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Floristic patterns, ecological gradients and biodiversity in the composite channels (Central Alps, Italy)

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ABSTRACT

Composite channels in the alpine region are heterogeneous environments resulting from a variety of erosive and depositional processes. They can have different ecological functions: habitats for plant species, conduits, filters, sources and sinks. They can contain sparse, intermittent vegetation cover, and are frequently free of vegetation except along the banks and levees. We hypothesised that this disturbed and fragmented landscape unit encourages biodiversity with characteristic plant species adapted to survive in the channel niches.

In this study, which was carried out mostly in the subalpine belt of the Adamello-Presanella Group, we aimed to characterize floristic and biodiversity patterns with respect to the dominant channel gradients by means of a canonical correspondence analysis (CCA) ordination approach and an analysis of diversity indexes. The frequency table and CCA results showed considerable floristic heterogeneity within the composite channels mainly as a function of nutrient availability and altitude. Different gradients of biodiversity (alpha, beta and gamma diversity) depended on the geomorphological disturbances (alpha and gamma) and environmental heterogeneity across the channel subunits.

Geomorphological processes seem to play key roles in the dispersal of seeds, spores and propagules and in the colonization, establishment and spread of plants in this complex environment. The composite channels could play an important refuge–habitat function for microthermic species during the widely accepted current trend of global warming.

1. Introduction

In recent years, interest in river and stream corridors and riparian habitats has increased, especially in regards to variations in vegetation structure and dynamics and in relation to differences in biodiversity gradients (Dynesius et al., 2004; Lyon and Gross, 2005; Nilsson and Svedmark, 2002). These environments have five principal functions: habitats for plant species, conduits, filters, sources and sinks (Butler, 2001). River and stream corridors produce heterogeneity by introducing strong ecological gradients that extend vertically, laterally and longitudinally with regards to natural disturbances and time (van Coller et al., 2000). In particular, disturbances deriving from geomorphological processes, at various spatial and temporal scales, seem to control species distribution (Ward et al., 2002). Moreover, environmental heterogeneity and disturbances influence plant species diversity patterns (Pollock et al., 1998).

There is a general agreement that climate changes could play a major role in modifying species distribution in mountain areas controlling disturbance effects upon vegetation. Azonal plant communities growing within channels seem to be less sensitive to climate change than zonal communities, since the major limiting factors of azonal assemblages are non-climatic in character (Kienast et al., 1998). On the other hand climatic warming may accelerate the invasion of alien plant species both in plain and mountain areas (Alexander et al., 2009; Hansen and Clevenger, 2005).

At the microscale, the spatial distribution of plants is mainly due to variations in the retention of nutrients (Osborne and Kovacic, 1993), in microclimatic conditions within streams (Grey and Eddington, 1969), or in the sedimentological and textural characteristics of deposits (Naiman and Décamps, 1997). Most studies that addressed the bio-ecological processes within rivers and corridors have been carried out in large- or medium-sized watercourses, generally in alluvial plains (Ward, 1998), in urbanized landscapes (Oneal and Rotenberry, 2008) and in arid

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environments (Tiegs et al., 2005); only a few authors have investigated arctic rivers or proglacial rivers (Gould and Walker, 1999; Gurnell et al., 1999). Furthermore, few specific studies have been conducted on floristic and diversity patterns within channels in the alpine region. Disturbance factors (fire, flooding, snow avalanches, etc.) play a major role in determining species distribution patterns and increase in diversity (Lenssen et al., 2004). In particular habitat diversity and species richness are considerably influenced by disturbances within avalanche tracks (Rixen et al., 2007). Snow avalanches are ecological agents that result in distinctive vegetation patterns in mountain environments (Stoeckli et al., 2005).

In our opinion, the floristic and biodiversity gradients within river/stream corridors are emphasised in the alpine regions, where typical species exist in high-quality environments. Along the valley slopes, geomorphic processes, such as running water, debris flow and snow avalanches (and, in part, also debris/rock fall), are extremely active and concentrated in the "central channel" (i.e. composite channel), a unit of the "composite alpine debris cones" (Baroni et al., 2007). Such processes, along with altitudinal gradients, seem to influence the dispersal (of seeds, spores and propagules), colonization, spread and establishment of these species in the alpine corridors.

In this study, we hypothesised that this disturbed and fragmented landscape unit favours floristic heterogeneity and biodiversity with characteristic plant species adapted to survive in the channel niches under selective environmental conditions. Our specific objectives were: (a) to assess and characterize the floristic patterns according to vertical, lateral and longitudinal ecological gradients and environmental indexes (i.e. Landolt indexes) within the composite channels; (b) to evaluate the spatial distribution of plant diversity in this environment in relation to geomorphic disturbances and (c) to stress the role of the channels as a means of dispersal/plant migration in the alpine environment.

2. Methods

2.1. Study area

The composite channels investigated are located in the Adamello-Presanella Group (Central Alps, Italy; Fig. 1A). The landscape in the highest elevation belt (above about 2500 m a.s.l.) is characterized by active glacial and periglacial landforms. The summit area of the group holds the largest glacier of the Italian Alps (Adamello Glacier, about 1813 ha in 1983, SGL 1992), as well as about 90 other minor glacial bodies.

The geological structure of the Adamello Group is mostly characterized by a Cenozoic large batholith, made up of tonalite, granodiorite and quartzdiorite rocks, and small basic plutons. In marginal sectors of the studied area, an older metamorphic basement and sedimentary cover surround the batholith (Callegari and Brack, 2002).

