many pastures have been abandoned since the end of the nineteenth century (Bätzing 1991). This highly contributed to the forest expansion toward higher elevations (Gehrig-Fasel et al. 2007; Vittoz et al. 2008b) and favored the arrival of plants from fallow and wood edge communities in the subalpine grasslands (Vittoz et al. 2009). Moreover, as a result of industrial, traffic, and agronomic emissions, tropospheric concentrations of nitrogen compounds have increased remarkably, reaching levels that are likely to affect the aboveground productivity of alpine plants (Bassin et al. 2007).

It has been demonstrated that nitrogen deposition causes a decrease in species richness in the Swiss montane grasslands, with oligotrophic, and usually rare, species being particularly disfavored (Roth et al. 2013). Subalpine and alpine grasslands are likely more vulnerable to negative effects of N deposition, as they have shorter growing seasons and generally thinner and nutrient poorer soils (Bowman et al. 2012). However, increased N depositions may have different consequences between habitats: using a plant trait analysis, Maskell et al. (2010) showed that eutrophication and acidification occurred, both of which can be responsible for species loss. Indeed, in a moss-dominated alpine heath of Northern Europe, N deposition seems to trigger a decline of plant diversity and of shrub, bryophyte and lichen covers, but an increase in the graminoid cover (Armitage et al. 2014).

A powerful and widely used tool to identify factors driving the vegetation changes is the species indicator values of Landolt et al. (2010) for the flora in the Alps or those of Ellenberg et al. (1991) in Central Europe. These semiquantitative parameters, although inferred from field experience and not from direct measurements, have been shown to give pertinent indications of the species ecological optima within small spatial areas in Alpine landscapes (Scherrer and Körner 2011). Specifically, the temperature indicator value is significantly correlated with the average soil temperature, which is far more representative of actual conditions experienced by low-stature alpine plants than the air temperature interpolated from meteorological stations (Scherrer and Körner 2011).

For the purpose of this study, 63 exhaustive plant inventories performed on six plant community types during the period 1964–1990 and located between the subalpine and alpine belts of the Swiss Alps have been revisited. Through a time comparison of species frequencies and cover, and with the help of indicator values, the following questions are targeted: (1) Are there observable changes in the subalpine–alpine vegetation over the last 25–50 years in species richness and community composition in the Alps? (2) Do the magnitude and direction of changes vary across different plant communities and how? (3) What are the environmental conditions that can explain the observed changes?

Materials and Methods

Study sites

Three study sites are located in the Northern Alps and western central Alps of Switzerland (Fig. 1). The Northern Alps are characterized by higher precipitations than

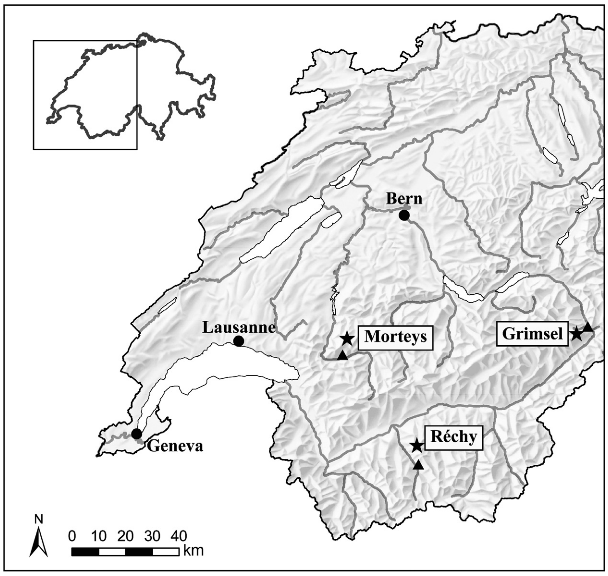

Figure 1. Study site area. Stars represent the three study sites, and triangles, the corresponding meteorological stations (Château-d'Oex for Morteys, Grimsel Hospiz for Grimsel, Evolène for Réchy).

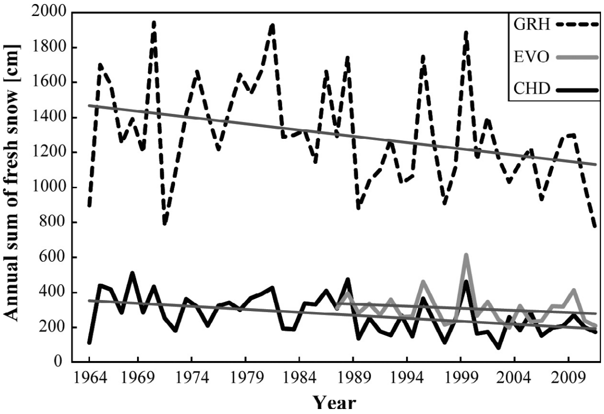

Figure 2. Annual sum of the fresh snow thicknesses daily measured at 5:40 a.m. from 1964 to 2011 (at Château-d'Oex – CHD, and Grimsel Hospiz – GRH weather stations) and from 1987 to 2011 at the Evolène (EVO) weather station (MeteoSwiss network, Begert et al. 2005). The overall decrease in the snow amount among the three stations is significant (ANCOVA test, *P*-value < 0.001).

the Central Alps. The Morteys area (46°32′N, 7°09′E) is situated on a calcareous bedrock with karstic geomorphology. The plots are located between 1698 and 2232 m a.s.l., in the transition from the subalpine to the lower alpine belt. The mean annual temperature is about 2.1°C, and the annual precipitations are 1650 mm (Zimmermann and Kienast 1999). The annual sum of fresh snow thickness decreased by 34.1 cm per decade between 1964 and 2011, while the mean summer temperature (from June to September) increased by 0.47°C per decade during the same period at the closest meteorological station (Château-d'Oex, 1029 m; Fig. 2 and Appendix S1).

