A survey of conservation, connectivity, and climate change in mountain regions: 1-18

RESEARCH ARTICLE

Vegetation trajectories in proglacial primary successions within Gran Paradiso National Park: A comparison between siliceous and basic substrates

Andrea Mainetti*[,1,2], Simone Ravetto Enri[1] and Michele Lonati[1]

[1]*Department of Agriculture, Forest and Food Sciences, University of Torino, Largo Paolo Braccini 2, 10095 Grugliasco (TO), Italy;* [2]*Botanical and Forest Conservation Office, Gran Paradiso National Park, Frz. Valnontey 44, 11012 Cogne (AO), Italy*

ABSTRACT

Global warming has a major impact on alpine environments and glacier retreat is the most noticeable consequence of rising temperatures. Ice-free screes and moraines are subjected to the colonization of biota thus providing a unique opportunity for the study of primary successions. Plant primary succession trajectories depend on several environmental factors, but bedrock type is one of the most important drivers of change. We studied the primary plant successions along two proglacial chronosequences, i.e. on siliceous and calcschist substrates, within the Gran Paradiso National Park (North-Western Italy). Both the chronosequences encompassed about 200 years and were located at high elevation (2,450–3,000 m a.s.l.). We focused on three functional species pools, namely early-successional pioneer, late-successional grassland and companion species. Plant species and phytosociological communities were recognized as indicators of several environmental features, such as sediment mobility and particle size. Despite the basic substrate generally hosts more plant species, we found a greater species richness and diversity in the gneissic chronosequence. The higher heterogeneity of the siliceous debris likely promoted plant establishment and vegetation development towards climax community, even if it was not reached. Conversely, the chronosequence on the calcschist substrate showed higher plant cover in the more developed stages, but still dominated by several pioneer species.

Key words: glacier foreland, chronosequence, alpine ecology, vegetation dynamics, pioneer species, plant colonization, phytosociology, calcschist, gneiss

*Corresponding author: andrea.mainetti@unito.it

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INTRODUCTION

The impact of global warming on the European Alps is dramatically shown by the retreat of the glaciers, a phenomenon documented by countless studies (e.g. Dyurgerov and Meier, 2000; Zemp et al., 2006; Pörtner et al., 2019). The increase in air temperature in the Alpine mountains over the past 50 years is approximately double the global average increase (Paul et al., 2004; Rebetez and Reinhard, 2008). The retreat of glaciers, begun at the end of the Little Ice Age (mid-19th century), has accelerated in recent decades and many small glaciers are disappearing or have already disappeared. In the area of Gran Paradiso National Park (GPNP) (south-western Italian Alps), glacier retreat is monitored annually by the Park's Surveillance Corp on more than 50 glaciers, which estimates the likely total disappearance of glacier cover within 20–30 years (GPNP, 2021).

Primary successions in proglacial environments have been studied since the end of the 19th and the beginning of the 20th century (Coaz, 1887; Cooper, 1923), but it still remains a fertile subject continually prone to new findings (Matthews and Vater, 2015; Erschbamer and Caccianiga, 2016; Eichel, 2019). However, the climatic, geological, ecological and phytogeographic variability which influences the successions is far from being fully explored.

Nowadays, the research in these environments is still based on the chronosequence approach (Egli et al., 2001; Caccianiga et al., 2006; D'Amico et al., 2017; Fischer et al., 2019), namely a space-for-time substitution, from recently ice-free moraines to the oldest ones (Pickett, 1989), where time since deglaciation assumes the role of key driver for ecosystem development.

Although plant communities have been extensively investigated along glacial chronosequences, a phytosociological description has been rarely adopted. The studies by Caccianiga and Andreis (2004) in the western and central Italian Alps and Raffl et al. (2006) in Austria serve as references in the Alps. In particular, Caccianiga and Andreis (2004) compare three different successions in different Alpine sectors and explore a wide geographical variability.

However, most of the studies have been conducted on siliceous debris, whereas vegetation developing on proglacial chronosequences on basic substrates has been poorly investigated (Erschbamer and Caccianiga, 2016). Moreover, a direct comparison of the vegetation dynamics between two chronosequences on different substrates, placed in the same group of the Alps (Graian Alps) and applying the same survey protocol is also something that has not been studied extensively (Schumann et al., 2016).

This paper aims to characterize and compare the different structures and trajectories of primary plant successions occurring at high altitude along both a siliceous and a calcschist proglacial chronosequence within the GPNP. More specifically, we described plant community development in terms of diversity and cover of different functional species pools in chronosequences of equal timespan. We hypothesized:

- a faster development of the primary succession on the basic lithotype towards the climax phytosociological community due to the lower mineral hardness compared to siliceous substrate;
- to observe a higher plant diversity on the basic substrate starting from the earliest pioneer phases.

MATERIALS AND METHODS

Study area

The study was conducted within GPNP (SAC/SPA IT1201000, North-Western Italy) in the proglacial forelands of Lauson (siliceous substrate) and Lavassey (basic substrate), in the valleys of Cogne and Rhêmes-Notre-Dame, respectively (Figure 1).

In both sites, the proglacial debris extended between the relative glacier terminus and the frontal moraines left by the glaciers at the end of the Little Ice Age (LIA), approximately in the 1850s. Outside the moraines the vegetation is mainly dominated by *Carex curvula* All. or *Carex myosuroides* Vill. communities at Lauson and Lavassey chronosequences, respectively.

The Lauson glacier foreland covered an area of about 0.65 km^2 for 1,300 m long, between 2,750 and 3,000 m a.s.l. The parent rock material was siliceous, mainly composed by paragneiss with a small amount of amphibolite (Le Bayon and Ballevre, 2006). Lavassey proglacial foreland extended over 0.90 km^2 for 2,300 m long, between 2,450 and 2,830 m a.s.l. Bedrocks were calcschists and metabasites (Polino, 2012; Carletti, 2015) which led to a soil basic reaction. Both sites were characterized by a continental climate with precipitations ranging between 700/800 mm year^{-1} at 1,700 m a.s.l. (Mercalli and Cat Berro, 2003).