The mean annual temperatures in the study area range from −2.8 to +0.5 °C near the summit areas to +7.5 to +10.7 °C in the bottom valleys (Ceriani and Carelli, 2000). The coldest month is January, when mean temperatures are under 0 °C. The warmest months are July or, at some stations, August, with mean temperatures ranging from 9 to 15 °C depending on the elevation. Annual thermic ranges vary from 11 to 16 °C (Baroni et al., 2004). In the study area, a general increase in mean air annual temperature has been registered during the last decades, as in the case of the Passo del Tonale meteorological station for the period from 1929 to 1999 (Fig. 1B).

The annual mean precipitation varies from about 800 mm in the bottom of valleys to about 1500 mm, with a strongly increase in trend according to elevation. The mean annual precipitation decreases from south to north, with lower values on the northern slopes of the massif (Baroni et al., 2004). Precipitation mostly occurs as snow, from November to May, and the total number of days per year with persistent snow cover can reach well over 200 (Baroni et al., 2007). In Fig. 1C, the trend of snow cover at the Passo del Tonale meteorological station is shown for the years 1969–1990. The accumulation of snow within channels during the winter and spring and its local persistence until late summer drastically shorten the length of the vegetative season.

Vegetation, growing above the upper forest limit, is characterised by a mosaic of plant communities, which is typical of the subalpine and alpine belts (Baroni et al., 2007).

2.2. Composite channel

The channels considered in the present study are polygenic landforms of the composite alpine debris cones of the Adamello-Presanella Group (Baroni et al., 2007). The channels generally cross cones in the central portion and are connected to deep gullies, cutting through rocky walls behind the cones. Gullies reach the glacial foreland in front of the Adamello-Presanella's glaciers, which are over 2900 m in altitude.

Geomorphic processes vary in intensity and frequency within channels, depending on season and altitude. The main processes related to channel incision are snow avalanche activity, running water, debris flow and debris/rock fall. Landforms and deposits of different origin, sedimentological character and texture are clearly distinguishable along the channel corridors (upper (u), medial (m) and lower (l) areas) and overlap to different extents.

The channels cut deeply into the composite cone-head and generate converging erosive scarps in the apical sectors, due to the erosive action of the snow avalanche movement. The maximum slope angles, around 30°, occur in the upper portions of the composite debris cone, while the minimum values are found in the lower sectors (about 7–10°). Channel depths range from several meters (more than 10 m) in the upper channels to about 0.5 m in the lower channels. The channels typically have concave profiles and become shallower down the valley, with widths ranging from 30–40 m (upper sectors) to 1–5 m (lower sectors). Such features demonstrate that erosion caused by the synergetic action of snow avalanches and running water is concentrated mainly in the upper channel. Deposits due to debris flow (levee and debris flow lobes) and scattered snow avalanche debris are more evident in the middle and lower portions of the channels. The upper and middle portions of the channels are also frequently affected by the debris and rock fall deposits. As a consequence, the upper (u) sectors of the channels and cones are richer in a sandy matrix and clearly demarcated by a gradient break from the middle (m) and lower (l) sectors.

In the transverse section, the channels consist of three distinct subunits: channel beds (CB), channel banks (Bk) and external bank-levees (EBL). Snow accumulates in the channels during winter and spring and persists in some places until late summer. Erosion in the active CB often causes collapses of Bk, particularly in the Bk subunits mainly consisting of massive diamicton or crudely stratified gravel with pebbles and boulders, which are clast-supported to matrix-supported and mainly formed by avalanches (Baroni et al., 2007). In the upper channel, EBL subunits are thin (generally less than 50 cm) and consist of scattered debris with heterogeneous grain size, and are rich in sandy matrix. Such deposits are due mainly to snow avalanche