The Grimsel area (46°32′N, 8°16′E) is situated on gneiss and granodiorite bedrocks (Oberhänsli et al. 1988). The slopes in the Grimsel Valley are covered by various moraine deposits from the last maximum glacier advances that occurred between 1860 and 1920 (Ammann 1979). The plots are situated in the lower alpine belt, between 2310 and 2650 m a.s.l., and are characterized by mean annual temperature and precipitations of −0.44°C and 2071 mm, respectively (Zimmermann and Kienast 1999). The annual sum of fresh snow thickness decreased in average by 71.2 cm per decade, and the mean summer temperature rose by 0.41°C per decade between 1964 and 2011 (Grimsel Hospiz, 1980 m; Fig. 2 and Appendix S1).

The Réchy area (46°10′N, 7°30′E) is located on a mixed bedrock composed by gneiss, mica schists, quartzite, calcshists, marble, and cornieule and is shaped by geomorphological processes related to glaciers, gravity movements, and cryoturbation. A mosaic of acid and alkaline soils characterizes the area. Elevation of the vegetation plots ranges from 2328 to 2697 m a.s.l., namely the tree line ecotone and the lower alpine belt of the region. The area is the coldest and the driest among the three study sites, with a mean annual temperature of −0.53°C and 1480 mm of annual precipitations (Zimmermann and Kienast 1999). The annual sum of fresh snow thickness decreased by 24.1 cm, whereas the mean summer temperatures increased by +0.25°C per decade (Evolène, 1825 m; Fig. 2 and Appendix S1) during the 1987–2013 time span (no data available before).

The three study sites have been partially included in natural reserves for several decades. Except for Grimsel, where there has been no cattle grazing since 1953, the two other sites are currently pastured in some parts. Thanks to the natural reserve management in Morteys, the land use (cow and goat grazing) has barely changed during the last 40 years. In Réchy, the type and amount of cattle have fluctuated since the 1970s with alternating cow and sheep grazing, proportions depending on both elevation and location.

The total nitrogen deposition in Morteys and Grimsel areas for the year 2007 amounted on average to 10.4 and 6.8 kg N·ha^{-1}·year^{-1}, respectively (according to Roth et al. 2013; data from FOEN Federal Office for the Environment). Data for the Réchy area were not calculated, but are comparable to those of Grimsel area because of the similar elevations and distance to main towns.

Vegetation data

In order to have a complete overview of reactions of subalpine–lower alpine vegetation to climate change, six common vegetation types, for which more historical data are available, were selected (Table 1 and Appendix S2). Each vegetation type corresponds to a phytosociological alliance given between brackets: calcareous grasslands (*Seslerion*) located in the subalpine–alpine belt, generally on very steep, south-exposed slopes; windy ridges (*Elynion*) in alpine belt, situated mostly on calcareous substrates; siliceous subalpine grasslands (*Nardion*); siliceous alpine grasslands (*Caricion curvulae*); typical snowbeds (*Salicion herbaceae*) associated with very long snow cover and acidic soil conditions; wet snowbeds (*Caricion bicolori-atrofuscae*) also associated with very long snow cover, but close to running water, brought by rivers or firn melting, or close to lakes.

Among the available data, a selection of the most promising historical records was performed according to criteria of reliability and possibility to relocate them. The historical records were achieved by several botanists from 1965 to 1990 (Table 1) with most data being collected during the 1970s (1980s in the case of wet snowbeds). The inventories were only partly published (Ammann 1974; Richard et al. 1977, 1993), but field books were available for most of them and they represented the main information source. Because of their localization on topographic or vegetation maps (1:25,000 or more precise), the plot areas were approximately localized in the field, with a precision of ± 10–50 m. Each area was extensively visited, and, on the basis of information contained in the historical field books (site description, elevation, surface, slope, and exposition), the possible plot sites were defined. The exact plot location was selected in order to have a species composition as close as possible to the historical one. This permits a conservative approach of potential changes. When no area corresponded to the historical description, or when vegetation was markedly different, the site was discarded. Only historical records separated by a distance >10 m were retained in order to avoid spatial autocorrelation. Finally, 63 plots have been localized with a high confidence level. A new exhaustive record of all vascular plants was performed during summers 2013 or 2014 at the phenological optimum, within the same area as the historical one. Species cover was visually estimated, as in historical inventories, according to cover classes of Braun-Blanquet (1964; Table 2). The plots were marked with metal plates in soil and the four corners measured with a high precision GPS (GeoXT, Trimble, Sunnyvale, CA) in order to enable their future use as permanent plots. Finally, the nomenclature of species is according to Aeschimann et al. (1996).

Data analyses

The potential mistakes in species identifications, or changes in nomenclature and aggregation level between the two periods, were corrected by a scrupulous check of possible synonymies and by aggregating the pairs of species with frequent confusions into the same taxon. One frequent problem in plant monitoring studies is the overlooked species in one of the surveys (Vittoz and Guisan 2007; Burg et al. 2015). This bias is particularly likely to cause artifact in this study, as recent inventories involved generally two botanists instead of one in the historical records, and because the historical inventories, especially those of Richard et al. (1977), were not performed for monitoring purposes, but for the classification of plant communities. Changes in diversity between pairs of records were not expressed in terms of species richness but using the Simpson diversity index, which is less sensitive to the species with low cover. This is justified in order to minimize the influence of a possible bias related to the fact that species with very low cover are mainly those overlooked (Vittoz and Guisan 2007).

Two conversions of Braun-Blanquet's scale were used for subsequent analyses. The Braun-Blanquet's scale was

Table 1. Number of plots, time spans, authors, and elevation ranges of historical and recent surveys ordered by study site (upper part) and plant community (lower part). The names of the historical botanists are abbreviated as follows: Jean-Louis Richard (JLR), Klaus Ammann (KA), Benoît Bressoud (BB), Olivier Duckert (OD). Numbers in brackets refer to medians.