Since the end of the LIA, the retreats of the Lauson and Lavassey glaciers have been tracked by historical and modern field monitoring (*Istituto Geografico*

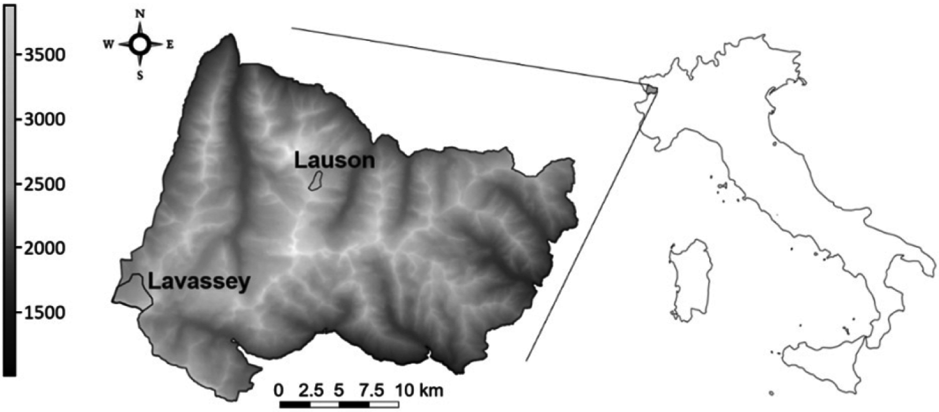

Figure 1 Location of the study areas of Lauson and Lavassey in the GPNP, North-Western Italy.

Table 1 Description of the identified chronosequence stages for both the study sites. In brackets, the time interval within the deglaciation age.

Chronosequence stage	*Deglaciation age in 2016* (yr)	*Distance from glacier terminus in 2016* (m)		*Altitude* (m a.s.l.)	
		Lauson (Siliceous)	Lavassey (Basic)	Lauson (Siliceous)	Lavassey (Basic)
1	~5	~35	~30	3,025	2,830
2	~10 (10–12)	~90	~120	3,015	2,800
3	~30 (18–42)	~180	~300	3,000	2,760
4	~65 (42–87)	~350	~600	2,970	2,700
5	~110 (87–135)	~800	~1000	2,885	2,600
6	~165 (135–197)	~1000	~1500	2,850	2,560

Militare and Gran Paradiso Surveillance Corp), aerial orthophotos, and satellite imagery (SPOT images). The resulting digitized historical forefronts allowed the identification of six different stages of a chronosequence in both study sites, from areas deglaciated less than 10 years ago, to areas deglaciated about 170 years ago (Table 1).

Vegetation surveys

At each of the six stages of the two chronosequences, three permanent plots were placed, for a total of 36 plots. Plot size was 25 m^2 at the Lauson foreland and reduced to 16 m^2 at the Lavassey one, due to the lower presence of large blocks and higher vegetation cover. In each plot, a botanical relevé was performed following the vertical point-quadrat method (Daget and Poissonet, 1971) using a 25 x 25 cm grid. At each grid node (for a total of 441 nodes in the plots of 25 m^2 and 289 in the plots of 16 m^2), plant species touching a steel needle were identified and recorded to account for the number of occurrences for each species (Figure 2). Since occasional species may be missed at the grid nodes, all other vascular species within each plot, not recorded with the steel needle, have been listed. Vascular plants were identified at species or subspecies level. For each relevé, the percentage cover of each species was obtained by dividing the number of occurrences by the total number of sampling nodes (i.e. 441 at Lauson and 289 at Lavassey). A cover of 0.1% was attributed to all occasional plant species as well, similarly to the classical phytosociological approach (Tasser and Tappeiner, 2005). Moreover, according to Grabherr and Mucina (1993), integrated with the works of Prunier et al. (2019) and Theurillat et al. (1994), three different Social Behaviour Types (SBTs, according to Bartha et al., 2008; Troiani et al., 2016) were identified: (i) early-successional pioneer species (T), including characteristic species of alpine debris (*Thlaspietea rotundifolii* and lower phytosociological units); (ii) late-successional grassland species (G), including characteristic (ingressive) species of

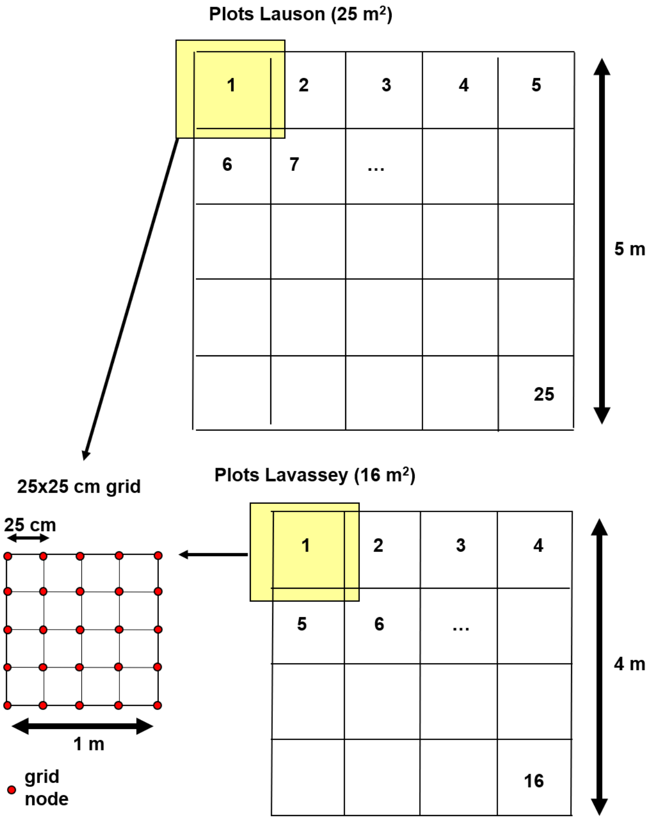

Figure 2 Sampling design adopted for the vegetation surveys for the two study areas.

acidophilic (*Caricetea curvulae* and *Salicetea herbaceae*) and basophilic (*Carici rupestris-Kobresietea bellardii* and *Seslerietea albicantis*) alpine grassland and snow-bed communities; and (iii) companion species (C).

For each relevé, the species richness, the total percentage cover and the Shannon-Wiener index (Magurran, 1988) were assessed within each SBTs.