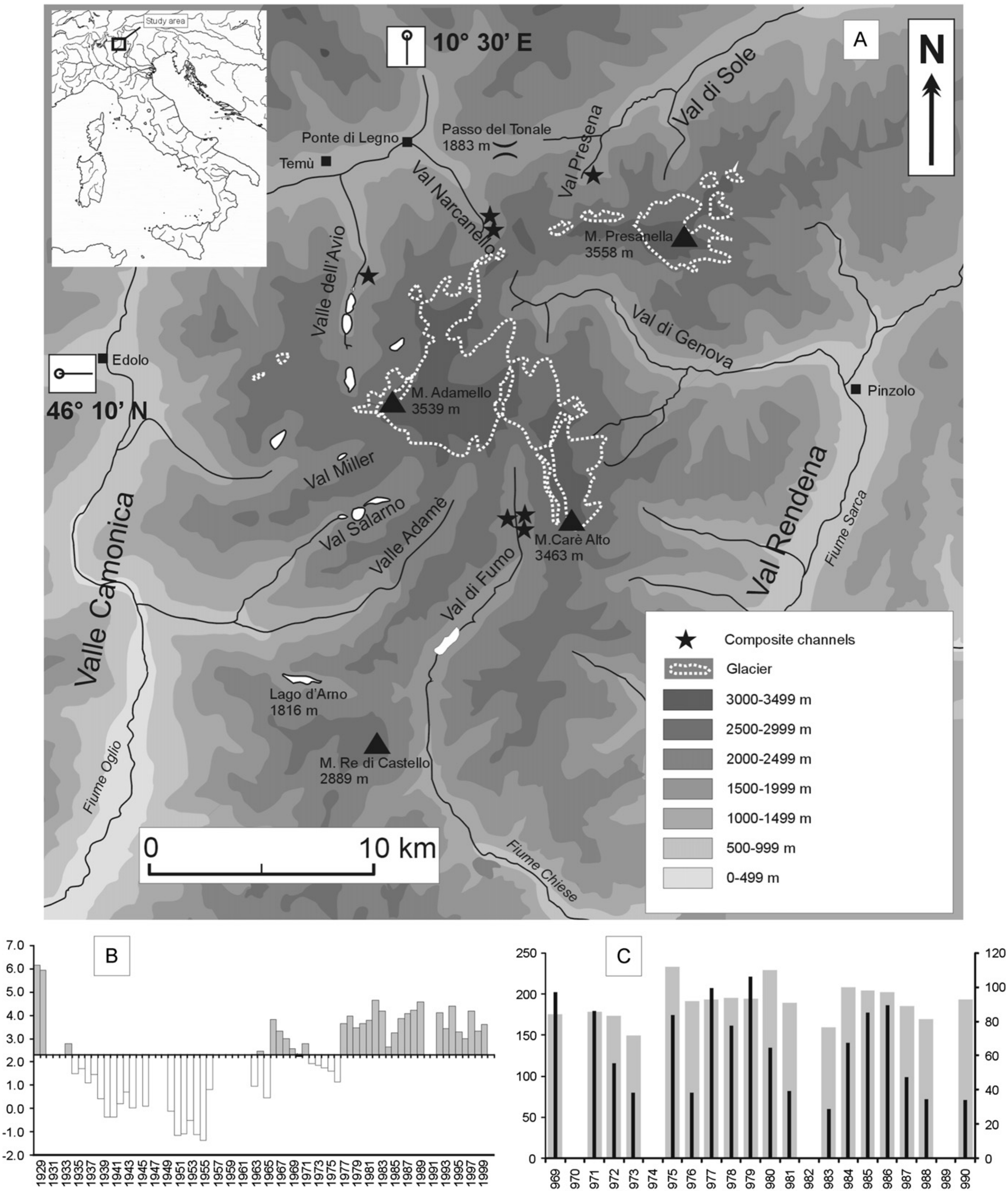

Fig. 1. (A) The study area. (B) Trend in deviations from mean annual air temperature [°C] during 1929–1999, recorded at the Passo del Tonale meteorological station (1850 m a.s.l.; TN). Years with values over the mean for the observation period are shown in grey. (C) Days with snow cover (grey, scale on the left) and mean thickness of snow cover from November to May (black, scale on the right; cm) at the Passo del Tonale meteorological station.

events. In the middle and lower parts of the channels, EBL is thick (generally more than 50 cm) and mainly formed by boulders with a scarce sandy matrix. The clast sets forming the levees are clearly imbricated (Fig. 2).

2.3. *Sampling*

The composite channels on which we carried out the vegetation surveys were chosen on the basis of the following

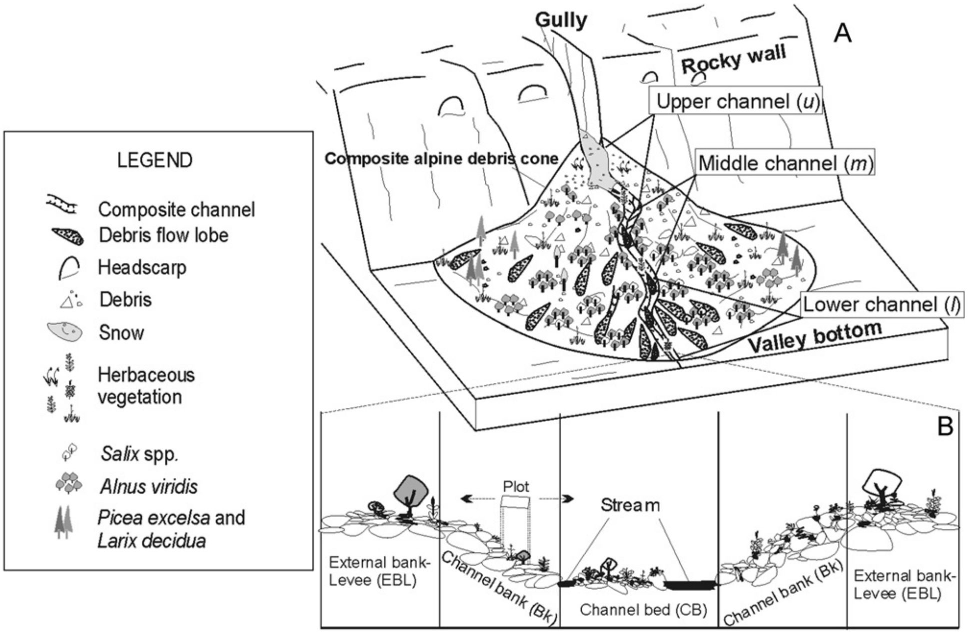

Fig. 2. (A) Geomorphologic and vegetation features of a composite alpine debris cone. (B) Transversal section of a channel showing the three main subunits.

criteria: (a) high frequency and activation degree of geomorphologic processes and (b) location in the subalpine belt. The vegetation sampling was conducted from July to September in 2004, 2005 and 2006.