Site	No. of plots	Historical survey	Author(s) of historical data	Elevation (m)
Morteys	12	1972–1979 (1973)	JLR	1698–2232 (1884)
Grimsel	25	1964–1973 (1970)	KA	2310–2650 (2329)
Réchy	26	1977–1990 (1981)	BB, JLR, OD	2328–2697 (2567)
Plant community				
Calcareous grasslands	10	1972–1973 (1973)	JLR	1698–2099 (1807)
Windy ridges	13	1975–1990 (1979)	BB, JLR, OD	2180–2697 (2430)
Siliceous subalpine grasslands	12	1964–1973 (1967)	KA	2312–2370 (2320)
Siliceous alpine grasslands	11	1965–1989 (1970)	JLR, KA	2300–2682 (2528)
Typical snowbeds	8	1970–1981 (1973)	BB, JLR, KA	2313–2685 (2460)
Wet snowbeds	9	1977–1990 (1988)	JLR	2468–2677 (2585)

Table 2. Braun-Blanquet's scale used in both historical and recent inventories to estimate plant cover, the corresponding cover range and medians, used in analyses of cover changes. Numerical codes used in all other analyses are also listed.

Braun-Blanquet's code	Cover range	Median of the cover range (%)	Numerical code (Gillet 2000)
r	1 or 2 individuals	0.05	0.1
+	<1%	0.5	0.5
1	1–5%	3	1
2	6–25%	15	2
3	26–50%	37.5	3
4	51–75%	62.5	4
5	76–100%	87.5	5

converted into the median of the cover class (Table 2), in order to test the changes in the species cover between the different periods. By contrast, for all other analyses (Simpson diversity, Bray–Curtis dissimilarity, PCA, mean ecological values), numerical codes (Gillet 2000) were used because they preserve the importance of the less abundant species, a crucial point in such analyses, by reducing the weight given to dominant ones (high cover).

A possible homogenization in plant composition between historical and recent records in a same vegetation type was tested with the Bray–Curtis dissimilarity. This index computes the beta-diversity between a given record and all the others during the same time period, considering their respective species composition and cover. Means of dissimilarity indices were computed for each record separately for historical and recent surveys. Pairwise Wilcoxon–Mann–Whitney tests were used to compare temporal differences between medians of Simpson diversity indices and mean Bray–Curtis dissimilarities. The Wilcoxon test was applied firstly in the bilateral mode, and, if it gave a significant result, the unilateral mode was applied as well. The *P*-values reported in the text refer to the unilateral mode.

The difference between recent and historical species frequencies was calculated and tested with a restricted permutation test following Kapfer et al. (2011) within each plant community. Treating historical and recent inventories separately, the occurrences of each plant species among plots were shuffled randomly 999 times and new frequencies were calculated for each repetition. Significance levels were assessed by counting the number of times the changes in frequency between random historical and recent data was larger or equal to the observed changes in frequency between observed historical and recent data. For the species present simultaneously in at least 25% of the historical and recent inventories, a mean cover was calculated considering only the plots where the species was observed. Changes in mean cover were tested with the same restricted permutation test used for species frequency but using the mean cover values instead (Kapfer et al. 2012).

The floristic shifts between historical and recent records were visualized using two principal component analyses (PCA, R *vegan* library): one based on species composition and cover, and the other based on presence–absence data. The cover values were previously submitted to Hellinger transformation, which is recommended when performing PCA with species cover data (Borcard et al. 2011). In order to test the significance of the temporal shifts in species composition and cover along the first three axes of PCA, a multivariate analysis of variance (MANOVA) was applied on the differences of axis scores against the intercept for each vegetation type individually (Vittoz et al. 2009).

Landolt ecological indicator values (Landolt et al. 2010) were used to investigate which of the environmental factors were related to the changes. These values, which are species specific, vary between 1 and 5 and express increasing species requirements in terms of air temperature (T), light (L), soil humidity (F), soil pH (R), and nutrient content (N). Mean indicator values per plot were calculated with the cover as a weight. Temporal changes of mean indicator values were checked using pairwise Wilcoxon–Mann–Whitney tests. All data processing and analyses were performed with R software, version 3.1.1 (R Core Team, 2014).

Results

Distribution among vegetation types

Sixty-three pairs of reliable records have been retained (Table 1): 10 in the calcareous grasslands, 13 in the windy ridges, 12 in the siliceous subalpine grasslands, 11 in the siliceous alpine grasslands, 8 in the typical snowbeds, and 9 in the wet snowbeds. A clustering analysis (using the Hellinger distance and the Ward aggregation algorithm) of cover-weighted historical and recent inventories together showed that all old and recent records were placed by pairs in the same group corresponding to their respective plant community, except for one snowbed plot (R3935), which shifted from the wet to the typical snowbeds. For subsequent analyses, this record was retained at its original group.

Diversity changes

Between the historical and the recent surveys, 47 of 63 plots show an increase in alpha-diversity and 16 show a decrease. The magnitude of the increase varies between vegetation types (Fig. 3). The windy ridges show the highest increase in the mean Simpson diversity index (+6.3 ± 6.0, difference between medians being significant with a *P*-value = 0.004), followed by the siliceous subalpine grasslands (+4.8 ± 6.7, *P*-value = 0.017) and the wet snowbeds (+4.1 ± 3.5, *P*-value = 0.004). The increase in alpha-diversity in the other plant communities is not significant.

Beta-diversity shows an opposite trend with a slight decrease in the mean Bray–Curtis dissimilarity index between historical and recent records in each plant community, except for the calcareous grasslands (Fig. 4), whose inventories always show the same low dissimilarity level. The highest homogenization is observed in the siliceous alpine grasslands, where the mean dissimilarity index decreased by 0.05 ± 0.03 (*P*-value = 0.002), followed by the windy ridges (−0.04 ± 0.04, *P*-value = 0.002) and the siliceous subalpine grasslands (−0.04 ± 0.04, *P*-value = 0.010). The two snowbeds also show a dissimilarity decrease, but not significantly.

