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Spatial and temporal biodiversity variations in a high mountain environment: the case of the proglacial margin of the Evettes, Natura 2000 area (Savoie, French Alps)

Variations temporelles et spatiales de la biodiversité en environnement de
haute montagne : le cas de la marge proglaciaire des Evettes, site Natura
2000 (Savoie, Alpes françaises)

Article 374

ABSTRACT/RÉSUMÉ

The aim of this paper is to contribute to the understanding of the changes in plant cover after the recent glacier retreat, in an alpine environment. The selected study site in Savoie in the French Alps (2502-2509m asl), belonging to the European network Natura 2000, provides favourable conditions for the study due to the flat glacier foreland, where the glacier did not advance since the Little Ice Age. Data collected from 110 botanical plots were correlated with dated glacial and proglacial landforms. Species diversity has been analysed using the Shannon-Weaver index, the Grime classification, and the uncommon species described in the European list of Natura 2000 European Network. Classical and multivariate analyses have been made to determine the impact of the glacial retreat on the biodiversity variation. We show that the changes in species richness and vegetation cover were related to the distance from the glacier front. The biodiversity index was less than 2.5 near the glacier but above 4 at the furthest point. The highest plant diversity, however, was observed at an intermediate position, where competitive and pioneer plants were equally represented in the field. This location, concurrently, showed the highest heterogeneity in the activity of periglacial processes. It seems that the most heterogeneous and disturbed soils, due to inherited deposits and currently active periglacial processes, are responsible for an increase in biodiversity.

L'objectif de cet article est de contribuer à la compréhension des changements en cours dans un environnement alpin, au front d'une marge proglaciaire, en relation avec un retrait glaciaire. Le secteur étudié correspond à la plaine proglaciaire du glacier des Evettes, situé en Savoie dans les Alpes françaises, vers 2500m d'altitude. Ce site appartient au réseau Natura 2000. Les conditions écologiques locales ont permis l'élaboration d'une vaste plaine proglaciaire en raison du retrait du glacier depuis la fin du Petit Âge Glaciaire (stades de retrait jalonnés depuis 1860). Les données collectées reposent sur l'échantillonnage floristique sur 110 placettes dont les résultats ont été analysés statistiquement avec plusieurs paramètres : la distance par rapport au front glaciaire actuel (et donc l'âge depuis la déglaciation), le contexte morphopédologique, la diversité spécifique déterminée à partir de l'indice Shannon-Weaver, la classification du type de stratégie dite de Grime et la valeur de la rareté de l'espèce lorsque celle-ci est signalée dans les listes du réseau européen de Natura 2000. Des analyses univariées et multivariées ont été appliquées afin de déterminer l'impact du retrait glaciaire sur la variation de la biodiversité. Si l'on aboutit très classiquement à la démonstration qu'il y a augmentation globale de la biodiversité en allant du front glaciaire actuel vers la marge la plus externe, notre étude prouve que la biodiversité la plus élevée concerne un point intermédiaire. Cette position correspond en réalité au secteur où les conditions locales périglaciaires permettent la cohabitation de plantes à la fois pionnières, rudérales et compétitrices. A terme, cette activité périglaciaire, ici responsable de l'augmentation de la biodiversité, est pourtant en régression sous l'impact du réchauffement.

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Introduction

In high mountain environments, the question of biodiversity is a major subject of scientific investigations (Matthews and Whittaker, 1987; Matthews, 1992; Chapin and Körner, 1995; Helm and Allen, 1995; Caccianiga et al., 2001; Kaufmann, 2002; Halloy and Mark, 2003; Körner, 2003; Caccianga and Andreis, 2004; Gaur et al., 2005; Stanisci et al., 2005; Walther et al. 2005; Rozema et al 2006), because it is useful to see whether biodiversity is affected by global climate change in the same way or differently, in comparison with other areas such as temperate grasslands or shrubs (Hoover and Parker, 1991; Loreau, 1998; Hector et al., 1999; Loreau, 2000; Loreau and Hector, 2001; Anthelme et al., 2003).

Changes in alpine environments, caused by climate warming (Haeberli 1994; Beniston et al., 1997; Diaz and Bradley, 1997; Watson et al., 1997; Beniston, 2003) following the end of the Little Ice Age (LIA) (Lamb, 1995; Magny, 1995; Watson et al., 1997; Hoelzle et al. 2003), can have serious impact on ecosystems and on landscapes (Matthews, 1992; Chapin and Körner, 1995; Helm and Allen, 1995; Caccianga et al., 2001; Kaufmann, 2002; Gaur et al., 2005; Stanisci et al., 2005; Walther et al 2005). Currently we observe an extension of recently deglaciated areas, the proglacial margins, where plants find pristine sites to establish. The colonisation of the new deglaciated areas is related to the age of the ice-free surface (Kaufmann, 2002; Tschirko et al., 2003). The age of a site since its deglaciation was observed to be linearly related to the number of plant species. The latter, therefore, may increase with the spatial distance from the current glacier limit (Matthews and Whittaker, 1987; Matthews, 1992; Chapin and Körner, 1995; Helm and Allen, 1995; Caccianga et al., 2001; Caccianga and Andreis, 2004). The biodiversity on glacier forelands (proglacial margins) is well studied and documented, particularly in the Alps (Guisan and Theurillat, 2001; Kaufmann, 2001; Kaufmann et al., 2001; Kaufmann, 2002; Kaufmann and Raffl, 2002; Anthelme et al., 2003; Gaur et al., 2003; Caccianga et al., 2004).

The aim of this paper is to illustrate biodiversity variations in a high alpine mountain environment related to glacial retreat. Vascular plant species richness and morphosedimentological parameters were used to assess temporal and spatial changes in biodiversity. In addition, the Reference List of Habitat Types and Species in the European Union (EEA, 2002) was used to examine the distribution of rare species.

Study area

The study area lies in the proglacial margin of the Evettes, located in the French Alps (Fig.1), in Savoie, near the Vanoise massif. It is the upper part of a watershed contributing the Arc river (Figure 1); the area belongs to European Natura 2000 network (FR8201780). The Evettes glacier (45°19'57" N; 7°55'16" E) is surrounded by summits exceeding 3500m asl (e.g. Ciamarella, 3549m, Albaron 3600m). The current ELA (Equilibrium Line Altitude) lies at around 3000m and the glacier tongue reaches 2559m asl. The foreland of the Evettes glacier is a flat plain, around 1600m in length and 320,000 m² in area, between the oldest known moraine (1860) and the

present one (Figure 2). Due to the flat topography of this proglacial margin, the stadial positions are well preserved and well documented (Vivian, 1975; Edouard, 1994; Marnezy, 1999). Actual climatic conditions are typical of this alpine environment, where the mean annual temperature is around 0°C and the solid precipitations reach 50% of the 1200 mm annual amount (Marnezy, 1999). The thickness of the snow varies locally with more or less great activity of the wind related to topographic configurations. One can find more than 10 m accumulated behind vellums and nothing on crests.