To evaluate the vegetation modifications along the composite channels of the Adamello-Presanella Group, twenty-one transects on seven channels were surveyed (three transects per channel) (Table 2) at elevations ranging from 2370 to 1560 m; one channel was in Valle dell'Avio, three were in Val di Fumo, two were in Val Narcanello, and one was in Val Presena (Fig. 1A). The transects were carried out in the upper (*u*), middle (*m*) and lower (*l*) portions of the channels following the longitudinal and transversal (CB, Bk, EBL) subdivisions proposed by Baroni et al. (2007) for alpine cones. Each transect was divided into equal-sized contiguous plots of 50 × 50 cm for each meter, in which presence/absence of species were recorded, and then allocated to geomorphologic subunits (Raffl and Erschbamer, 2004). As highlighted by Tamás et al. (2001), the presence/absence scale is particularly suitable for the floristic approach in which interest is focused on species list for landscape units or sample plots.

2.4. Data analysis

In total, 387 floristic plots were surveyed, 142 of which were not colonised by plants (Table 1). A frequency table was built with the floristic matrix (Table 2).

A canonical correspondence analysis (CCA) ordination was carried out for the 57 most frequent species in the surveyed plots with respect to selected environmental variables. Dominant channel gradients, such as elevation, distance down the channel and horizontal distance from the centre of the channel (Table 2), were evaluated. To minimise the diminution of the channel width with altitude, the product of the two variables, down-channel and horizontal distances, was included (van Coller et al., 2000). The distance down the channel (i.e. distance from the cone-head; Fig. 2) was indicated as follows: upper channel, value 1; middle channel, value 3; lower channel, value 5.

For the ecological characterization of the channel sites, Landolt's average indicator values (Landolt, 1977) for soil nutrient (*N*), soil moisture (*F*) and dispersion (*D*; i.e: grain size) were also included in the CCA analysis. The Monte Carlo permutation test was performed in order to assess both the significance of the environmental variables and the ordination axes (forward selection under CANOCO output). The rare species (under a frequency of 6) was not included in the multivariate analysis. The software employed for the ordination of the plots was CANOCO version 4.5 (Lepš and Šmilauer, 2003).

The floristic matrix, ordered according to the landform subunits, was analysed for assessing the diversity variations on the base of three characteristics: alpha diversity, beta diversity and gamma diversity (Whittaker, 1972; Williams et al., 2003). The alpha diversity (it measures differences in species diversity within particular units, areas or habitats) was measured as the mean number of species registered in the plots for each landform-vegetation subunit. The beta diversity (it measures differences in species diversity across units, areas or habitats) was described using the mean of Jaccard's coefficient. Differences in the alpha and beta diversities (Jaccard's coefficient) were tested using non-parametric methods (e.g. Kruskal–Wallis test). The gamma diversity (it measures differences in species diversity over different ecosystems or habitats within a region) was calculated as the total number of species recorded in each subunit of the channel within the survey area. The observed gamma diversity was defined using the presence–absence estimator *Mao Tau* (Colwell et al., 2004) and by calculation of "species accumulation curves" from the species lists, with 95% confidence intervals for each channel subunit using EstimateS 7.5.0 software (Colwell, 2005). The Michaelis–Menten formula was used to estimate the total number of species per subunit (Raaijmakers, 1987).

2.5. Nomenclature

All species are named according to Pignatti (1982). The seed dispersal strategies cited in the text and tables follow Müller-Schneider (1986).

Table 1
Distribution and number of vegetation and empty plots per channel subunit, in the upper, middle and lower portions. Mean altitude and main exposure are also shown for each channel.

Upper channel

	Fumo 1	Fumo 2	Fumo 3	Narcanello 1	Narcanello 2	Presena	Avio	Mean	Sd
Mean altitude (m)	2370	2350	2300	2050	2020	1985	1705	2111	242
Exposure	W	E	W	N	SW	N	NW		
Empty plots									
Channel bed	6	4	2	10	3	9	12		
Bank	7	0	3	1	1	0	4		
External bank-levee	2	0	1	1	1	0	1		
Plots with plants									
Channel bed	0	3	2	4	0	0	0		
Bank	3	4	9	2	7	15	13		
External bank-levee	1	3	4	3	5	4	6		

Middle channel

	Fumo 1	Fumo 2	Fumo 3	Narcanello 1	Narcanello 2	Presena	Avio	Mean	Sd
Mean altitude (m)	2290	2275	2240	1985	1980	1940	1620	2047	241
Exposure	W	E	W	N	SW	N	NW		
Empty plots									
Channel bed	6	2	2	5	3	9	8		
Bank	6	0	2	0	0	0	5		
External bank-levee	0	1	1	0	0	0	0		
Plots with plants									
Channel bed	0	3	2	2	0	2	6		
Bank	2	6	6	4	7	7	9		
External bank-levee	4	3	3	4	5	5	4		

Lower channel

	Fumo 1	Fumo 2	Fumo 3	Narcanello 1	Narcanello 2	Presena	Avio	Mean	Sd
Mean altitude (m)	2210	2190	2175	1940	1930	1850	1560	1979	235
Exposure	W	E	W	N	SW	N	NW		
Empty plots									
Channel bed	6	0	1	1	1	4	5		99
Bank	0	0	0	0	0	0	3		32
External bank-levee	1	0	0	0	0	0	2		11
Tot. empty plots									142
Plots with plants									
Channel bed	0	1	2	2	2	5	3		39
Bank	3	5	3	4	9	8	6		132
External bank-levee	3	3	2	2	4	3	3		74
Tot. plots with plants									**245**
Total plots									**387**

3. Results

3.1. Floristic patterns

In total, 126 species were found within the channels. Most of them were occasional and were found only once (39 species) or twice (13 species). The most frequent species along the channels, with a presence in more than 50 plots (out of a total of 245 plots with plants), were *Agrostis schraderana* (37.5%), *Alnus viridis* (35.1%), *Luzula alpino-pilosa* (24.1%), *Rumex scutatus* (22.5%) and *Poa alpina* (21.6%).