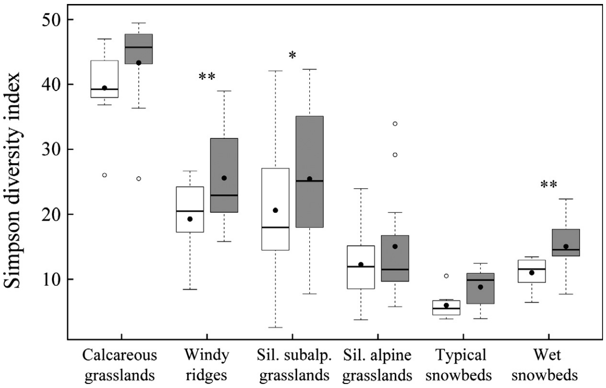

Figure 3. Simpson diversity index for historical (white boxes) and recent (gray boxes) inventories in six plant communities. "Sil.": siliceous; "subalp.": subalpine. Black dots represent the mean values, the black line is the median, and boxes are limited by 1st and 3rd quartiles. Stars above the boxes indicate a significant change between historical and recent inventories, according to a pairwise Wilcoxon–Mann–Whitney test: **P* < 0.05; ***P* < 0.01.

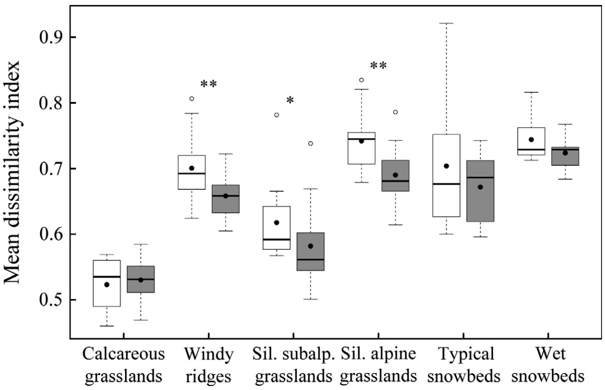

Figure 4. Averages of Bray–Curtis dissimilarity indices among historical (white boxes) and recent (gray boxes) inventories in six plant communities. Same symbols as in Figure 3.

Shifts of plant communities

The six plant communities display different directions and amplitudes in their temporal shifts in the cover-weighted PCA (Fig. 5). The first two axes of PCA explain 23.3% of the total variance (PC1: 13.0%; PC2: 10.3%). The most evident shifts are those of snowbeds: the typical ones show a significant (*P*-value = 0.012) unidirectional trend toward the siliceous alpine grasslands, while the recent species composition of the wet snowbeds is significantly closer (*P*-value = 0.006) to the typical snowbeds than the historical composition. The windy ridges plots shift in two main directions (*P*-value = 0.047), either toward calcareous grasslands or the siliceous ones. The three grassland communities have no significant shift in species composition. In particular, the calcareous grasslands display a high stability in terms of species composition. Similar trends, in direction and magnitude, are displayed when presence–absence data are considered (Fig. 6). However, four couples of records originally attributed to the siliceous alpine grasslands are here assimilated to the typical snowbed group, sharing with it the same unidirectional trend toward siliceous grasslands. These records have a species composition similar to those of typical snowbeds, but, because of the dominance of some grassland species, they are assimilated to the alpine grassland group when cover is taken into account. Hence, they can be considered as transition between snowbeds and siliceous alpine grasslands.

Changes in species frequency and cover

In all the vegetation types but the calcareous grasslands, the number of species, whose frequency increased since the historical survey, exceeds species whose frequency decreased (data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.q82j0), and only increasing frequencies are significant. Regarding changes in species cover, most of the species in the calcareous grasslands, the siliceous subalpine, and alpine grasslands show a decrease in the mean cover, whereas most of the species in the windy ridges, the typical, and wet snowbeds increase in cover. But very few cover changes are significant.

In the calcareous grasslands, five species with their optimum mostly at the subalpine belt increase significantly: *Festuca ovina aggr.*, *Globularia cordifolia*, *Cirsium*

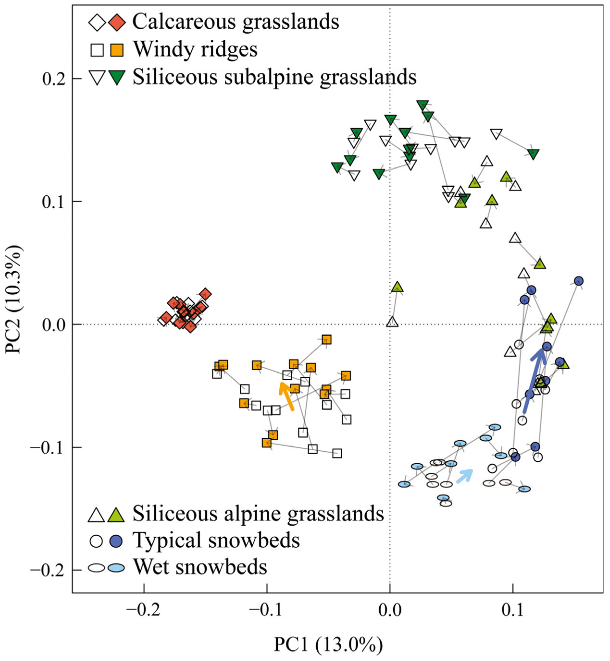

Figure 5. Principal component analysis based on species composition and cover. The first axis represents 13.0% of the variance and the second 10.3%. Couples of historical (empty symbols) and recent (full symbols) records are connected with thin arrows. Thick arrows represent a significant shift of the plant community centroids.