Taxonomic nomenclature followed the new checklist of the Italian vascular flora (Bartolucci et al., 2018). The syntaxonomic nomenclature followed Grabherr and Mucina (1993).

Statistical analysis

For both the chronosequences, we assessed between-stages differences in terms of overall species richness, species cover and Shannon-Wiener index of the three functional species pools, by performing one-way ANOVAs. Assumptions of normality and homoscedasticity were checked with Shapiro-Wilk's and Levene's tests, respectively and, in case of assumption violation, logarithmic and square-root transformations were applied to variables prior to carrying out the ANOVAs. Whenever normal distribution or homoscedasticity did not occur, even after transformations, we performed the non-parametric Kruskal-Wallis test. Tukey's and Dunn's post-hoc tests were adopted for one-way ANOVA and Kruskal-Wallis, respectively, in case of significant differences ($p \leq 0.05$).

RESULTS AND DISCUSSION

1. Floristic characterization and syntaxonomy

Glacier foreland on the siliceous substrate (Lauson, Cogne) – Table 2

Along the Lauson chronosequence, 65 different vascular species were recorded.

The proglacial foreland hosted a flora strongly affected by the acidic parent material as highlighted by the frequent occurrence along the whole chronosequence of siliceous species such as *Saxifraga bryoides* L., *Cerastium uniflorum* Clairv. and *Saxifraga exarata* Vill. subsp. *exarata* (Delarze and Gonseth, 2008; Landolt et al., 2010).

Among the most constant species, eight were characteristic of the alliance *Androsacion alpinae*, typical of sparsely vegetated, rather stable, high-altitude siliceous debris. Plants like *Geum reptans* L. and *Androsace alpina* (L.) Lam. marked this facies of the community at higher altitudes: they venture to extreme elevations in Aosta Valley, up to 3,800 and 4,245 m a.s.l., respectively (Bovio, 2014). Within the pioneer communities, 13 species were found, belonging to the *Thlaspietea rotundifolii* class (and lower units). Among them, *Saxifraga oppositifolia* L. subsp. *glandulifera* Vacc., *Artemisia genipi* Weber ex Stechm. and *Arabis alpina* L. subsp. *alpina*, were the most frequent in the relevés.

The siliceous lithotype also affected the ingressive grassland species belonging to the class *Caricetea curvulae* (and lower units), as suggested by the frequency of *Leucanthemopsis alpina* (L.) Heywood and *Agrostis rupestris* All. in the relevés.

Overall, 15 species were strictly related to grassland functional pool, namely *Caricetea curvulae*, *Carici rupestris-Kobresietea bellardii* and *Seslerietea albicantis*. Siliceous snow-bed species were mainly represented by *Sagina saginoides* (L.) H. Karst (found in 14 out of 18 relevés), *Veronica alpina* L. and *Salix herbacea* L.

Glacier foreland on the basic substrate (Lavassey, Rhêmes-Notre-Dame) – Table 3

At the Lavassey foreland, the 18 relevés allowed the identification of 49 different vascular species.

Saxifraga oppositifolia and *Poa minor* Gaudin were the most frequent species along the chronosequence. Five species were characteristic of the *Drabetalia hoppeanae* (and lower units), a typical pioneer vegetation of high-altitude calc-schists substrates. The most frequent species was *Saxifraga biflora* All. subsp. *biflora*, recorded in eight out of the 18 relevés. In likely wetter sites, where drainage

Table 2 Phytosociological table for Lauson (gneissic) proglacial foreland.