Most of the empty plots were surveyed in the channel bed units (particularly in the upper channel). In the vegetation plots of this unit (CB_*u*) only two species showed a high frequency of occurrence: *Epilobium fleischeri* and *Saxifraga stellaris* (Table 1, 2).

On the contrary, in the bank subunits (particularly in the Bk_*u*), many species had frequency values of at least 30%, showing a high specificity, such as *Arabis alpina*, *Cardamine resedifolia*, *Cirsium spinosissimum* (53.8%), *Linaria alpina* (57.9%), *L. alpino-pilosa*, *P. laxa*, and *Silene exscapa*. Also, in the external bank/levee subunits, several species with high frequencies were present, including *Juncus trifidus*, *P. glauca*, *Polygonum viviparum*, *Rubus idaeus* and *Salix helvetica*.

In the Bk and EBL subunits, the number of empty plots progressively decreased. The plots without plants also decreased from the upper to lower channel regions (Table 1).

3.2. Ecological gradients

CCA ordination (Fig. 3) was used to verify relationships between the distributions of the 57 most frequent species in the study area with respect to the dominant channel gradients: altitude, horizontal distance from the centre of the stream, longitudinal distance down the channel, product between horizontal and down-channel distances, soil nutrient (*N*), soil moisture (*F*) and dispersion value (*D*).

The CCA ordination resulted in medium eigenvalues and low cumulative percentage variances of the species data (Table 4), which are indicative of a noisy data set (high number of plot). The Monte Carlo permutation test indicated statistically significant eigenvalues for the ordination axes (p=0.001, with 999 permutations). The biplot of the first two axes, accounting for 56.5% of this variance, highlights the distribution of the selected species relative to the variables (Table 3A). Moreover, there were strong species/environment relationships with all four axes, which together accounted for 82.9% of the variance explained by the environmental data. The Monte Carlo permutation test indicated that the effects of the environmental variables are highly significant (p=0.001 for all ones, with 999 permutations). In particular, the factors explaining most of the variance (highest fitness: Table 3B) were the nutrients (*N*; lambda=0.47), soil moisture (*F*; lambda=0.28), altitude (Alt; lambda=0.23) and grain size (*D*; lambda=0.23).

The CCA diagram ordinated the species due to altitude (Alt) and nutrient (*N*) availability along the first axis (Fig. 3). The second axis indicated a main gradient in the soil moisture (*F*). Herbaceous pioneer species (*L. alpino-pilosa*, *Oxyria digyna*, *P. laxa*, *Doronicum clusii*, etc.) within the channels correspond to an increase in altitude and soil moisture gradients; they were mainly found along the positive axis 1. The stands characterized by a higher gradient of nutrients (*N*) correspond to shrub and megaforb species (*A. viridis*, *E. angustifolium*, *S. appendiculata*, *Senecio nemorensis*).

Grassland species and more thermophilous species (*Carduus carlinaefolius*, *S. rupestris*, *Thymus polytrichus Trifolium pratense*,

Table 2

Floristic table reporting the frequency of the species in the channel subunits and the values table according to the main channel characteristics. Abbreviations for seed dispersal strategies (for terminology see (Vittoz and Engler, 2007): Ab=anemochory-boleochory; Am=anemochory-meteorochory; Ac=anemochory-chamaechory; AU_bal=autochory (ballistic); Zep=epizoochory; Zen=endozoochory; Hb=hydrochory-bythisochory; *X*=undefined.