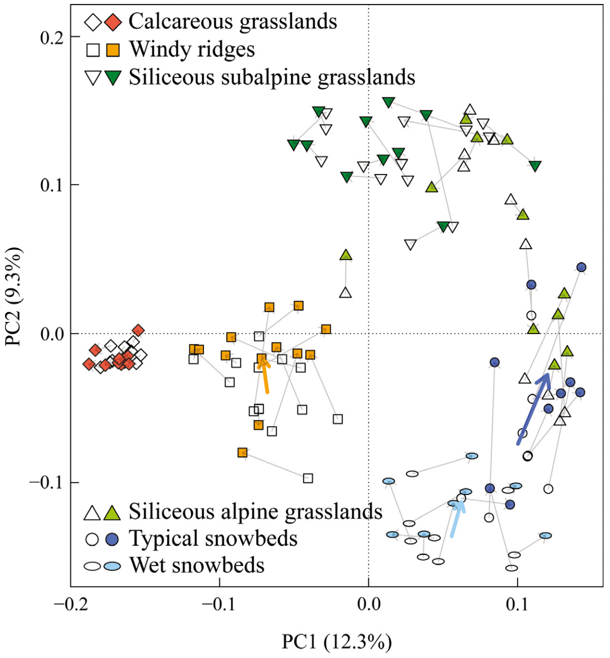

Figure 6. Principal component analysis based on species composition (presence–absence). The first axis represents 12.3% of the variance and the second 9.3%. Same symbols as in Figure 5.

acaule, *Plantago atrata s.str.*, and *Polygala alpestris*. Interestingly, *Globularia cordifolia*, a typical species of upper montane–lower subalpine belt according to the temperature indicator value (Landolt et al. 2010), was absent in the historical survey, but is present in 50% of the recent plots. *Carex sempervirens* shows a strong decrease in mean cover (−15%, *P*-value = 0.001). In windy ridges, species from both calcareous (*Anthyllis vulneraria* subsp. *alpestris* and *Selaginella selaginoides*) and siliceous grasslands (*Hieracium angustifolium*), or from the ridge community itself (*Agrostis alpina*) and generalist species (*Campanula scheuchzeri*), display a significant frequency increase.

The occurrence of three subalpine species (*Solidago virgaurea* ssp. *minuta*, *Trifolium pratense* ssp. *nivale*, and *Arnica montana*) is significantly higher in recent siliceous subalpine grassland surveys than in the historical ones. *Nardus stricta* markedly decreases in mean cover (−11.5%, *P*-value = 0.029). In the siliceous alpine grasslands, four species typical of this community (*Euphrasia minima*, *Agrostis rupestris*, *Homogyne alpina*, and *Hieracium alpinum*) are distributed more widely among recent surveys than in the historical ones.

The species, whose frequency and cover greatly increased in typical snowbeds, are mostly from siliceous alpine grasslands as well: *Leontodon helveticus* increases by 62.5% in frequency (*P*-value = 0.019) and 3.3% in cover (not significant), while *Helictotrichon versicolor* was absent in the historical survey, but is present in half of the recent plots (marginally significant, *P*-value = 0.057). Between the other species increasing both in frequency and cover (defined as “winners”, Appendix S3c), most of them are typical of grasslands and are generalists (*Ligusticum mutellina, Nardus stricta)*. In contrast, the species with the most important, but not significant, cover decrease (*Carex foetida*) is typical of snowbeds.

In the wet snowbeds, some species mostly associated to typical snowbeds, such as *Sibbaldia procumbens*, increase in frequency (+55.6%, *P*-value = 0.019), while *Juncus triglumis*, *Saxifraga androsacea,* and *Gentiana bavarica*, three species growing in wet snowbeds, decrease in terms of mean cover (−26.3%, *P*-value = 0.008; −18.4%, *P*-value = 0.026; −15%, *P*-value = 0.047, respectively).

Ecological indicator values

The six vegetation types display mean temperature indicator values (Landolt et al. 2010) that reflect their distribution in elevation, with highest values for the calcareous grasslands (Fig. 7A). The calcareous grasslands and the typical snowbeds are the only plant communities showing a significant increase in their mean temperature values between inventories (*P*-value = 0.010 and *P*-value = 0.004, respectively). Similarly, the value for soil humidity (F) reflects the moisture conditions of the plant communities, with the four types of grasslands having lower values than the two snowbed communities (Fig. 7B). Species present in the recent records of the typical and wet snowbeds have, on average, lower values than the composition of historical surveys, indicating their preference for drier conditions. However, only the decrease in the latter one is significant (*P*-value = 0.004). None of the studied plant communities show significant variations between historical and recent surveys in terms of soil nutrient requirements (Fig. 7C), light, and soil pH (Appendices S4 and S5), according to the corresponding mean ecological indicator values.

Discussion

The results of this study clearly indicate that vegetation changed over a 25- to 50-year time span at the subalpine–alpine level in the Swiss Alps. The six plant communities display similar alpha- and beta-diversity changes, but also various reactions to past environmental changes in terms of species composition.

Alpha- and beta-diversity

The increase in species richness, expressed as Simpson diversity index at the plot scale, is observed in each plant community. There are three possible explanations: (1) new species arrived since the historical time; (2) the recent inventories were more exhaustive than the historical ones, or (3) the new species are the result of inaccurate location of the plots. The last option can be excluded because it cannot result in a systematic increase for all the vegetation types. The second option could be meaningful only for the least frequent species (i.e., occurring in one or two new plots), but not for those with a considerable increase (for example, *Globularia cordifolia* in the calcareous grasslands). Moreover, many of these species are easily visible in terms of size and/or difficult to confuse with other species. Therefore, the colonization of plots by new species is at least partly responsible for the observed increase in alpha-diversity. Many previous studies observed the same trend over the last three decades on alpine plant communities (Kudernatsch et al. 2005; Britton et al. 2009; Vittoz et al. 2009; Sandvik and Odland 2014), or even just over 6 years in snowbeds (Carbognani et al. 2014; Pickering et al. 2014). Olsen and Klanderud (2014) observed that species-poor communities were more susceptible to species invasion than highly diverse species communities. Our results do not confirm such a trend, as the highest species increase was observed on the windy ridges community, which are more diverse than typical snowbeds.