Chronosequence stage Years from deglaciation Altitude (m a.s.l.)	1 ~5 3025			2 ~10 3015			3 ~30 3000			4 ~65 2970			5 ~110 2885			6 ~165 2850				
Relevé	Rel1	Rel2	Rel3	Rel4	Rel5	Rel6	Rel7	Rel8	Rel9	Rel10	Rel11	Rel12	Rel13	Rel14	Rel15	Rel16	Rel17	Rel18	Count	Frequency
Plot size (m^2)	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25		
Taxon																				
Charact. species of the *Androsacion alpinae*																				
Saxifraga bryoides L.	.	.	.	+	+	.	0.5	0.7	0.2	0.9	1.1	2.0	6.1	6.1	5.7	4.5	6.6	5.4	14	IV
Cerastium uniflorum Clairv.	.	.	+	0.2	+	+	3.9	2.9	2.7	5.7	9.5	2.0	1.8	+	0.2	.	.	.	13	IV
Saxifraga exarata Vill. subsp. *exarata*	+	+	.	+	.	.	0.2	0.5	.	0.2	0.2	+	+	+	.	.	.	+	11	IV
Oxyria digyna (L.) Hill	.	.	.	0.2	.	.	+	0.2	+	0.5	0.9	0.2	0.2	0.2	+	.	.	.	10	III
Androsace alpina (L.) Lam.	.	.	.	.	.	.	0.2	+	+	+	0.2	0.2	.	+	0.2	+	0.2	.	10	III
Geum reptans L.	.	.	.	.	.	.	.	+	.	0.2	+	.	0.7	0.2	+	+	.	+	8	III
Ranunculus glacialis L.	.	.	.	+	.	+	+	+	+	0.2	.	+	.	.	.	.	.	.	7	II
Poa laxa Haenke	.	.	.	.	.	+	0.2	0.7	.	0.7	0.5	+	.	.	.	.	.	.	6	II
Charact. species of *Thlaspietea rotundifolii* (and lower units)																				
Saxifraga oppositifolia L. subsp. *glandulifera* Vacc.	0.2	+	.	0.7	0.9	1.6	8.4	5.9	3.6	0.2	+	+	+	.	0.2	.	.	+	14	IV
Artemisia genipi Weber ex Stechm.	.	.	.	.	+	+	+	+	+	0.2	0.2	1.6	0.9	0.5	0.2	+	+	0.5	14	IV
Arabis alpina L. subsp. *alpina*	.	.	.	+	+	0.2	+	+	+	+	0.2	.	.	.	+	.	.	.	9	III
Saxifraga biflora All. subsp. *biflora*	.	+	.	+	+	+	+	+	+	.	+	.	.	.	.	.	.	.	8	III
Draba fladnizensis Wulfen	.	.	.	.	.	+	+	+	.	+	.	.	.	+	+	+	.	.	7	II
Hornungia alpina subsp. *brevicaulis* (Spreng.) O. Appel	.	.	.	.	.	.	0.2	+	+	+	+	.	+	.	+	.	.	.	7	II
Linaria alpina (L.) Mill.	.	.	.	.	0.2	+	0.2	+	.	0.2	+	.	.	.	.	.	.	.	6	II
Carex parviflora Host	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	3.4	+	3	I
Cardamine resedifolia L.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	2	I
Sedum atratum L.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	2	I
Trisetaria distichophylla (Vill.) Paunero	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.5	.	.	0.5	2	I
Salix retusa L.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1	I
Saxifraga androsacea L.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	1	I
Companion species																				
Ingr. species of *Caricetea curvulae* (and lower units)																				
Leucanthemopsis alpina (L.) Heywood	+	.	.	.	+	.	+	+	.	.	+	+	0.7	1.4	0.9	0.5	2.0	1.4	12	IV
Agrostis rupestris All.	.	+	+	+	.	.	.	+	.	+	0.2	.	.	.	.	+	+	.	8	III
Cherleria sedoides L.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	+	1.4	0.5	1.6	6	II
Minuartia recurva (All.) Schinz and Thell.	.	.	.	.	.	.	.	.	+	.	.	.	+	+	+	.	.	+	5	II
Luzula spicata (L.) DC. subsp. *conglomerata* (W.D.J.Koch) Murr	.	.	.	.	.	.	.	.	.	.	.	.	0.2	0.5	0.2	+	.	.	4	II
Festuca halleri aggr.	.	.	.	.	.	.	.	.	.	.	.	.	+	0.2	.	+	0.2	.	4	II
Hieracium glanduliferum Hoppe	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	+	3	I
Euphrasia minima Jacq. ex DC.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	0.2	0.2	3	I
Carex curvula All. subsp. *curvula*	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	0.2	.	2	I
Antennaria dioica (L.) Gaertn.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	0.2	.	2	I
Ingr. species of *Carici rupestris-Kobresietea bellardii* and *Seslerietea albicantis* (and lower units)																				
Erigeron uniflorus L.	.	.	.	.	.	.	.	.	.	.	.	+	1.1	0.7	1.1	2.0	1.4	2.0	7	III
Festuca pumila Chaix	.	.	.	.	.	.	.	.	.	.	.	.	0.5	0.2	+	0.2	.	.	4	II
Carduus defloratus L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1	I
Draba aizoides L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	1	I
Salix serpillifolia Scop.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	I
Ingr. species of *Salicetea herbaceae*																				
Sagina saginoides (L.) H. Karst.	.	.	.	+	+	+	0.2	+	+	0.9	+	0.2	+	+	1.1	.	+	+	14	IV
Veronica alpina L.	.	.	.	.	.	.	.	+	.	+	.	0.2	+	+	0.7	0.2	+	0.2	9	III
Salix herbacea L.	.	.	.	.	.	.	.	+	.	+	+	+	+	0.2	2.0	2.0	.	0.5	9	III
Omalotheca supina (L.) DC.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	.	6	II
Sibbaldia procumbens L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	0.7	2.5	.	3	I
Cardamine alpina Willd.	.	.	.	.	.	.	.	.	.	.	+	.	0.2	.	.	.	.	.	2	I
Alchemilla pentaphyllea L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	.	+	.	2	I

Table 2 Continued.

Chronosequence stage Years from deglaciation Altitude (m a.s.l.)	1 ~5 3025			2 ~10 3015			3 ~30 3000			4 ~65 2970			5 ~110 2885			6 ~165 2850				
Relevé	Rel1	Rel2	Rel3	Rel4	Rel5	Rel6	Rel7	Rel8	Rel9	Rel10	Rel11	Rel12	Rel13	Rel14	Rel15	Rel16	Rel17	Rel18	Count	Frequency
Plot size (m^2) Taxon	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25		
Other species																				
Poa alpina L.	+	.	.	.	+	+	0.2	0.2	0.2	1.6	0.9	3.4	4.1	2.5	3.2	3.4	1.8	4.8	15	V
Silene acaulis (L.) Jacq. subsp. *bryoides* (Jord.) Nyman	.	.	.	+	.	.	0.2	0.5	.	1.8	1.1	1.4	1.6	2.7	6.1	5.0	3.9	4.5	12	IV
Campanula cenisia L.	.	.	.	.	.	.	0.2	+	.	+	+	.	+	+	+	.	.	.	7	II
Achillea nana L.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	1.8	3.9	1.1	1.6	1.4	6	II
Taraxacum cfr. sect. *Alpina* G. E. Haglund	.	.	.	.	.	.	.	.	.	.	.	.	0.5	.	+	0.2	+	+	5	II
Noccaea corymbosa (J. Gay) F.K. Mey.	.	.	.	.	.	.	+	0.2	.	+	0.2	.	.	.	.	.	.	.	4	II
Gentiana brachyphylla Vill.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	+	3	I
Botrychium lunaria (L.) Sw.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	2	I
Phyteuma globulariifolium subsp. *pedemontanum* (Rich. Schulz) Bech. ex Greuter, Burdet and G.Long	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	0.5	2	I
Salix helvetica Vill.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	1	I
Sedum alpestre Vill.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	1	I
Jacobaea uniflora (All.) Veldkamp	.	.	.	.	.	.	.	.	.	.	.	.	0.2	.	.	.	.	.	1	I
Achillea erba-rotta All. subsp. *erba-rotta*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1	I
Adenostyles leucophylla (Willd.) Rchb.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1	I
Sempervivum montanum L. subsp. *montanum*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.5	.	.	1	I
Campanula scheuchzeri Vill.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	.	1	I
Oxytropis helvetica Scheele	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	.	1	I
Myosotis alpestris F.W. Schmidt	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1	I
Anthyllis vulneraria L. subsp. *valesiaca* (Beck) Guyot	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	1	I
Cerastium arvense L. subsp. *strictum* Gaudin	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	1	I
Sempervivum arachnoideum L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	1	I
Primula pedemontana Thomas ex Gaudin	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	I

was limited and solar radiation less intense, the basic snow-bed vegetation was well represented by the order *Arabidetalia caeruleae* (and lower units) with species like *Arabis caerulea* All., *Salix reticulata* L. and *Salix retusa* L. Additionally, other pioneer species like *Campanula cochleariifolia* Lam. and *Cerastium latifolium* L. clearly denoted the calcschists-derived substrate. Among grassland units, only four species belonged to *Caricetea curvulae* (and lower units) while nine belonged to *Carici rupestris-Kobresietea bellardii* and *Seslerietea albicantis* (and lower units).