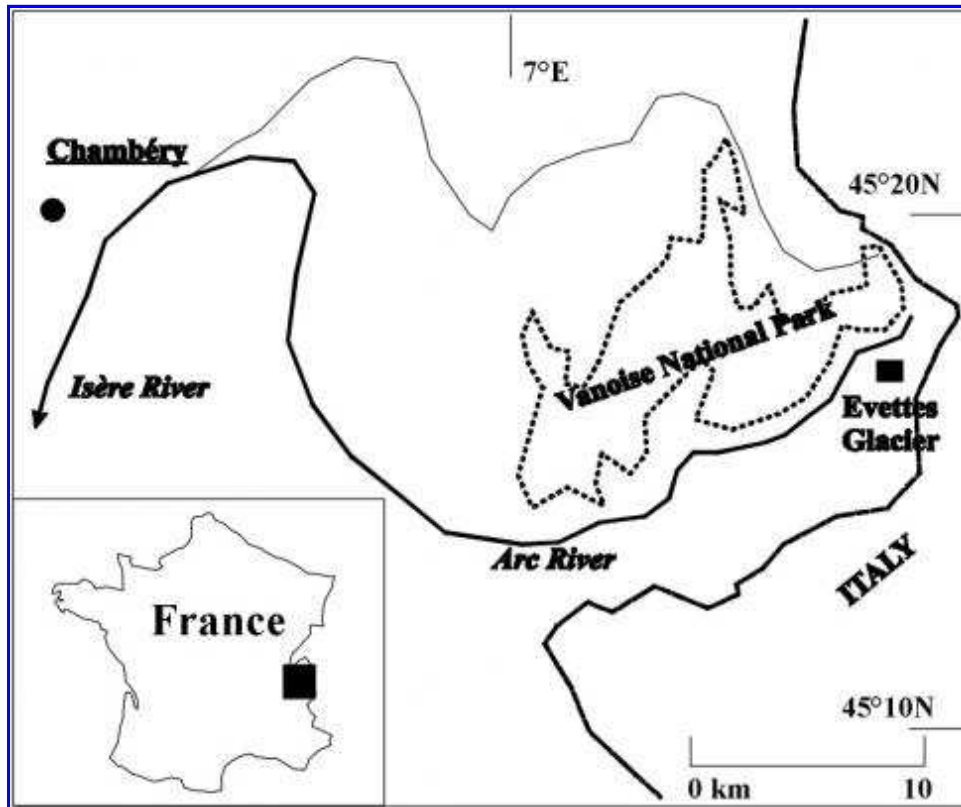


Figure 1: location map

Since the end of the Little Ice Age, i.e. around the middle of the 19th century, climate conditions in the Alps have been warming more or less regularly by 1 to 2°C per 100 years (Le Roy Ladurie, 1983; Lamb, 1995; Magny, 1995; Watson *et al.*, 1997; Böhm *et al.*, 2001; Beniston, 2003). The dynamics of glacial retreats since the end of the Little Ice Age are well known in the Alps (Vivian, 1975; Beeler, 1981; Le Roy Ladurie, 1983; Burca, 1985; Furrer, 1985; Maisch, 1987; Biju-Duval, 1991; Hoelzle *et al.* 2003). The history of this retreat shows successive stands, around 1920-1925, for example, corresponding to temporarily worsening climate conditions in a general warming trend (Vivian, 1975; Lamb, 1995; Magny, 1995).

Many observations have already been made in this sector of the Evettes foreland and can be used to map the evolution the successive positions of this glacier since the middle of the 19th century. In order to date such a retreat since the end of the LIA, we used archives such as local documents or Napoleonic Land Registers, old maps (from IGN, National French Geographic Institution) and old aerial photographs as previously used by Vivian (1975), Edouard (1994) and Marnezy (1999). We determined the successive positions of the glacier using the maps or documents presented in Table I. From these materials, we derived the precise proglacial and glacial retreat between each dated front moraine, as shown in Figure 2. It was possible to determine five successive positions of the glacier between the oldest positions and today (Tables I, II and Figure 2)

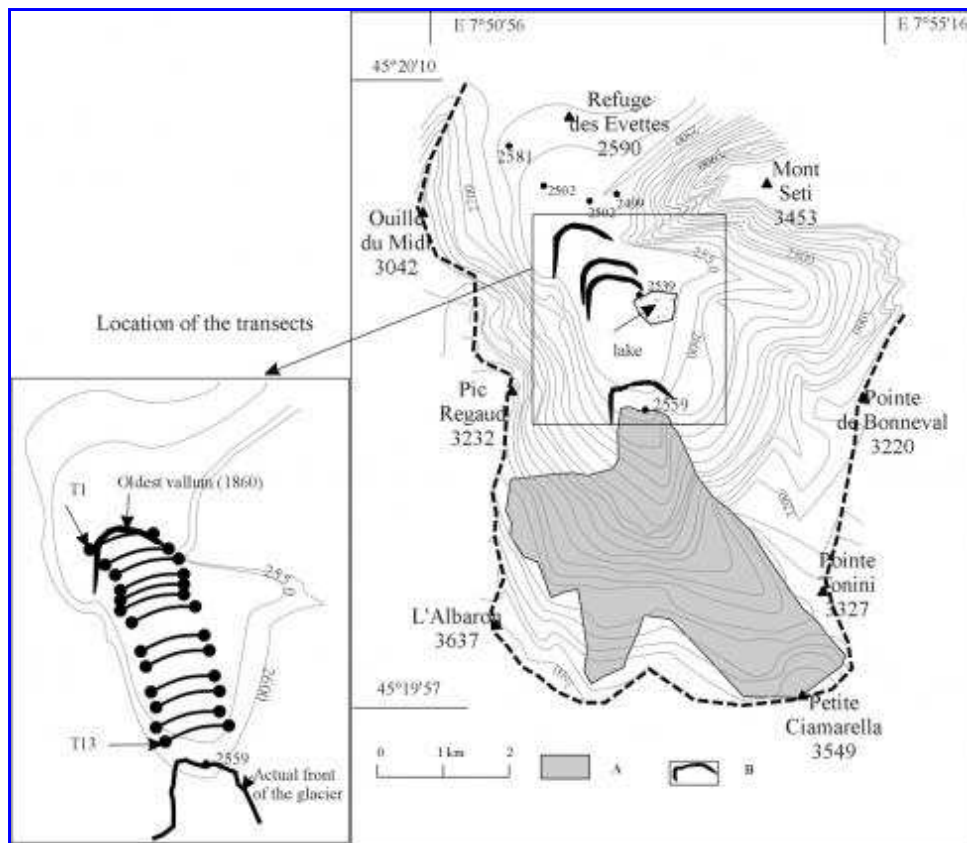


Figure 2: The proglacial margin of Evettes : A: contemporary glacier; B: ancient ridges).