N	**Abbrev.**	**Species**	**Channel Bed_*u***	**Channel Bed_*m***	**Channel Bed_*l***	**Bank_*u***	**Bank_*m***	**Bank_*l***	**External Bank_*u***	**External Bank_*m***	**External Bank_*l***	**Mean Altitude**	**SD**	**MIN**	**MAX**	**Mean dist. downch.**	**SD**	**Mean horiz. dist.**	**SD**	**Dist. downch. X horiz. dist.**	**Seed dispersal**
			Percent frequency values								**Altitude values**					**Distance values**					
92	Agr_sch	*Agrostis schraderana* Becherer	0	7.6	6.5	14.1	23.9	17.4	5.4	10.9	14.1	1909	247	1550	2275	3.4	1.5	6.6	4.2	22.2	Am
86	Aln_vir	*Alnus viridis* (Chaix) DC.	0	5.8	7.0	5.8	22.1	19.8	8.1	17.4	14.0	1808	172	1550	2010	3.5	1.4	7.6	4.1	27.0	Am/Hb
59	Luz_alp	*Luzula alpino-pilosa* (Chaix) Breist.	15.3	11.9	6.8	**33.9**	11.9	6.8	11.9	1.7	0	2118	184	1600	2370	2.1	1.5	4.4	2.9	9.0	Zen
54	Rum_scu	*Rumex scutatus* L.	0	9.3	5.6	**33.3**	13.0	18.5	13.0	5.6	1.9	1829	152	1550	2010	2.6	1.7	7.4	4.5	19.3	Am/Zd
53	Poa_alp	*Poa alpina* L.	1.9	5.7	5.7	**30.2**	15.1	13.2	7.5	9.4	11.3	2049	218	1600	2330	2.8	1.7	5.3	3.4	14.8	Am
44	Car_res	*Cardamine resedifolia* L.	6.8	6.8	2.3	**40.9**	15.9	6.8	11.4	9.1	0	2043	222	1600	2330	2.0	1.3	5.5	3.4	11.1	AU_bal
38	Leu_alp	*Leucanthemopsis alpina* (L.) Heyw.	0	7.9	10.5	**31.6**	18.4	13.2	2.6	7.9	7.9	2042	210	1600	2330	2.9	1.6	5.0	3.2	14.7	Ab/Hb
37	Dor_clu	*Doronicum clusii* (All.) Tausch	2.7	8.1	0	16.2	24.3	5.4	13.5	18.9	10.8	2185	131	1940	2330	2.7	1.4	5.4	2.9	14.5	Am
29	Peu_ost	*Peucedanum ostruthium* (L.) Koch	0	0	10.3	20.7	17.2	17.2	13.8	10.3	10.3	1864	207	1600	2300	3.1	1.7	8.3	4.7	25.5	Am
28	Agr_rup	*Agrostis rupestris* All.	0	10.7	0	21.4	25.0	10.7	7.1	25.0	0	1990	290	1600	2370	2.6	1.2	6.8	4.0	17.9	Am/Hb
28	Sal_app	*Salix appendiculata* Vill.	0	10.7	7.1	0	7.1	28.6	7.1	21.4	17.9	1684	172	1550	2010	3.9	1.3	8.1	4.6	31.7	Am
28	Sal_hel	*Salix helvetica* Vill.	0	0	3.6	0	10.7	10.7	25.0	**32.1**	17.9	2127	145	1940	2300	3.1	1.5	6.8	3.4	21.3	Am
27	Ade_leu	*Adenostyles leucophylla* (Willd.) Rchb.	0	3.7	0	29.6	22.2	11.1	22.2	11.1	0	2140	131	1985	2300	2.2	1.4	6.1	3.4	13.3	Am
24	Cer_uni	*Cerastium uniflorum* Clairv.	12.5	20.8	12.5	16.7	16.7	8.3	4.2	8.3	0	2071	258	1600	2370	2.8	1.5	4.5	3.2	12.3	Ab/c
22	Ant_alp	*Anthoxanthum alpinum* Love et Love	0	9.1	4.5	27.3	22.7	18.2	0	0	18.2	1950	281	1600	2275	3.3	1.7	5.8	4.3	18.8	Am/Zen
22	Leo_hel	*Leontodon helveticus* Merat	0	4.5	4.5	18.2	13.6	9.1	18.2	9.1	22.7	2170	127	1940	2330	3.0	1.7	5.9	3.6	17.7	Am
22	Oxy_dig	*Oxyria digyna* (L.) Hill	22.7	13.6	4.5	27.3	9.1	4.5	0	18.2	.	2029	220	1550	2370	2.2	1.3	5.1	3.0	11.2	Am
20	Epi_ang	*Epilobium angustifolium* L.	0	5.0	10.0	0	15.0	**30.0**	0	15.0	25.0	1766	182	1550	1980	4.3	1.0	7.1	4.2	30.4	Am
19	Lin_alp	*Linaria alpina* (L.) Miller	5.3	0	0	**57.9**	21.1	0	10.5	0	5.3	1959	245	1600	2300	1.6	1.2	7.1	4.2	11.5	Ab/Hb
18	Rho_ros	*Rhodiola rosea* L.	0	11.1	5.6	16.7	11.1	11.1	27.8	11.1	5.6	1777	171	1550	2050	2.6	1.6	10.3	4.6	26.4	X
18	Rub_ida	*Rubus idaeus* L.	0	0	11.1	0	0	27.8	5.6	22.2	**33.3**	1884	62	1700	1940	4.3	1.2	8.1	3.0	35.1	Zen
18	Sen_nem	*Senecio nemorensis* L.	0	5.6	5.6	0	5.6	**50.0**	16.7	5.6	11.1	1801	183	1550	1985	4.0	1.6	7.4	3.3	29.6	Am
16	Gal_ani	*Galium anisophyllum* Vill.	0	12.5	0	12.5	6.3	25.0	18.8	12.5	12.5	1841	185	1600	2235	3.1	1.7	7.7	5.5	23.9	Zep
16	Lig_mut	*Ligusticum mutellina* (L.) Crantz	0	6.3	0	18.8	18.8	31.3	0.0	0	25.0	2139	138	1940	2275	3.8	1.6	4.1	3.0	15.2	Zen
15	Ach_mos	*Achillea moschata* Wulfen	0	0.0	0	20.0	**33.3**	6.7	26.7	13.3	0	2266	38	2175	2300	2.2	1.3	6.2	2.9	13.6	Ab
15	Cal_vil	*Calamagrostis villosa* (Chaix) Gmelin	0	.	6.7	0	13.3	26.7	26.7	13.3	13.3	1913	63	1850	1985	3.4	1.7	8.8	3.2	30.0	Am
15	Thy_pol	*Thymus polytrichus* Kerner	0	6.7	0	20.0	13.3	6.7	26.7	20.0	6.7	1778	176	1600	2010	2.3	1.4	9.8	5.3	22.8	Am

Table 2 (*continued*)