The different parent rock material of the two glacier forelands had a relevant effect on vegetation, as highlighted by the presence of contrasting pioneer phytosociological alliances and orders within *Thlaspietea rotundifolii* class (i.e. *Androsacion alpinae* on the siliceous Lauson substrate; *Drabetalia hoppeanae* and *Arabidetalia caeruleae* on the basic Lavassey substrate). However, as already observed for *Caricetea curvulae* characteristic species, the species frequency of the grassland functional pool at Lauson was double that at the Lavassey site, while species belonging to *Carici rupestris-Kobresietea bellardii* and *Seslerietea albicantis* showed an opposite trend. At the species level, the lithologic vicariance shown by *Carex curvula* was emblematic: on the siliceous substrate of Lauson it was recorded only *Carex curvula* subsp. *curvula* All., while at Lavassey only *Carex curvula* subsp. *rosae* Gilomen in line with their respective ecological preferences (Aeschimann et al., 2004).

2. Vegetation diversity and dynamics along the chronosequences

At Lauson, the first stage of the chronosequence (relevés 1 to 3), deglaciated for *ca*. 5 years, was colonized by very few pioneer species under extreme harsh conditions. Surprisingly, at Lavassey no species was able to establish in the first stage, likely because of the over-mobility of the glacial till, despite in general the processes of mineral weathering are faster on basic substrates. Indeed, such disturbance as well as other abiotic constraints (i.e. water flows, solar radiation, etc.) and nutritional limitations (i.e. Carbon and Nitrogen availability, etc.) are known to strongly affect the germination and establishment of plant species in these environments (Marcante et al., 2012, 2014; Neuner and Buchner, 2012). The glacial till of Lavassey was finer and more homogeneous than at Lauson, where several medium and large blocks were dispersed throughout the proglacial debris (Figure 3). Indeed, large rocks effectively stabilize the glacial till while reducing erosion determined by the huge inputs of nival and glacial meltwater (Erschbamer and Caccianiga, 2016; Eichel, 2019). Moreover, this process leads to the formation of micro safe-sites (*sensu* Harper et al. 1961) where species such as *Saxifraga oppositifolia* can germinate and survive. Such 'nursery effect' played by rocks is not limited to a sheltering function, but the water funnelled between rocks can be also nutrients-enriched, thus facilitating the uptake by pioneer species (Göransson et al., 2016).

Since there is no evidence to suggest otherwise, we assume that the input of viable propagules on the two chronosequences was comparable. Indeed, outside the LIA moraines we observed, for both the glacier forelands, patches of pioneer and quasi-climax plant communities at higher altitudes than the proglacial debris, as reported also by Erschbamer and Caccianiga (2016).

The number of pioneer species was more constant at the Lauson foreland than at Lavassey. While at Lauson the *Androsacion alpine* was the unique pioneer alliance established from very few years from deglaciation to more than a century and a half, at Lavassey there was a clear changing pattern of the early-successional community. The first non-sporadic species (i.e. only three different species) were those characteristics of *Drabetalia hoppeanae*, establishing after 65 years from deglaciation. However, these species became sporadic along the chronosequence as the characteristic species of *Arabidetalia caeruleae* emerged. In particular, we observed the establishment of the *Salicetum retuso-reticulatae* association, a pioneer community more nutrient-demanding, hardly able to anchor to the gravel.

Looking to the SBTs, the number and cover of species belonging to *Thlaspietea rotundifolii* followed a similar trend in both glacier forelands (Figure 4A–D). At Lauson, the cover was lowest in recently deglaciated areas, increasing with terrain age (peaking at *ca*. 30 years after glacier retreat), while the species number decreased

Table 3 Phytosociological table for Lavassey (calscist) proglacial foreland.