Table I: Sources of the data used to built the map of the chronosequences of the Evettes glacier retreat between 1860 and 2000 (see references at the end of the paper)

Age (years)	Distance from front (in m)	Landform and sediment association
1818	>1675	sandur
1860	1675	vallum
1860-1893	1675-1235	sandur
1893-1905	1235	vallum
1905-1920	1235-1135	recessive moraine
1920-1925	1135	vallum
1925-1935	1135-935	sandur
1935-1955	935-255	recessive moraine
1955-1975	255-70	sandur
1975-1982	70	vallum
1982-2003	70-0	recessive moraine

Table II: Chronosequences of stadal positions and of the retreat of Evettes glacier (Savoie, French Alps)

Although it has been shown in many areas that the general glacial retreat since the end of the Little Ice Age was temporarily reversed by short-term climatic oscillations (Vivian, 1975; Menzies a, b, 1995; Vincent et al., 2005), for the Evettes glacier there have been no advances but only stadal positions when climate conditions became colder, as in 1920-1925, for example, and this cold period is already well documented (Leroy Ladurie, 1983; Berger, 1992; Lamb, 1995; Magny, 1995; Diaz and Beniston, 1997; Beniston, 2003). Locally, the retreating glacier has uncovered three types of successive morphologies (Jochimsen, 1970; Bennett and Glasser, 1996): frontal moraines ridges also called vallums, proglacial outwashes also called sandurs and recessional moraines. One morainic vallum is situated in the most outer position. According to Bonaparte (1890) and Mougin (1903) it is dated around 1860 (Vivian, 1975; Leroy Ladurie, 1983; Magny, 1995). Looking at the Napoleonic Land Register of 1834, it could well be in the same place. In fact, this morainic ridge is so important in the landscape that we have to consider that the stagnation lasted long enough for it to be built from heterogenic and coarse materials coming from the Evettes. Consequently, the area beyond this vallum is necessarily older. The next oldest and better known one is the front moraine vallum of 1893-1905. The position of the glacier was also well known around 1920 and it probably remained until 1925. The eastern margin of the proglacial lake of the Evettes appeared in 1935 and its western margin appeared in 1943 (Edouard, 1994), when the glacier retreated from this lake (Figure 2)

The climatic conditions are typical of an alpine environment, here: mean annual precipitation of 1300mm, mean annual temperature of about -1°C (lowest and highest are -7°C and 8°C, respectively). The growing season is short: frozen conditions begin around October and continue until May. Snow cover is the major determinant of surface temperatures and of soil freezing in winter. Snow accumulates in depressions such as sandurs, where it protects from low winter temperatures, whereas the crests of the moraines are more affected by cryoturbation, owing to a reduced or absent winter snow cover.

The Evettes proglacial plain was interesting for our study because the topographical conditions are exceptionally flat and the habitat heterogeneity is mainly caused by the age and the variable micro-topography of the glacial foreland. The expansion of plants can be dated precisely.

Methods

Biodiversity spatial variability: our theoretical approach

Our study followed two distinct strategies. First of all, we investigated the changes in species richness and plant cover over time, i.e. the chronosequences, without taking account of the morphosystems: this was made by using quantitative and qualitative approaches (Magurran, 1988; Pielou, 1993, Chapin and Körner, 1995; Caldecott et al., 1996; Samson and Knopf, 1996; Vanpeene-Bruhier et al., 1998; Huston et al., 2000; Guisan and Theurillat, 2001; Kaufmann and Raffl, 2002; Anthelme et al., 2003; Körner, 2003; Caccianga et al., 2004; Stanici et al., 2005). Secondly, we investigated the role of these morphosystems in changing plant cover and biodiversity (Jochimsen 1970). This was made by successively analysing the chronosequences and then studying for each chronosequence several parameters, as floristic components, plant density, and the habitat parameters such as the morphosedimentological components. The aim of our study was to identify which species grow on each morphosystem, corresponding to the stadial positions of the glacier when it retreated.

In order to take account these two distinct approaches, a statistical comparison between the different morphosystems was made focusing on changes in the number of plants and of species from the inner part, near the present front glacier, to the outer sector. The local geomorphic conditions, vallums, sandurs and recessive moraines were considered because they may determine biodiversity variations in relation to the variability of the complexity of their biotope, such as the slopes or the sedimentological components, and the current morphodynamic activities, such as frost or rill wash actions.

Morphosedimentology of the proglacial margin

Formerly, the most frequently studied morphology was morainic fronts and we also documented the other types of morphologies by field studies, in particular by taking morphosedimentological measurements. The slopes were calculated using a clinometer (precision: 0.5°); soil samples were collected to describe the granulometric composition, in order to understand which morphodynamic process had built the successive morphologies, vallums, sandurs and recessive moraines. In another hand, we studied the active morphodynamic processes, using the micro-morphologies such as sorted soils or cryoreptation landforms well documented in such environments (Pech, 1996).

Plant sample design

Because of severe climate conditions in such a high mountain environment, we only collected samples during the summers of 2000, 2003 and 2005 and it was not possible to study the plant changes over a longer period. Vegetation data were recorded in plots along 13 transects (= "T") parallel to the front side of the Evettes glacier (Figure 2). The position of each transect was determined by the successive topographical and morphological conditions (vallum, sandur, recessive moraine). On each transect, species recording was carried out in 5 and 10 plots of 4m x 4m size; the number of plots per transect depended on complexity of the micro-morphology: 5 plots for sandurs and more for moraines. This yielded a total of 110 plots, where vascular plant species cover and the surface percentage covered by vegetation were recorded according to Braun-Blanquet (1954). Species names follow the nomenclature in *Flora Europaea* (Tutin et al., 1964-1980) and local species lists (Gensac, 1974; Gensac, 1990). This study area lies within a Natura 2000 site (Nr is FR 8201780), a protected area of the European Natura 2000 network (European Commission, 2003). Rare plants were identified using the reference list of habitat types and species of the Natura 2000 network elaborated by the European Environment Agency (2002) and especially the n°240 which are the alpine pioneer formations of *Caricion bicoloris-atrofuscae*. The rare plants are *Saxifraga florentula*, *Trifolium saxatile* (codes: 1527 and 1545).

Finally, on each transect, we also picked one sample of soil in order to determine the granulometric and mineralogical composition, which was studied with French Series Afnor sieves and with X-Ray diffraction of clay minerals.

Biodiversity indices

First, we studied the dominant species relative to the age of the topography. This protocol has been used by other researchers (Moiroud, 1976; Mathews and Withattaker, 1987; Matthews, 1992; Helm and Allen, 1995;

Kozłowska and Rączkowska, 2002).

We evaluated an index of abundance (Fortin et al., 1999):

$$I = P_n / A_p$$

where I is the index, P_n is the number of species and A_p is the area covered by vegetation.

Then, in order to evaluate the species diversity we used the Shannon-Weaver index, which represents ? biodiversity showing local richness (Shannon and Weaver, 1949; Magurran, 1988; Frontier and Pichot-Viale, 1998; Vanpeene-Bruhier, 1998; Faurie et al., 2003; Gosselin and Laroussinie, 2004).

The Shannon-Weaver index is:

$$H = -\sum p_i \log_2 p_i$$

Or simplified by Pielou (1993), $H = -\sum (n_i / N) \log_2 (n_i / N)$

where N = total number of plants in the plot, n_i = the number of plants of each i species in the plot.

We adopted this index because it expresses two major aspects of biodiversity (Magurran, 1988; Samson and Knopff, 1996; Grime, 1997; Vanpeene-Bruhier et al., 1998; Schwartz et al., 2000; Anthelme et al., 2003; Arques, 2005): information about the plant population and the evenness of each species.

Finally, in order to classify the species by reference to their strategies in different ecological conditions, we used Grime's C-S-R model (Grime, 1974, 1977, 1988 and 2001). Three types of species correspond to the strategies:

R species are adapted to disturbances, because of the frost movement of the soils or the impact of morphodynamic periglacial processes or runoff.

S species can tolerate stress conditions such as severe cold or wind.

C species grow in stabilized areas, where the competition is of particular relevance.