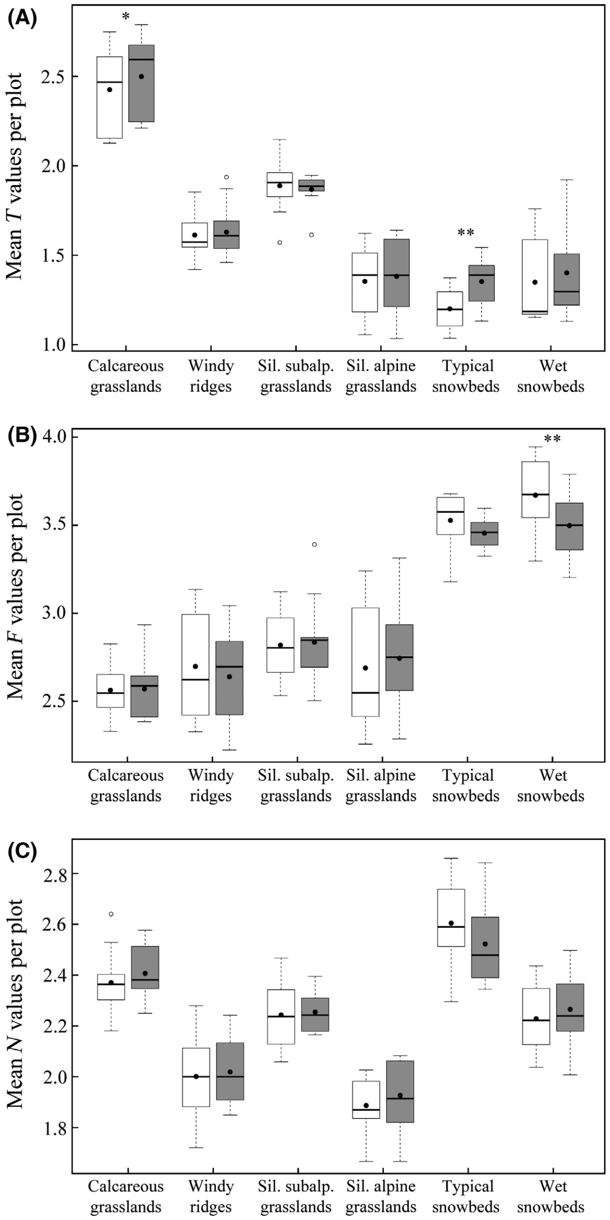

Figure 7. Cover-weighted means of indicator values (Landolt et al. 2010) for temperature (A), soil humidity (B), and soil nutrient content (C) in historical (white boxes) and recent (gray boxes) inventories. Same symbols as in Figure 3.

The increase in species richness is related to an increase in the floristic similarity inside the plant community, except in the calcareous grasslands. Similar homogenization was first highlighted on seven European Alpine summits by Jurasinski and Kreyling (2007), and on a variety of alpine plant communities since then (Britton et al. 2009; Ross et al. 2012; Carbognani et al. 2014). According to their observations, the biotic homogenization results from two processes: the invasion of widespread and generalist species, and a decline of rare and specialized species. Generalist species may be able to spread in new areas previously unsuitable, thanks to less constraining conditions for their establishment and survival, such as longer growing seasons through climate warming, or increased nutrient availability (Britton et al. 2009). Indeed, such a pattern is apparent in this study, where snowbed specialists decrease in cover, while grassland generalist species increase in frequency and cover (see Appendix S3). An increasing alpha-diversity coupled with a homogenization can be explained by the arrival of previously missing species in the community, completing the typical species ensemble for a given vegetation type (e.g., *Agrostis alpina* in the windy ridges, *Arnica montana* in the siliceous subalpine grasslands).

Snowbeds

The main changes in plant composition are observed in the typical snowbeds, which show a marked shift of species composition and cover toward the siliceous alpine grasslands, and in the wet snowbeds, whose composition tends toward the typical snowbeds (Figs 5 and 6). Therefore, the snowbeds are now more similar to the siliceous alpine grasslands than they were in the 1970s. This is confirmed by the observed colonization by species from siliceous alpine grasslands (*Helictotrichon versicolor*) in the typical snowbeds or their increase in both frequency (*Leontodon helveticus)* and cover (*Nardus stricta*). This expansion of grassland species is reflected in the increase in the temperature indicator value and in the decrease in the humidity one (Fig. 7A,B). These conclusions are consistent with results from previous long-term monitoring across alpine areas of the Scandes (Virtanen et al. 2003; Kapfer et al. 2012; Sandvik and Odland 2014), Scotland (Britton et al. 2009), Caucasus (Elumeeva et al. 2013), Japan (Kudo et al. 2011), and Greenland (Daniëls et al. 2011).