Chronosequence stage Years from deglaciation Altitude (m a.s.l.)	1 ~5 2830			2 ~10 2800			3 ~30 2760			4 ~65 2700			5 ~110 2600			6 ~165 2560				
Relevé	Rel1	Rel2	Rel3	Rel4	Rel5	Rel6	Rel7	Rel8	Rel9	Rel10	Rel11	Rel12	Rel13	Rel14	Rel15	Rel16	Rel17	Rel18	Count	Frequency
Plot size (m^2) Taxon	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16		
Charact. species of *Drabion hoppeanae* and *Drabetalia hoppeanae*																				
Saxifraga biflora All. subsp. *biflora*	.	.	.	1.7	1.0	1.7	4.2	2.4	3.8	+	+	+	.	.	.	.	.	.	9	IV
Artemisia genipi Weber ex Stechm.	.	.	.	.	.	.	.	.	.	0.7	+	1.4	.	.	+	.	.	+	5	II
Hornungia alpina subsp. *brevicaulis* (Spreng.) O. Appel	.	.	.	.	.	.	.	+	.	0.3	+	+	.	.	.	.	.	.	4	II
Gentiana terglouensis Hacq. subsp. *schleicheri* (Vacc.) Tutin	.	.	.	.	.	.	.	.	.	.	.	.	.	0.3	1.0	.	+	+	4	II
Herniaria alpina Chaix	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	2	I
Charact. species of *Arabidion caeruleae* and *Arabidetalia caeruleae*																				
Arabis caerulea All.	.	.	.	.	+	.	.	.	.	2.4	1.7	2.4	0.3	+	0.3	0.7	+	0.3	10	IV
Saxifraga aizoides L.	.	.	.	.	.	+	+	0.3	+	.	+	+	.	.	.	.	.	.	6	III
Salix reticulata L.	.	.	.	.	.	.	.	.	.	.	.	.	6.6	4.5	5.2	2.8	5.5	10.7	6	III
Salix retusa L.	.	.	.	.	.	.	.	.	.	.	.	.	2.8	1.7	0.3	6.9	9.3	11.4	6	III
Silene acaulis (L.) Jacq. subsp. *cenisia* Vierh.	.	.	.	.	.	.	.	.	.	.	.	.	0.7	1.0	2.1	8.7	5.2	6.6	6	III
Omalotheca hoppeana (W.D.J.Koch) Sch. Bip. and F.W. Schultz	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	2	I
Cirsium spinosissimum (L.) Scop.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	1	I
Charact. species of *Thlaspietea rotundifolii* (and lower units)																				
Saxifraga oppositifolia L. subsp. *glandulifera* Vacc.	.	.	.	1.0	0.3	1.4	5.9	5.9	10.0	18.7	12.1	13.8	5.2	3.8	6.2	9.0	10.7	2.8	15	V
Poa minor Gaudin	.	.	.	+	+	.	+	+	+	2.1	3.1	2.1	.	0.7	+	1.4	+	.	12	V
Linaria alpina (L.) Mill.	.	.	.	.	.	.	.	.	.	+	+	+	.	+	+	.	+	+	7	III
Scorzoneroides montana (Lam.) Holub	.	.	.	.	.	.	.	.	.	.	.	.	.	0.7	1.4	2.1	0.7	1.0	5	II
Arabis alpina L. subsp. *alpina*	.	.	.	.	.	.	.	.	.	1.0	+	+	.	.	.	.	.	.	3	II
Campanula cochleariifolia Lam.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	1	I
Cerastium latifolium L.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	1	I
Ranunculus glacialis L.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	1	I
Companion species																				
Ingr. species of *Caricetea curvulae* (and lower units)																				
Euphrasia minima Jacq. ex DC.	.	.	.	.	.	.	.	.	.	.	.	1.0	.	0.3	+	0.3	0.3	+	6	III
Jacobaea incana (L.) Veldkamp	.	.	.	.	.	.	.	.	.	.	0.3	.	.	.	.	+	+	+	4	II
Cherleria sedoides L.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	1	I
Hieracium glanduliferum Hoppe	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.3	1	I
Ingr. species of *Carici rupestris-Kobresietea bellardii* and *Seslerietea albicantis* (and lower units)																				
Salix serpillifolia Scop.	.	.	.	.	.	.	.	.	.	.	.	.	20.8	13.8	14.9	9.7	7.3	4.2	6	III
Bartsia alpina L.	.	.	.	.	.	.	.	.	.	.	.	.	1.0	2.1	1.7	0.3	1.4	2.1	6	III
Leontopodium alpinum Cass.	.	.	.	.	.	.	.	.	.	.	0.3	+	0.3	.	.	.	0.7	.	4	II
Pedicularis rosea Wulfen subsp. *allionii* (Rchb. f.) Arcang.	.	.	.	.	.	.	.	.	.	.	.	.	0.3	1.0	0.7	0.3	.	.	4	II
Antennaria carpatica (Wahlenb.) Bluff and Fingerh.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	3	II
Erigeron uniflorus L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	2	I
Dryas octopetala L.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1	I
Carex curvula subsp. *rosae* Gilomen	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.3	1	I
Festuca pumila Chaix	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	I

Table 3 Continued.

Chronosequence stage	1			2			3			4			5			6				
Years from deglaciation	~5			~10			~30			~65			~110			~165				
Altitude (m a.s.l.)	2830			2800			2760			2700			2600			2560				
Relevé	Rel1	Rel2	Rel3	Rel4	Rel5	Rel6	Rel7	Rel8	Rel9	Rel10	Rel11	Rel12	Rel13	Rel14	Rel15	Rel16	Rel17	Rel18	Count	Frequency
Plot size (m²)	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16		
Taxon																				
<u>Ingr. species of *Salicetea herbaceae*</u>																				
Sagina saginoides (L.) H. Karst.	.	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.	.	4	II
Veronica alpina L.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	2	I
Arenaria biflora L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.3	.	+	.	2	I
<u>Other species</u>																				
Achillea nana L.	.	.	.	.	.	.	.	.	.	+	0.3	+	1.0	2.8	3.5	3.5	3.1	2.4	9	IV
Campanula cenisia L.	.	.	.	.	.	.	.	.	.	2.1	2.1	0.3	+	+	+	+	.	+	8	III
Poa alpina L.	.	.	.	.	.	.	.	.	.	.	+	+	.	0.3	.	0.3	+	1.7	6	III
Euphrasia officinalis subsp. *rostkoviana* (Hayne) Towns.	.	.	.	.	.	.	.	.	.	.	.	.	0.3	+	+	+	2.1	1.4	6	III
Anthyllis vulneraria L. subsp. *valesiaca* (Beck) Guyot	.	.	.	.	.	.	.	.	.	.	.	.	.	0.3	+	1.0	0.3	0.7	5	II
Botrychium lunaria (L.) Sw.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	0.3	5	II
Gentianella tenella (Rottb.) Börner	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	2	I
Silene acaulis (L.) Jacq. subsp. *bryoides* (Jord.) Nyman	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	1	I
Erysimum jugicola Jord.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	1	I
Solidago virgaurea subsp. *minuta* (L.) Arcang.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	1	I
Lotus corniculatus L. subsp. *alpinus* (DC.) Rothm.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1	I
Sempervivum ara chnoideum L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1	I
Sedum alpestre Vill.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	1	I

in the more developed stages. At Lavassey, species number of *Thlaspietea rotundifolii* unit grew in the first 30 years after glacier retreat and then stabilized, while overall species cover increased gradually along the chronosequence reaching values three to four times higher than at Lauson. By comparing the two chronosequences, it emerged that pioneer species pattern was different in the two glacier forelands. At Lauson, characteristic species of *Thlaspietea rotundifolii* declined with time and were almost replaced by late-successional grassland species (Figure 4C). The stabilising effect played by large blocks likely fostered soil development and nutrient build-up while limiting leaching processes (Wojcik et al., 2020). Since at Lavassey the debris was very fine, several processes interfered with ecosystem development even if plant species covered a larger area (*ca.* 50% of the available area, in the eldest stage) than at Lauson (Figure 4C and 4D). Indeed, surface erosion and soil cryoturbation probably assumed a crucial role, creating and maintaining harsh conditions suitable only for extreme pioneer species even after a century of development. This process was well highlighted by the high number and cover of species belonging to *Thlaspietea rotundifolii* class in the latter stages of the Lavassey chronosequence (Figure 4B and 4D). The number of species belonging to grassland SBT was remarkable in both the chronosequences matching that of the generalist