The R and S species are to be found particularly in areas where the vegetation is generally young and where disturbance is high. In glacier forelands, such conditions are predominantly caused by periglacial morphodynamic activities; therefore we combined R and S species to SR and opposed them to C species (competitive species), which are found in grassland environments.

Statistical methods

Classical and univariate statistical approaches such as linear functions and regressions were used, first followed by a multivariate analysis (PCA, Principal Component Analysis, and MCA, Multiple Correspondence Analysis) to determine the impact of the age of the landscape and of the type of biotope on biodiversity.

PCA, Principal Component Analysis, and MCA, Multiple Correspondence Analysis, are statistical analyses that use multi-variation patterns with a population of distances or of plants and nine quantitative variables. With PCA, only quantitative values are used; with MCA only qualitative ones. The nine variables are:

Eff: total number of plants on the plot

App: number of appearances of new plants

Disp: number of disappearances of plants

Eff_R: total number of rare plants on the plot

App_R: number of appearances of rare plants

Disp_R: number of disappearances of rare plants

Tx: rate of plant cover on the plot

SR: percentage of pioneer plants

NB_reap: number of re-appearances of rare plants

Results

The micro-morphology of the foreland

From the outer to the inner part of the proglacial plain it is possible to identify several situations. The retreat of the glacier left three types of landforms (Figure 3):

Sandurs, which are proglacial flat plains whose granulometric material is composed alternatively of roundish pebbles, sands or silt. The mean value of the granulometric composition of the sediment is shown in Figure 3, where the cumulative granulometric curve shows a unimodal distribution, which is characteristic of fluvial transport in front of a stationary ice margin (Bennett and Glasser, 1996);

Recessional moraines, which are chaotic topographies built by very coarse materials and erratic blocks. They are ablation moraines (Bennett and Glasser, 1996). The curve (Figure 3) shows how the material is unsorted in such sediments.

Morainic ridges (vallum), which are dissymmetric ridges formed from stratified heterometric and unsorted materials (Figure 3). The sedimentary structures may be associated with the dynamics of a push moraine (Bennett and Glasser, 1996).

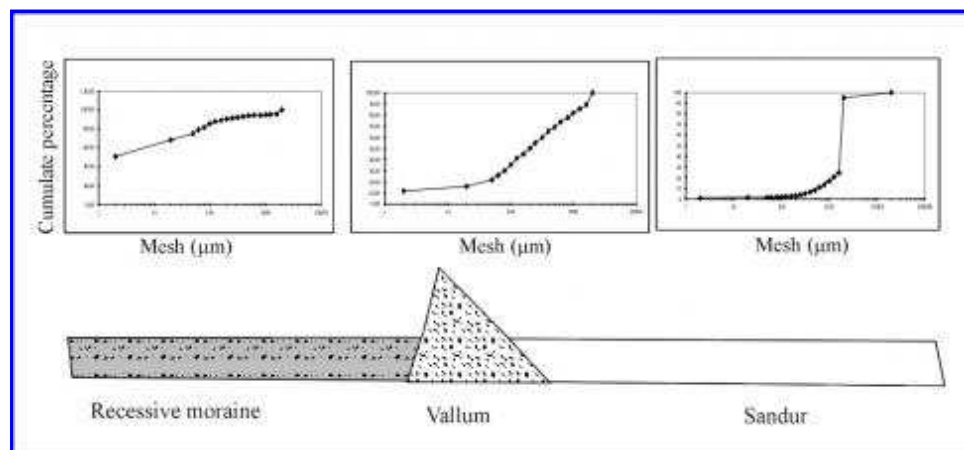


Figure 3: Morphosedimentology of the proglacial margin units (Evettes, glacier foreland, Savoie, French Alps)

The comparison of fine granulometric components of successive glacial and proglacial deposits shows the incipient weathering (Table III), because primary minerals remain (chlorite) and the percentage of free iron is insignificant (Walden et al., 1996).

Landform and sediment association	date	percentage of minerals					Iron		
		mica	plagioclase	chlorite	illite	kaolinite	total Fe ₂ O ₃	Free Fe ₂ O ₃	%Free/total iron
Sandur	1955-1975	4.9%	32.7%	42.1%	20.3%	0%	7.09	0.42	5.92
Recessive moraine	1960	0%	6.4%	49.9%	43.7%	0%	6.90	0.44	6.37
Recessive moraine	1935	0%	0%	67.6%	32.4%	0%	5.44	0.43	7.90
Sandur	1935	0%	0%	68.3%	31.7%	0%	5.51	0.44	7.99
Vallum	1860	0%	0%	34.3%	54.9%	10.8%	7.92	1.65	20.83

Table III: X-Ray and geochemical (free and total iron) studies of successive glacial and proglacial deposits of the proglacial margin of the Evettes glacier (Savoie, French Alps)

Temporal variations and botanical chronosequences

The number of species per plots was significantly related to the age of the site (time since deglaciation), see Figure 4: Curve of the change in number of species from the inner to the outer areas (many plots were on the same age merged): simplified model of the dynamic trend of number species and of plant cover in a proglacial margin in an alpine environment (Evettes, Savoie, French Alps). As shown in Table IV, the botanical composition becomes increasingly complex along the gradient from the glacier tongue to the 1860 end moraine position. There is an overall increase in biodiversity, if we assume the cumulate number of species as shown in Figure 5: Cumulative number of species from the inner to the outer areas in the proglacial margin of Evettes glacier (Savoie, French Alps): the linear relationship between the time in years and the cumulate number of species in the area studied is significant (0.05; level $R^2 = 0.9173$). Figs.4 and 5 respectively show the shift in number of species per plot, related to time, itself related to distance in the field from the present front glacier. They show an increase in number of species from inner to outer positions in this proglacial margin. Such a change is also found for the area covered by plants on each plot. In Figure 6: Change in percentage of plant cover on each transect area (mean value of the plots studied: many plots are merged), we see an overall increase in the percentage of the area covered by plants on plots from inner to outer parts of the proglacial margin of the Evettes glacier. $R^2 (=0.6181)$ shows a relationship between the age of the area and the percentage of the surface covered by the vegetation.

distance from floor of the glacier	T0	27	41	55	65	80	10	10	12	13	14	1475m	G s
Transects	T1	T1	T1	T9	T8	T7	T6	T5	T4	T3	T2	T1	
<i>Campanula crenata</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Linaria alpina</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Saxifraga aizoides</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Saxifraga floribunda</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Tinifolium saxatile</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Saxifraga oppositifolia</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Artemisia austriaca</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Cerastium lasiofolium</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Hieracium alpinum</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Salix haemata</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Achillea millefolium</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Arabis alpina</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Arabis bellidifolia</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Arenaria ciliata</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Betrychium lanatum</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Engelmannia stricta</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Euphrasia alpina</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Pritzelago alpina</i> L.	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Salix reticulata</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Salix retusa</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Salix supralibana</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Silene acaulis</i> ssp. <i>caesia</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Silene acaulis</i> ssp. <i>extensa</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Tussilago farfara</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Epidendrum flexuosum</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Hieracium glandulosum</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Pedicularis spicata</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Salix helvetica</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Saxifraga bryoides</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Sedum atratum</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Veronica alpina</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Bernia alpina</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Doronicum grandiflorum</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Dryas octopetala</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Pedicularis kermari</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Pedicularis rotunda</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Biscutella laevigata</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Cryptogonon fragile</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Epidendrum spicatum</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Polygonum viviparum</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Valeriana tripteris</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Astragalus alpinus</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Crepis aurea</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Gentianella senella</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Helianthemum oelandicum</i> ssp.	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Euphrasia minima</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Scirpus alpina</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Solidago virgaurea</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Minuartia saxatilis</i>	*	*	*	*	*	*	*	*	*	*	*	*	SR
<i>Hieracium alpinum</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Potentilla aurea</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Minuartia verna</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Campanula scheuchzeri</i>	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Leontodon pyramidalis</i> ssp.	*	*	*	*	*	*	*	*	*	*	*	*	C
<i>Minuartia sedoides</i>	*	*	*	*	*	*	*	*	*	*	*	*	C