N	**Abbrev.**	**Species**	**Channel Bed_*u***	**Channel Bed_*m***	**Channel Bed_*l***	**Bank_*u***	**Bank_*m***	**Bank_*l***	**External Bank_*u***	**External Bank_*m***	**External Bank_*l***	**Mean Altitude**	**SD**	**MIN**	**MAX**	**Mean dist. downch.**	**SD**	**Mean horiz. dist.**	**SD**	**Dist. downch. X horiz. dist.**	**Seed dispersal**
			Percent frequency values									**Altitude values**				**Distance values**					
14	Ara_alp	*Arabis alpina* L.	7.1	7.1	0	**35.7**	21.4	21.4	0	0	7.1	1889	148	1600	2050	2.7	1.7	5.2	2.8	14.1	Ab/Hb
14	Lot_alp	*Lotus alpinus* DC. Schleicher	0	0	0	**35.7**	0	28.6	14.3	0	21.4	2017	197	1700	2235	3.0	2.1	5.7	4.1	17.1	AU_bal
14	Sed_alp	*Sedum alpestre* Vill.	0	0	0	28.6	14.3	7.1	28.6	7.1	14.3	2271	84	2010	2330	2.3	1.7	5.8	1.9	13.2	Ab/Hb
13	Cir_spi	*Cirsium spinosissimum* (L.) Scop.	0	0	0	7.7	23.1	**53.8**	7.7	0	7.7	2165	144	1940	2330	3.9	1.6	3.2	2.4	12.4	Am/Zd
13	Sil_aca	*Silene acaulis* (L.) Jacq.	0	23.1	0	**38.5**	7.7	7.7	15.4	7.7	0	2067	321	1600	2370	2.1	1.3	5.7	3.0	11.8	Ab
12	Pet_alb	*Petasites albus* (L.) Gaertn.	0	0	16.7	16.7	16.7	25.0	0	8.3	16.7	1588	57	1550	1700	3.8	1.6	7.8	4.0	29.7	Am
11	Eup_ros	*Euphrasia rostkoviana* Hayne	0	0	9.1	18.2	0	27.3	18.2	18.2	9.1	2110	258	1550	2300	3.2	1.9	6.7	4.5	21.3	Ab
11	Sax_bry	*Saxifraga bryoides* L.	0	0	18.2	27.3	18.2	0	**36.4**	0	0	2186	232	1550	2300	2.1	1.6	5.9	3.2	12.4	Ac
11	Tri_pra	*Trifolium pratense* L.	0	0	0	18.2	27.3	27.3	9.1	18.2	0	1918	111	1700	2010	3.0	1.5	5.9	4.7	17.6	Am/Zen
10	Poa_gla	*Poa glauca* Vahl	0	0	0	20.0	20.0	10.0	0	**40.0**	10.0	1819	152	1600	1985	3.0	1.3	9.6	3.2	28.8	Zep
9	Cam_sch	*Campanula scheuchzeri* Vill.	0	0	0	11.1	11.1	22.2	**33.3**	11.1	11.1	1898	115	1700	1985	2.8	1.9	9.7	5.0	27.0	Ab
9	Sax_asp	*Saxifraga aspera* L.	0	0	0	22.2	22.2	11.1	**44.4**	0	0	2030	249	1700	2370	1.9	1.5	7.7	4.7	14.5	Ab/Hb
8	Epi_fle	*Epilobium fleischeri* Hochst.	0	**37.5**	12.5	0	**37.5**	0	0	0	12.5	1630	127	1550	1940	3.5	0.9	5.4	4.1	19.0	Am/Hb
8	Jun_tri	*Juncus trifidus* L.	0	0	0	25.0	0	0	**50.0**	25.0	0	2258	101	2010	2300	1.5	0.9	8.2	1.7	12.3	Am
8	Poa_lax	*Poa laxa* Haenke	12.5	12.5	0	**50.0**	12.5	0	12.5	0	0	2196	159	1985	2330	1.5	0.9	5.3	2.6	8.0	Am
8	Sax_ste	*Saxifraga stellaris* L.	**37.5**	25.0	25.0	0	0	12.5	0	0	0	2074	267	1550	2330	3.0	1.9	2.3	1.0	6.9	Ab/Hb
8	Vio_bif	*Viola biflora* L.	0	0	0	12.5	0	**37.5**	12.5	25.0	12.5	1924	72	1850	2050	3.5	1.8	8.4	3.0	29.5	AU_bal
7	Cha_hir	*Chaerophyllum hirsutum* L.	0	0	0	**42.9**	0	0.0	28.6	14.3	14.3	1808	136	1700	1985	1.9	1.6	11.9	3.3	22.0	Ab
7	Pol_viv	*Polygonum viviparum* L.	0	0	14.3	0	0	**42.9**	0	0	**42.9**	2108	115	1940	2175	5.0	0.0	2.5	1.3	12.5	Am
7	Sax_pan	*Saxifraga paniculata* Miller	0	0	14.3	28.6	28.6	14.3	0	0	14.3	1761	208	1550	2010	3.3	1.8	6.6	4.3	21.8	Ab
6	Myo_alp	*Myosotis alpestris* F. W. Schmidt	0	0	0	**50.0**	0	**33.3**	16.7	0	0	2025	199	1700	2235	2.3	2.1	7.3	5.3	16.9	Ab/c
6	Sil_rup	*Silene rupestris* L.	0	0	0	0	**33.3**	**33.3**	16.7	16.7	0	1910	105	1700	1980	3.3	1.5	6.1	4.8	20.3	Ab
5	Car_car	*Carduus carlinaefolius* Lam.	0	0	0	20.0	20.0	0	**60.0**	0	0	1680	45	1600	1700	1.4	0.9	13.9	3.6	19.5	Am
5	Cer_fon	*Cerastium fontanum* Baumg./arvense	0	0	0	20.0	20.0	**40.0**	20.0	0	0	1972	193	1700	2240	3.0	2.0	6.3	4.3	18.9	Ab
5	Hie_lac	*Hieracium lachenalii* Gmelin	0	0	0	**60.0**	0	0	**40.0**	0	0	1700	0	1700	1700	1.0	0.0	13.9	2.1	13.9	Am
5	Sax_aiz	*Saxifraga aizoides* L.	0	20.0	**40.0**	20.0	20.0	0	0	0	0	1832	197	1550	1985	3.4	1.7	3.0	1.2	10.2	Ab/Hb
5	Sax_opp	*Saxifraga oppositifolia* L.	0	20.0	0	20.0	20.0	0	0	**40.0**	0	1697	167	1600	1985	2.6	0.9	9.2	5.9	23.9	**Ab/Hb**
5	Sil_vul	*Silene vulgaris* (Moench) Garcke	0	20.0	0	0	20.0	**40.0**	20.0	0	0	1828	168	1600	1980	3.4	1.7	4.8	6.6	16.3	Ab
5	Tha_aqu	*Thalictrum aquilegifolium* L.	0	**40.0**	0	20.0	20.0	0	20.0	0	0	1640	55	1600	1700	2.2	1.1	8.7	7.2	19.1	Am
5	Ver_alp	*Veronica alpina* L.	0	20.0	0	20.0	20.0	20.0	0	20.0	0	2082	244	1700	2275	3.0	1.4	5.2	5.2	15.6	Ab/ZM