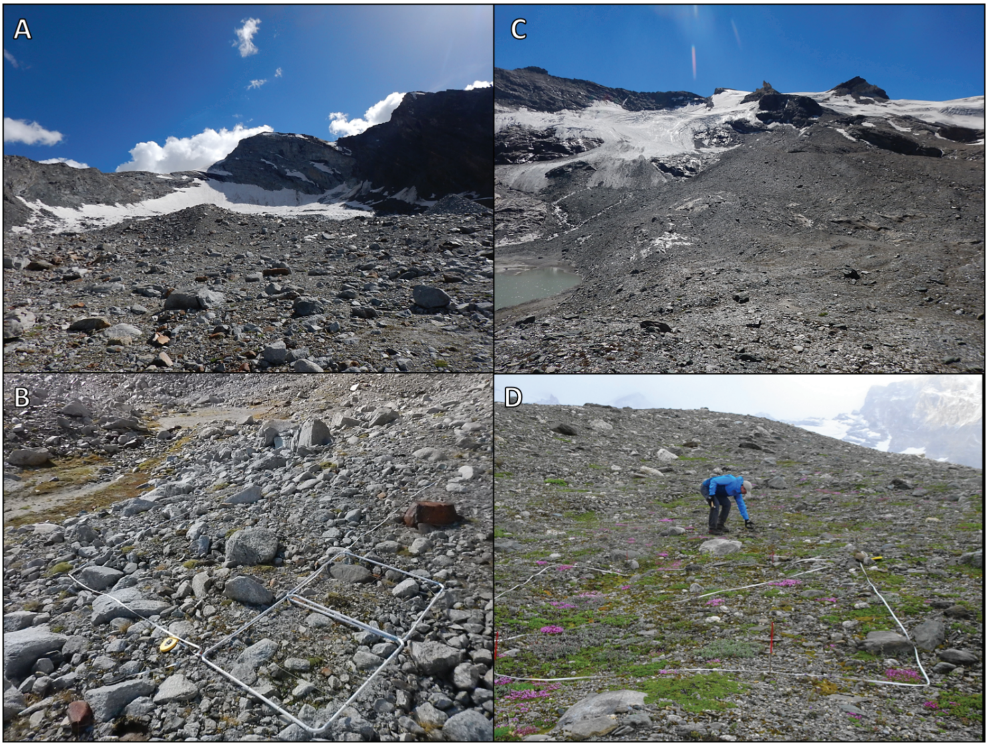

Figure 3 Overview and close-up photos of the proglacial foreland of Lauson (A and B) and Lavassey (C and D). The different plant cover between the two proglacial debris is clear, much greater in the calcschist chronosequence of Lavassey (D) than in the siliceous one of Lauson (C).

companion species (Figure 4A and 4B). Further, for both the chronosequences, we observed a clear increasing trend of grassland ingressive species number and cover with age after *ca*. 110 years from deglaciation. Nevertheless, at Lauson, the grassland species cover remained lower or comparable to that of companion species, while at Lavassey it was considerably higher, with a remarkable cover also of woody species. After 110 years from deglaciation, the woody species *Salix serpillifolia* Scop. covered a huge area (Table 3) and likely promoted the consolidation of the fine sediment by growing year after year for decades, extending its long branches, thus acting as an 'ecosystem engineer' (Jones, 2012; Eichel, 2019).

The pattern of the Shannon-Wiener index along the two chronosequences, subdivided among the three SBTs, provided some interesting insights. In the early phases after glacier retreat, few pioneer species dominated the scarce available safe-sites. With soil system development, the establishment of novel species favoured a more equal distribution among SBTs, resulting in higher values of the Shannon-Wiener index on older moraines (Figures 4E and 4F). At the Lauson glacier foreland, the pioneer *Saxifraga bryoides* was still abundant on the more developed soils (Table 2) and thus causing a decreasing trend (even if not statistically significant) of Shannon-Wiener index of the pioneer functional pool (Figure 4E). However, this process was counterbalanced by the more even distribution among grassland species and companion ones that gave to the entire community a more heterogeneous composition. At Lavassey, there was no strongly dominant species among pioneer ones and the relative portion of Shannon index slightly increased along the chronosequence, even after a century of community development (Figure 4F). Grassland and companion species proportions were similar for both the chronosequences with an increasing relative importance with time since deglaciation. In literature, older moraines are generally reported to be dominated by few late-successional grassland species (e.g. Caccianiga and Andreis, 2004), thus resulting in decreasing diversity index values. At the Lauson and Lavassey proglacial forelands, this pattern was not observed, likely because of the overall low cover and consequent low competition.

At the Lauson glacier foreland, the process of primary succession towards grassland communities (i.e. *Caricetum curvulae*) was faster than at Lavassey, despite the higher elevation and lower vegetation cover. The abundance of safe-sites, likely nutrient-enriched by pioneer plant turnover (Mainetti et al. 2021), created favourable conditions for hosting more competitive species that overcome pioneer early-successional species. In contrast, at Lavassey late-successional grassland species struggled to survive, reproduce and spread (with the exception of *Salix* spp.) while the pioneer ones dominated throughout the chronosequence, leading to uncommon vegetation composition of the later stages. Overall, in both study areas the vegetation dynamics were slow compared to other proglacial chronosequences (Andreis et al., 2001; D'Amico et al., 2014) and the climax community was far from being reached even at Lauson.

CONCLUSIONS

This study allowed the identification and characterization of primary plant succession trajectories of two glacial forelands within the GPNP. Glacier retreat is particularly severe within the Park and large areas of debris are continually exposed to plant colonization. Among the several lithotypes on which they can develop, the main two considered in this work represent the most common. Plant species act as indicators of several environmental features, such as sediment mobility and particle size, without the need of direct measures in this field. Despite basic substrates often being considered more favourable for plant colonization and richer in species, we found a greater species richness and even cover distribution among species in the siliceous chronosequence of Lauson. The glacial till heterogeneity promoted the creation of greater ecological niches (i.e. safe-sites) likely differentiated in terms of nutrient availability, protection against extreme hazards and creating favourable soil moisture and temperature conditions. However, where plants were able to survive on basic finer debris, especially prostrate woody species (i.e. at Lavassey), they grew year after year covering large surfaces, rather than at Lauson where the abundant rocks do not allow such extensive plant cover.