Table IV: Species composition by transects, from the inner to the outer positions of the proglacial margin of the Evettes glacier, Savoie, French Alps (G s: Grime's strategy = SR: plants growing on disturbance places with periglacial processes; C: competitive plants growing in more homogeneous cover, grassy cover)

With rare species approach and the consideration of differences in the species composition, the results are quite a bit different. Plant cover is increasing from the present front to the morainic vallum of 1975-1982. Thus, though the number of species seems to remain constant (Figure 4), in Figure 5 we see a constant increase in the number of new species from the inner to the outer positions of the areas studied. The variety of plants changes from the inner to the outer positions, some species, such as *Saxifraga biflora*, have disappeared, and new species have appeared, several decades later, such as *Salix reticulata*, *Salix retusa*, *Silene acaulis*. In the older positions (1860), we observe other new species such as *Campanula scheuchzeri*, *Leontodum montanum*, *Minuartia sedoides*.

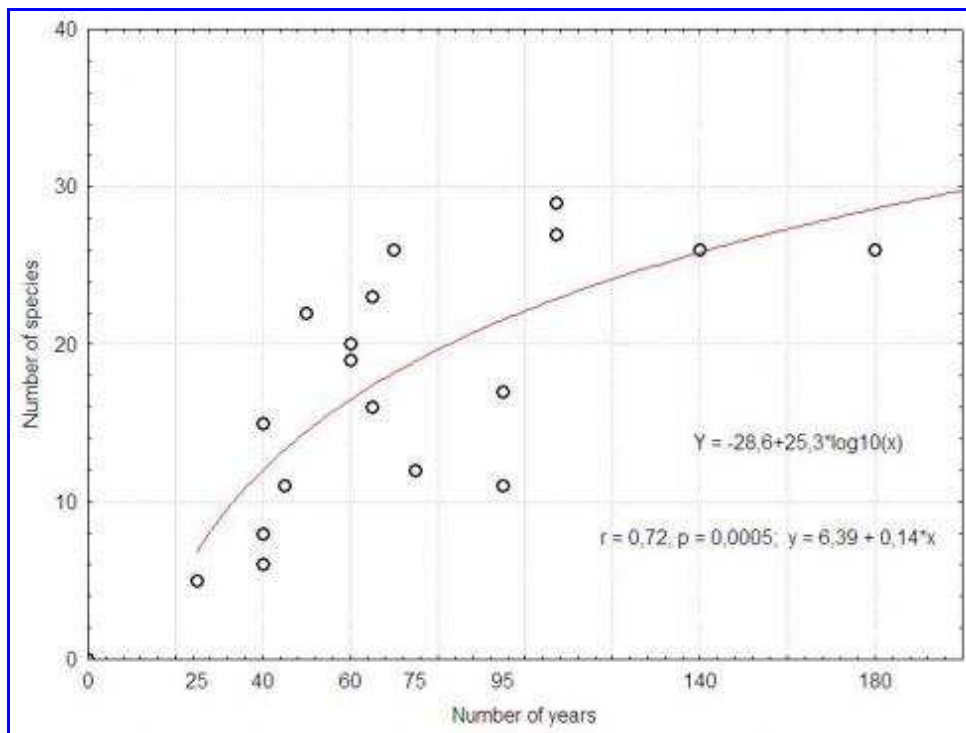


Figure 4

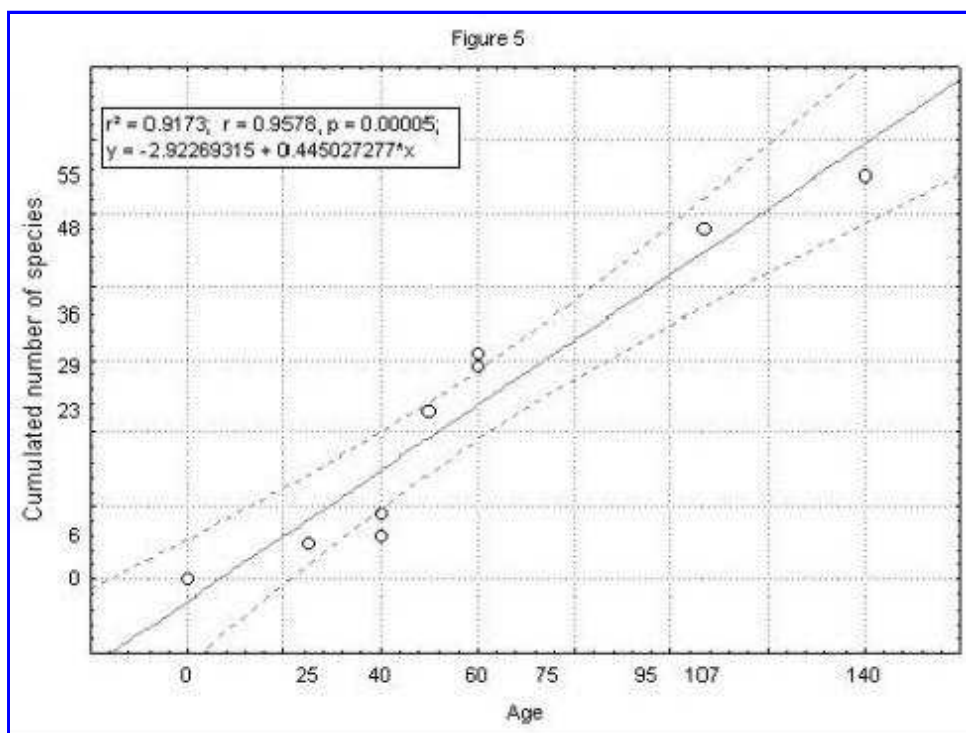


Figure 5

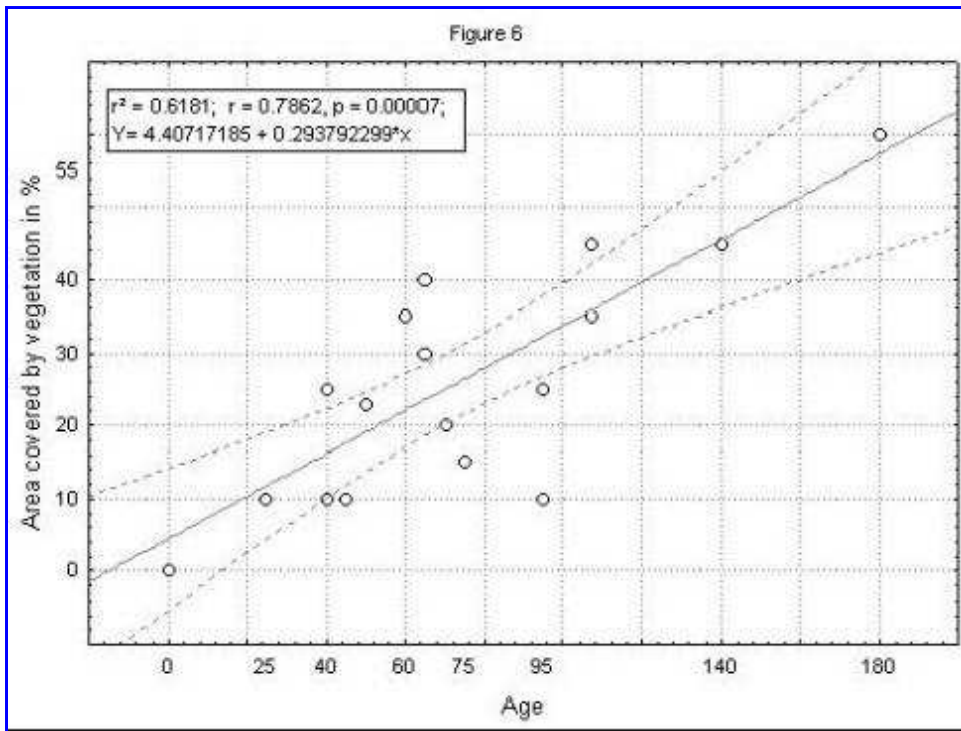


Figure 6

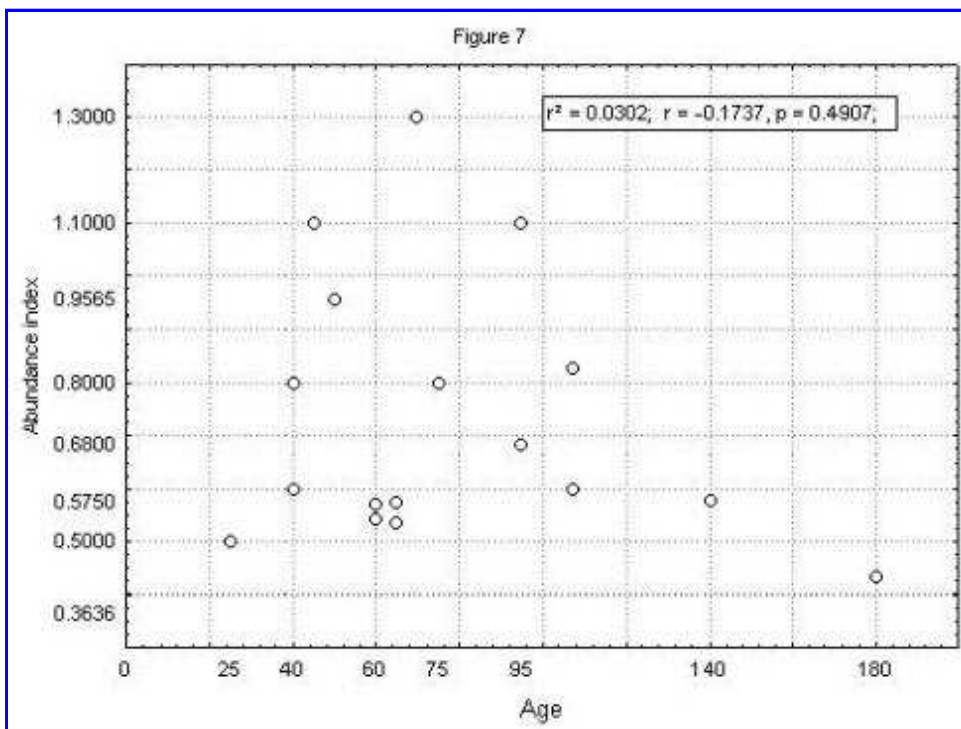
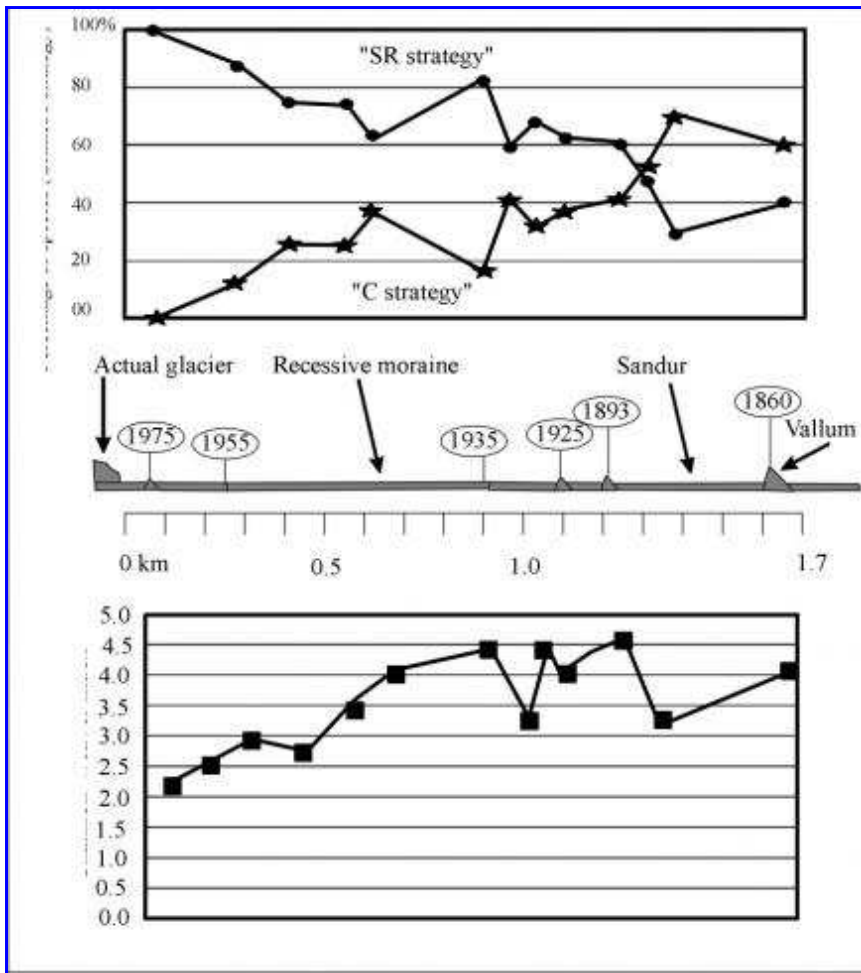


Figure 7: Relationship between the time and the abundance index

Figure 7 shows no significant relationship between the abundance index (I) and the age of the surface. The highest values correspond to central sectors of the proglacial margin. Equally, Figure 8 and Table V show a change in species diversity from the inner to the outer positions. The curves of SR and C species percentages show a change (Figure 8b), in which the competitive species grow in number and in surface from the youngest to the oldest positions. Table V and Figure 8 clearly show the turnover along the temporal gradient from SR and C species, which is a usual result.