Similar changes have been observed even on shorter timescales, as in 6-year surveys from Italy (Carbognani et al. 2014) and Australia (Pickering et al. 2014). All these studies agree that the arrival and expansion of grassland species in the snowbed communities is likely a consequence of longer growing seasons induced by earlier snowmelt dates. The melt-out date, which is an important driver of arctic and alpine plant growth (Jonas et al. 2008), shifted earlier by 1–4 days per decade between 1998 and 2015 at 2110–2630 m.a.s.l. next to our three study sites (Appendix S6a). This shift, although not significant and covering a short time period, is corroborated by satellite observations in the high-latitude and high-elevation areas of the Northern Hemisphere (Dye 2002). This is probably the consequence of two associated factors: firstly, the increase in mean annual temperature, which has been calculated as 1.82 K between 1961 and 2008 in Switzerland (Serquet et al. 2013), which is equivalent to the double of the mean change for the Northern Hemisphere (Rebetez and Reinhard 2008), and secondly, the decrease in the snowfall/precipitation ratio estimated to be around 0.25% per year at the beginning and the end of the snow season from 1961 to 2008 (Serquet et al. 2013). The spring decreasing trend of snowfall/precipitation day ratio has been observed even at 2500 m a.s.l. by Marty and Meister (2012) but is generally more pronounced at lower elevations (Scherrer et al. 2004; Serquet et al. 2013). In the three present study sites, despite a high interannual variability, the annual sum of fresh snow thickness decreased by 0.49–0.96% per year between 1964 and 2011 (Fig. 2). The autumn and spring months seem to be crucial for snow duration, because at that period of the year, air temperatures are closer to the melting point than during the winter (Serquet et al. 2011), and a slight increase is sufficient to reduce the snowfall part of precipitations. The lower snow amount and earlier melting dates observed in the study sites were accompanied by lagged snow falls in autumn (Appendix S6b). The resulting longer growing season (+5 to 14 days per decade between 1998 and 2015, not significant, Appendix S6c) allows the invasion of generally more competitive species, such as graminoids (Dullinger et al. 2007). These species now have enough time to accomplish their life cycle in a snowbed. The establishment of species from adjacent communities could have been enhanced by (1) the proximity of grasslands to snowbeds (mostly <20 m from the study sites), (2) the snowbed potential of trapping seeds (Larsson and Molau 2001), and (3) the high dispersal capacity of certain grassland species. Indeed, the increase in frequency of *Leontodon helveticus* could be associated to its pappus appendage, which was shown to give an advantage to plant species in colonizing new Alpine summits (Matteodo et al. 2013).

Moreover, snow is an efficient scavenger of atmospheric pollutants, which are leached through the snowpack, mainly at the beginning of the melt period (Johannessen and Henriksen 1978). The consequent high load of nitrogen into the snowbed soils can damage certain species (as the moss *Kiaeria starkei*; Woolgrove and Woodin (1996)) and favor the establishment of acquisitive (nutrient-rich) plants. For example, graminoid cover has been shown to be directly related to nitrogen deposition in acidic grasslands (Dupré et al. 2010). However, an increase in the mean nutrient indicator value (Landolt et al. 2010) that could support this hypothesis has not been observed in the study sites (Fig. 7C). But, we cannot exclude that higher temperatures, combined with relatively high nutrient level in the soil, allow more thermophilous species (grassland species) to establish in the snowbeds, independently from the length of the growing season.

The snowbed species are able to respond positively to experimental warming (Arft et al. 1999; Sandvik and Totland 2000) and can theoretically profit for earlier snow-free habitats. But they are restricted to snowbed habitats because of lower competition from co-occurring plants (Heegaard and Vandvik 2004). The arrival of taller species from the surrounding grasslands might increase the competition and induce a decrease in typical snowbed species. Hulber et al. (2011) suggested that the presence of neighbors in snowbed systems leads to competitive effects rather than facilitative ones, which can be expected in such harsh environmental conditions (Choler et al. 2001). Moreover, the role of competition might increase with warming, as experimentally observed by Olsen and Klanderud (2014). In the study sites, no significant decrease is observed, but the strong decrease in cover of *Carex foetida* could be a first sign of such an evolution.

Similar to the typical snowbeds, but over a shorter time period (median of historical records years = 1988, Table 1), the wet snowbeds show increasingly dry conditions. Reductions in snow precipitation, combined with higher temperatures, likely shorten the amount and duration of water supply (Beniston et al. 2003) to these communities, mostly located under melting firn. The cover decrease in typical alliance species and the diffusion of snowbed species, in parallel with the reduction in the mean humidity indicator value (Fig. 7B), indicate that these sites are rapidly shifting toward typical snowbed communities. The same drying trend was observed with the expansion of some graminoids and shrub species in Norwegian wet snowbeds (Sandvik and Odland 2014), on soligenous and ombrogenous mires (Virtanen et al. 2003; Ross et al. 2012), and springs (Britton et al. 2009). These last vegetation types do not belong to snowbeds, but they are subject to the same water-logged conditions, which limit the growth of taller plants. Diverse alpine plant communities, directly related to high water supply, seem to respond similarly to climate changes.

Grasslands

In contrast to plant communities related to long snow cover, calcareous and siliceous grasslands demonstrate a high stability of species composition and cover, whatever the bedrock type (Figs 5 and 6). Similar results were obtained by warming experiments on subalpine meadows in the Rocky Mountains (Price and Waser 2000), on calcareous grasslands in northern England after a 13-years exposure to climate changes (Grime et al. 2008), and observed too by long-term surveys in the Alps (Vittoz et al. (2009), Windmaißer and Reisch (2013). These authors identified many possible explanatory factors. Firstly, the high plant density and belowground phytomass of subalpine grasslands, compared to the sparse vegetation of alpine and nival summits or to the low species abundance in snowbeds, lead to high competition levels for light and soil resources, which restricts the establishment of new species (Choler et al. 2001). Secondly, the extreme longevity of some grass species (*C. curvula* can reach a maximum of 5000 years; de Witte et al. 2012), the persistence of their shoot and root systems, and their clonal growth, that allows the continuous recolonization of vegetation gaps, result in a high resilience to interannual variations (Hillier et al. 1990) with a consequent long-term persistence. For example, *Laserpitium siler*, which was a dominant species in half of the plots in calcareous grasslands, is highly competitive in terms of light and water resources and occupies a wide elevation range, thus likely preventing colonization by new species. Thirdly, the steep slopes where the calcareous grasslands are established could also explain their stability. According to Theurillat and Guisan (2001), slopes steeper than 40° (which is often the case in this study) may act as barriers to upward dispersal of species.