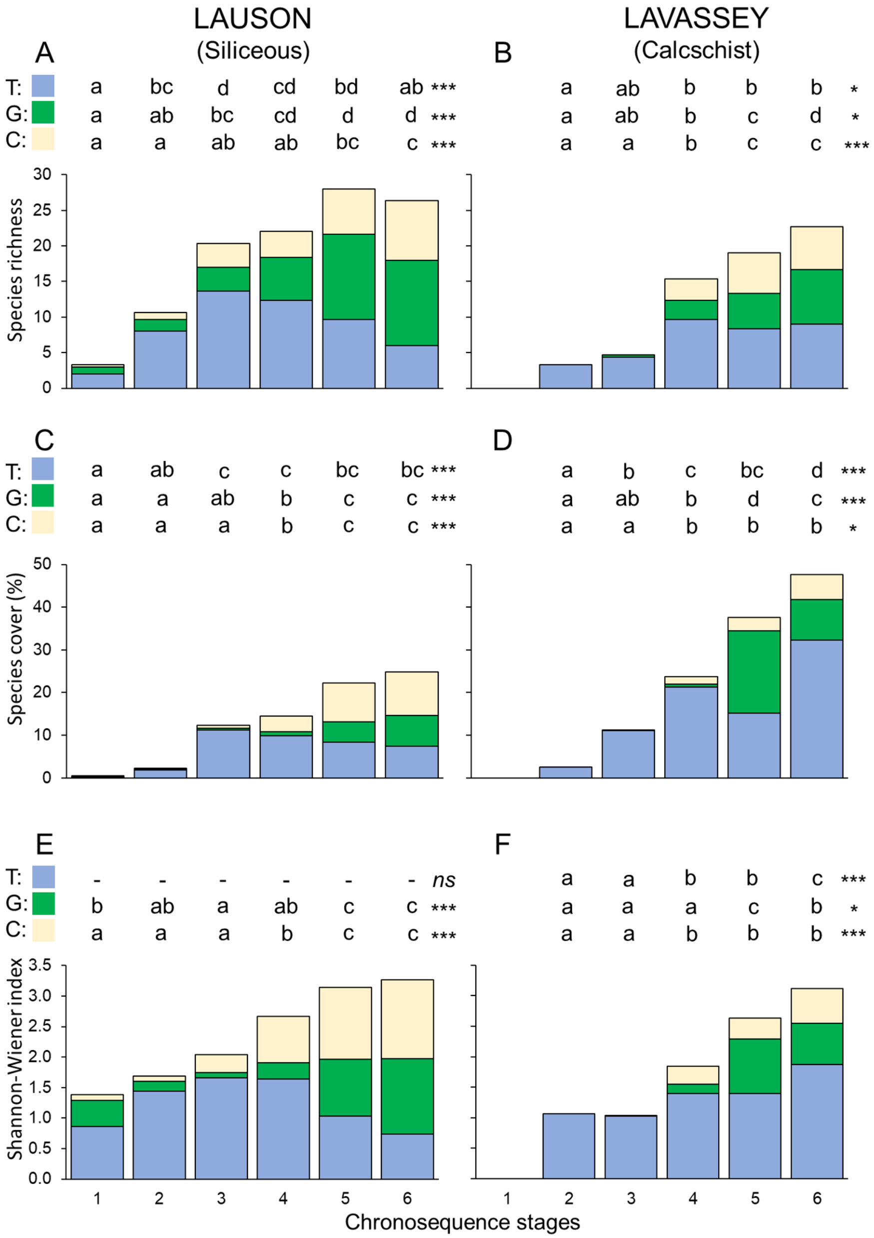

Figure 4 Plant species richness (A, at Lauson siliceous foreland; B, at Lavassey calcschist foreland), cover (C, at Lauson; D, at Lavassey) and Shannon-Wiener index (E, at Lauson; F, at Lavassey) along the six stages of both the chronosequences. Different colours refer to different Social Behaviour Types: the blue portion of the histograms (T) refers to the contribution of pioneer species (belonging to *Thlaspietea rotundifolii* Br.-Bl. 1948 class and subordinate units); the green portion (G) to the late-successional grassland species (ingressive alpine grassland species) and the yellow portion (C) to the companion species. Different letters indicate significant differences (p <0.05) among stages according to Tukey's HSD test.

The comparison of these two primary successions revealed an interesting contrast in terms of successional development and overall plant cover: they do not necessarily progress simultaneously. At the siliceous Lauson foreland the succession was more developed toward grassland communities but with scarce plant cover, whereas on the basic substrate of Lavassey pioneer species dominated also at the older stages with the higher plant cover.

SYNTAXONOMIC LIST OF THE COMMUNITIES OF LAUSON AND LAVASSEY PROGLACIAL FORELANDS

THLASPIETEA ROTUNDIFOLII BR.-BL. 1948
  DRABETALIA HOPPEANAE ZOLLITSCH 1968
    Drabion hoppeanae Zollitsch 1968
  ARABIDETALIA CAERULEAE RÜBEL EX NORDHAGEN 1936
    Arabidion caeruleae Br.-Bl. in Br.-Bl. et Jenny 1926
  ANDROSACETALIA ALPINAE BR.-BL. IN BR.-BL. ET JENNY 1926
    Androsacion alpinae Br.-Bl. in Br.-Bl. and Jenny 1926
CARICI RUPESTRIS-KOBRESIETEA BELLARDII OHBA 1974
SESLERIETEA ALBICANTIS OBERD. 1978 CORR. OBERD. 1990
CARICETEA CURVULAE BR.-BL. 1948
SALICETEA HERBACEAE BR.-BL. 1948

OTHER SYNTAXA QUOTED IN THE TEXT

Caricetum curvulae Rübel 1911
Salicetum retuso-reticulatae Br.-Bl. in Br.-Bl. et Jenny 1926

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