Figures 8a et 8b: Biodiversity trend and plant strategy in the proglacial margin (Evettes, glacier foreland, Savoie French Alps; a- Shannon-Weaver index and b- Grime's strategy)

Such a change may be found using the Shannon-Weaver index (= Alpha biodiversity). As seen in Fig.8a, the index increases gradually up to the central part of the deglaciated plain but there is a decrease near the outer areas. From the recently deglaciated area, both plant cover and species diversity increase. In the habitats of the oldest deglaciated areas, the vegetal communities are more uniform.

Distance from front of the glacier	Number of new species	Number of disappearing species	% of new species on total number of species	SR %	C %
70m	5	0	100	100	0
275m	4	1	50	87.5	12.5
415m	14	1	64	74.4	25.6
550m	6	6	30	75	25
650m	2	4	10.5	62.5	37.5
900m	0	5	0	83	17
1000m	5	1	20.8	58.4	41.6
1050m	5	4	20	68	32
1075m	0	10	0	62.5	37.5
1235m	4	1	14.8	59.3	40.7
1300m	3	6	11.1	48.2	51.8
1425m	3	8	15	30	70
1675m	4	8	15.3	42	58

Table V: Spatial changes of the biological dynamism of the proglacial margin of the Evettes glacier, Savoie, French Alps; the distinction between SR and C are due to Grime's classification of plant strategies (Grime, 1974, 1977, 1988 and 2001)

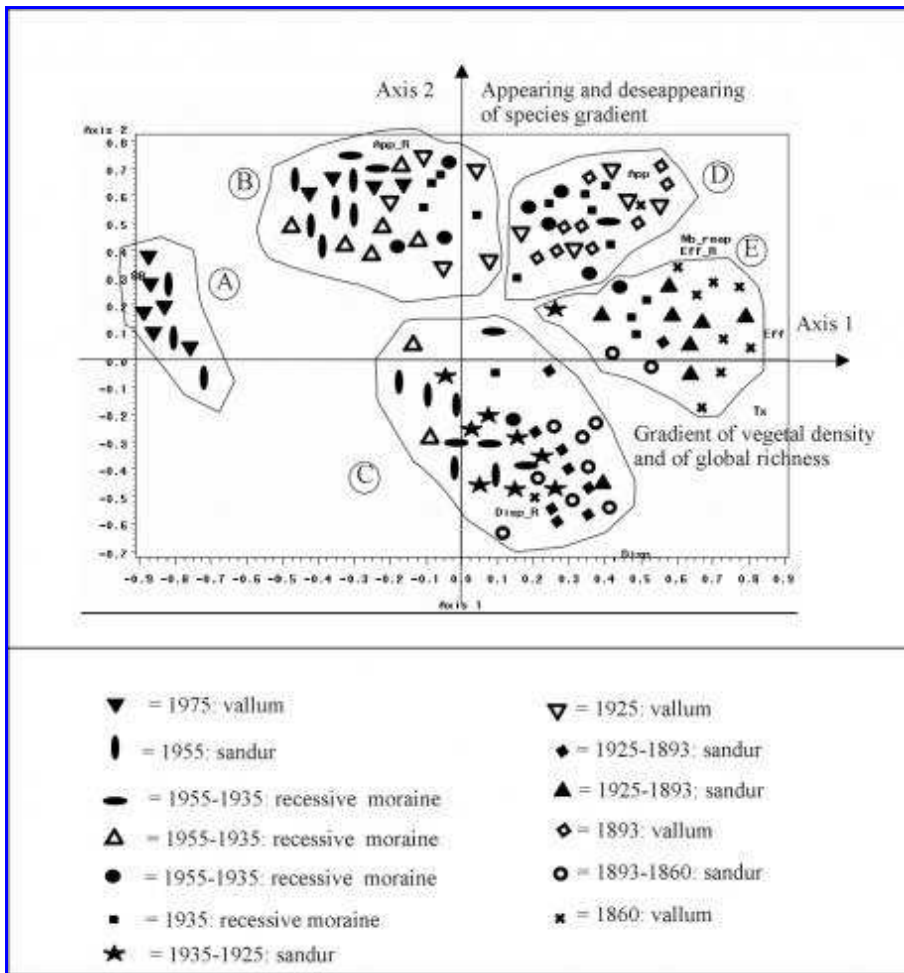


Figure 9

In Figure 9: Position of the plots on the two axis of the PCA (principal component analysis). Ordination diagram of vegetal types. Detrended component analysis are scaled in standardized units, so that 1.0 equals standard deviation of mean vegetation distribution range across the vegetation gradient, from the front of the glacier to the outer position, axes 1 and 2 correspond to plane λ_1 ? λ_2 , which summarizes most of the information, i.e. 67.79%. On the first axis, there is an opposition between:

On the left, the distribution of pioneer plants (SR), which concern the recently deglaciated areas and also sectors where periglacial activity is too intense (vallums) to facilitate easy development of continuous plant cover.

On the right, areas where there is a very high number of plants and a high number of rare plants, and a high species diversity index. These areas are the furthest away from the glacier, and this fact is attested by the shift of the ? diversity in Figure 8a.

On the positive part of the second axis, the highest side summarizes the factors determining the appearance of all plants and of rare plants, while the lowest side corresponds to the loss of plants. These correspond to the right side, which is the most plant-covered and not the nearest to the glacier.

Using MCA (Maillet and Melois, 2005), we find that dense vegetation covers soils like sandurs but their species richness in terms of number of species is lower than on other more heterogeneous soils. Multivariate procedures may test significant results based on factor analysis: in fact it is easy to determine five classes which summarize the information. These five plots are, as shown in Figure 9:

A: gathers the plots near the front glacier, where there is low plant cover, a small number of plants and where the major floristic component is pioneer plants;

B: summarizes the plots in the recently deglaciated areas, where the pioneer plants are still dominant but the plant cover is growing in density and the number of new species appearing is high;

C: is a group of plots where there is a good density but where plants, and especially pioneer ones, disappear and leading outputs are a kind of loss in biodiversity;

D: is a group where the plots have a great biodiversity and a great density in vegetal cover;

E: although the vegetal density is high, it is a poor group in terms of biodiversity because there is a loss of pioneer plants.

Consequently, these five categories highlight the interpretation of the shift. From the inner position to the outer one, if there is an overall increase in density, there is a change in the floristic component and we have to interpret this double shift in order to determine whether or not there is or not there is a loss of biodiversity.

Discussion

Our results confirm previously documented changes in biodiversity and plant cover in glacial forelands (Caccinga et al., 2001; Kaufmann and Raffl, 2002; Anthelme et al., 2003; Gaur et al., 2003; Caccinga and Andreis, 2004). First of all, there is evidence of a relationship between the age of the surface and the increase in both plant cover and number of species (Helm and Allen, 1995; Caccianga et al., 2001; Kaufmann, 2002; Kaufmann and Raffl, 2002; Gaur et al., 2003; Caccianga and Andreis, 2004). Pioneer vegetation is, as usual, more frequent near the front glacier and decreases as soon as more distant areas are considered, where, conversely, the number of competitive plants increases. One of the most original aspects shown up through our analysis is that, in the intermediate position, the relative percentage of the two populations is equally represented (Figure 8) and, in such an area, biodiversity seems greater.