Nevertheless, this general stability is also accompanied by new species or increase in frequency. Some of these species (*Globularia cordifolia*, *Cirsium acaule*), although frequently associated to calcareous grasslands, have their optimum at lower elevations. Conversely, the only significantly declining species, *Carex sempervirens,* has its optimum at the lower alpine rather than the subalpine belt. These changes in composition are reflected by a significant increase in the mean indicator value for temperature observed across the calcareous grasslands (Fig. 7A). In conclusion, although displaying a high stability, these grasslands seem to experience the arrival of species from lower elevations, as repeatedly observed on alpine and nival summits (see Stöckli et al. 2011 for a review). Interestingly, in long-term studies focused on lower elevation grasslands (Britton et al. 2009; Vittoz et al. 2009; Ross et al. 2012; Elumeeva et al. 2013; Windmaißer and Reisch 2013), most of the species decreasing in frequency and/or cover have an alpine-to-arctic distribution, while those increasing have broader or lower elevation ranges.

Siliceous subalpine and alpine grasslands show a different trend with supplementary species either having very widespread distribution (*Euphrasia minima*, *Homogyne alpina*) or arriving from the same species pool (*Arnica montana, Hieracium alpinum*). This process, known as range filling, was already observed in the Italian Alps by Cannone and Pignatti (2014) and seems to be predominant compared to the upward shift. Indeed, neither did montane species colonize the siliceous subalpine grasslands, nor did subalpine species move upward and colonize the siliceous alpine grasslands. The abovementioned stabilizing factors appear to be important in these siliceous grasslands.

According to Dullinger et al. (2012), the elevational shift of plant species observed on alpine summits may display faster cool edge expansion than warm edge retreat because of the potentially long persistence of declining populations under unsuitable conditions. The stability of the subalpine and alpine grasslands, while snowbeds are changing, seems to confirm this prediction and indicates that, during the last few decades, subalpine and lower alpine species expanded upwards from their elevational range rather than shifting it.

Windy ridges

The community on windy ridges shows a significant change in species composition according to the PCA (Figs 5 and 6). Indeed, the centroid shifts toward the calcareous grasslands, although some of the recent inventories are closer to the siliceous grasslands instead. The species increasing in frequency confirm this pattern, with some related to the calcareous grasslands and others to the siliceous ones. The different shifts seem to be related to soil pH, as shown by soil analyses, but a higher number of plots would be necessary for a better understanding of these divergences. Research on comparable habitats (such as alpine heaths on windy ridges) shows diversified reactions to past climatic changes, from very limited changes (Elumeeva et al. 2013), to an increase in dwarf shrubs (Virtanen et al. 2003) or graminoid increase related to a dwarf shrub and forb decrease (Ross et al. 2012). The only common feature is the lichen decrease, attributed either to summer reindeer grazing (Virtanen et al. 2003), or to nitrogen deposition (Armitage et al. 2014), trampling, and climate warming (see Ross et al. 2012 and references therein). Unfortunately, the majority of our historical inventories do not give any indication of lichen covers (Appendix S2). Consequently, this study cannot confirm such a trend.

Long-term implications

This study is the first of its kind to assess the way different plant communities in the subalpine and lower alpine belts of the European Alps reacted to climate changes over the last two to four decades. It demonstrates that reactions differ considerably between vegetation types, with the most important changes in those linked to long snow cover. The vulnerability of *Salicion herbaceae* (typical snowbeds) was already suspected by Braun-Blanquet (1975). Indeed, monitoring eastern Switzerland vegetation of a very late snowmelt patch dominated by the moss *Polytrichum sexangulare* from 1921 to 1947, Braun-Blanquet (1975) observed an increasing cover of snowbed plant species in response to shorter snow cover and warmer temperatures. Moreover, he hypothesized that snowbeds will be progressively invaded by species from the surrounding siliceous grasslands. Therefore, it is likely that, during the last few decades, some snowbed communities took refuge in *Polytrichum sexangulare* communities, altering their species composition. Simultaneously, snowbed species colonized many summits and slopes, where, as a result of glacier and snow cover reductions, new snowbed areas were available for colonization (Grytnes et al. 2014). Therefore, snowbed species can still find suitable areas in the coldest microhabitats, but with potential detrimental consequences for the communities currently present. This corroborates the theory of Scherrer and Körner (2011), who sustained that alpine terrain offers a variety of thermal microhabitats over very short distances, which will be suitable for the majority of species.

Beniston et al. (2003) predicted that, with a temperature rise of 4°C in 2071–2100 (Christensen et al. 2002), the snow volume in the Alps at 2000 m may reduce by 50% and the melting season advanced by 50–60 days. As this study clearly demonstrates, changes in snow precipitations may have a stronger impact on the subalpine–alpine plant communities than warmer temperatures, at least for communities directly dependent on snow cover as a limit to the growing season. However, very probably, the grasslands will not be able to stand such a temperature increase without important changes as well. But, with the available data, it is not possible to conclude whether changes will still be very slow, like those observed until now, which will induce a large local extinction debt (Dullinger et al. 2012), or whether strong and sudden changes are expected after forest colonization, successive years of drought, development of diseases (Ayres and Lombardero 2000), or the arrival of new herbivores (Pellissier et al. 2014). Future monitoring of alpine grasslands will be particularly important to address these questions.

Acknowledgments

We thank Marie-José Petétot, Loïc Liberati, and Swanee Messerli for their help in the field; Beat Rihm (Meteotest) for providing calculation of nitrogen deposition on our study sites; François Gillet, Stéphanie Grand, and Vanessa Rion for their suggestions and contributions in the statistical analyses; Benoît Bressoud for his contribution to the record data; Karin Verrecchia for checking the English version; and two anonymous reviewers for their useful comments on an earlier version of the manuscript.

Conflict of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. Mean summer temperature variations in the three study sites.

Appendix S2. Characteristics of the 126 inventories.

Appendix S3. Relative change in cover versus relative change in frequency of the most frequent species.

Appendix S4. Cover-weighted means of indicator values for light (L).

Appendix S5. Cover-weighted means of indicator values for soil pH (R).

Appendix S6. Variations of the last snow day, first snow day, and growing season length in the three study sites.

Appendix S7. Principal component analysis based on species composition and cover of the calcareous plant communities.

Appendix S8. Principal component analysis based on species composition and cover of the siliceous plant communities.