Using PCA and MCA (Maillet and Melois 2005) statistical analysis, the results confirm the non-linearity of the increase in species diversity from the inner to the outer positions. Species richness varies with respect to the kind of local micro-forms (Jochimsen 1970). Analysis of the plots suggests that spatial variations in species follow both the chronology and the three major geomorphological landforms: sandurs, recessional moraines and morainic ridges or vallums. Therein lies the essential factor to distinguish between several original biotopes, as shown by Kozłowska & Rączkowska (2002). Sandurs are flat, fine-textured morphosystems, which increase the plant cover. Consequently, we find species typical of outwash deposits (Bennett and Glasser, 1996), such as *Achillea nana*, *Saxifraga aizoides*, *Herniaria alpina* (Gensac, 1974). Morainic ridges are generally drier, because their slope topography and coarse grading do not allow the water to remain in the soil. Consequently, xerophilous plants can more easily colonize this landform. Morainic ridges, which are moreover slope environments with periglacial morphodynamic activities, can support lithophilous and scree plants such as *Campanula cenisia* or *Cerastium latifolium*. Furthermore, morainic ridges have well distinct southern and northern exposures. In the northern position, snow cover remains longer and plants specific to this kind of snowy environments grow, such as *Salix reticulata* and *Salix retusa* (Barry, 1960). Recessional moraines, which are characterized by many interstices due to coarse materials and erratic blocks, can also retain snow longer and thus preserve moist conditions. There it is possible to find plants typical of moist conditions, such as *Salix hastata* (Gensac, 1974). Moreover, on these recessional moraines, where current periglacial activities are responsible for the instability of the ground, scree species such as *Artemisia mutellina* can be found. The highest values of biodiversity are due to local cohabitation of competitive plants, because of the age of the topography, and also of pioneer plants, since periglacial morphodynamic processes or runoffs maintain a kind of instability of soils. Most natural disturbances (Fortin et al., 1999), such as periglacial processes, play a major role in the maintenance of biodiversity by creating mosaic landscapes. Plant diversity on glacier forelands also includes species of conservation concern, such as *Trifolium saxatile* and *Saxifraga florentula*.

Conclusion

This change in plant dynamics shows a change and renewal of the flora, from the more recent to the older deglaciated areas. The better we are able to date the morphological changes, i.e. the ecological environment

of the plant cover, the better we can understand the succession of plant communities at the time. Today, the heterogeneity of the plant cover is due to the chronology of the successive stages of glacier retreat. If the climate conditions do not change, we assume that plant cover will be homogeneous in less than 50 years, such as in the fifth stage. With this model of flora evolution, it should be possible to predict the future of this proglacial landscape, if climate warming conditions do not change. Thus, if we see a growth in plant density and a change in the plant composition, the shift in biodiversity is not really linear. In Fig.8a, the distribution of the species diversity index shows an increase in index in relation to the conservation of pioneer species in the middle of more stable or competitive species. At the same time, species diversity is poorer in the oldest area, which is the most stabilized and the least periglacial environment (Table IV). The question here is to know if the pioneer species which grow during the first stage of this deglacial area will continue to exist, because they are one of the essential factors of biodiversity. We have seen that some of them survive and fight, with difficulty, against inter-specific competition which occurs in parallel with the changes in plant species. Nevertheless, the age of the deglaciation does not completely explain this plant dynamics. Other factors disturb this shift, such as runoff, frozen ground activity and mountaineering. Although some areas, such as morainic ridges or crests in recessional moraines, are old, pioneer species still grow because frost actions in this periglacial environment, such as frost-heaving or frost-cracking, are due to the lack of snow which is blown away by winds. Small scale periglacial processes are responsible for the increase in diversity of species because there is a fragmentation of habitats and of ecological conditions.

Nevertheless, today general global warming is responsible for the glacial retreat (Haeberli 1994; Vallon et al. 1998; Vincent et al. 2000). The meteorological data collected in France and in the Alps (Diaz and Beniston, 1997; Bougeault et al. 2002), in particular in the Mesoscale Alpine Programme (MAP of IGPB-WCRP), show an increase in temperatures of between 1.01 and 1.2°C over one century. This warming is responsible for the increase in plant cover in high mountain environments because bare grounds are extending caused by glacier retreat. Although the cover density is increasing, the variety of species is decreasing because of the inter-specific competition as shown by different authors (e.g., Gusian and Theurillat 2000 or Kaufmann 2002 for invertebrates). Recent experimental work (Hector et al. 1999; Loreau 1998, 2000, 2001) provides clear indications about relationships between environmental changes and biodiversity changes. Here, as shown by other authors (Gusian and Theurillat 2000; Kaufmann 2002), we show that there is a kind of weakness in species diversity, in a high mountain environment, with warming, for two reasons:

Firstly, the increase in plant cover, where pioneer plants decrease in number,

Secondly, the fact is more general for the entire alpine landscape, the warming conditions decrease the extent of the periglacial environments, which are responsible for the occurrence of more varied and rare ecological habitats for plants.

Mountain environments in the Alps above the treeline commonly host a small-scaled patchwork of more stable and dynamic plant communities (Arques 2005). Many plant species are adapted to low temperatures and may thus be particularly vulnerable to impacts of climate change. For example, shifts in biodiversity may be intensified under scenarios of global warming (Haeberli 1994; Price and Barry 1997; Haeberli and Beniston 1998; Houghton et al. 2001; Grabherr et al. 2003; Walther et al 2005). It is now widely accepted that climate change is an important driving force in determining plant-cover changes (Myers et al. 2000; Halloy and Mark 2003; Rozema et al. 2006). Climate change has produced numerous shifts in the distributions and abundances of species (Grabherr et al. 1994; Reich et al. 2001; Körner 2003; Parmesan and Yohe 2003; Root et al. 2003; Walther et al. 2005). Changes in biodiversity are studied in high mountain environments (Matthews and Whittaker 1987; Matthews 1992; Grabherr et al. 1994; Helm and Allen 1995; Kullmann 2000; Klanderud and Birks 2003), in the Alps (Gottfried and Pauli 1994; Körner 1995; Schwartz et al. 2000; Guisan and Theurillat 2001; Kaufmann 2001; Kaufmann et al. 2002; Kaufmann and Raffl 2002; Anthelme et al. 2003; Körner 2003) and in New Zealand (Halloy and Mark 2003). For invertebrates, Kaufmann (2002) shows the relationship between the increase in temperature and the rate of community variation. In the Himalaya, Gaur et al. (2003) pointed that the species richness has increased remarkably, partially due to the invasion of plant species from lower alpine belt. Such a climate warming-induced shift along altitudinal gradient is also assumed for the Apennines (Italy; Stanisci et al. 2005) and was already observed in the Alps and in the Scandes (Grabherr and al. 1994; Kullmann 2002; Klanderud and Birks 2003) in relation to the elevation in mean temperatures. For temperate high mountains such as the Alps, global and local warming reduces glaciers and periglacial environments (Haeberli 1994) and the question is now to consider if there will be an erosion in biodiversity

related to the development of invasive plants from lower belts. Glacier forelands are rather special environments within high mountains (Erschbamer and Retter 2004), where any changes in species richness and cover are primarily a mostly natural process following deglaciation; impacts arising from climate warming are here foremost secondary effect of the glacier retreat, following the simple fact that formerly ice-covered land has opened for colonisation. Nevertheless, such sites can be used to study the dynamics of a primary succession, which was shown here. Such dynamics, particularly the temporal dimension, will be very different in the zonal vegetation along an elevation gradient.

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