Note (a): species with a presence under the value 5 were omitted.
Note (b): frequency values over 30% are written in bold.

etc.) corresponded to a decrease in the soil moisture (along second axis) and to an increase in the horizontal distance from the centre of the channel.

In regards to the seed dispersal strategies of the species (symbols in diagram), we found that: (a) the "Am" strategy and other strategies did not show particular trends with respect to the channel gradients; (b) the "Ab" and Ab/Hb strategies corresponded with a decrease in the nutrients and with an increase in the altitude and grain size gradients.

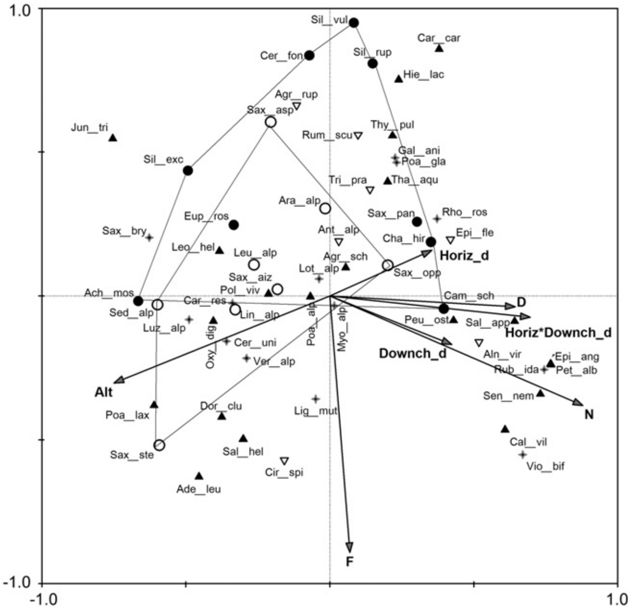

Fig. 3. CCA ordination showing the 57 most frequent species (abbreviated plant names) and related seed dispersal categories (signatures) scored with respect to the dominant riparian gradient: Alt=Altitude; Horiz_*d*=Lateral distance from water table; Downch_*d*=distance down channel; *N*=nutrients; *F*=soil moisture; *D*=dispersion (i.e. grain size). For species abbreviations, see Table 3. Symbols for dispersal ability: (1) black filled circle: Ab; (2) white, empty circle: Ab/Hb; (3) black filled, upright triangle: Am; (4) white, empty, down-oriented triangle: Am/others; (5) plus sign: others. Ab and Ab/Hb symbols are distributed in spaces enclosed by connecting lines.

3.3. Biodiversity

3.3.1. Alpha diversity

Species richness calculated for the channel subunits showed a greater number of species on average in those levee subunits which are more stabilized and less disturbed than others. In contrast, a scarce number of species was found in the CB_*u* subunit (0.5), which represents the most active surface (Table 4). Comparisons of the different plant assemblages among all the channel subunits by means of the Kruskal–Wallis test showed significant differences between the mean numbers of species in the different subunits ($p < 0.01$).

3.3.2. Beta diversity

Jaccard's coefficients of similarity, calculated for each pair of vegetation plots within each channel subunit, showed that the CB_*u* subunits had higher values (i.e. samples were more uniform) than the other channel subunits. Differences in Jaccard's coefficients between the channel subunits, which were estimated with the Kruskal–Wallis test, were highly significant ($p < 0.01$).

3.3.3. Gamma diversity

The highest level of gamma diversity was in the EBL_*u* subunit, which had 67 species in total, representing 53.2% of the regional diversity (with 12 exclusives species). The values of the channel banks were also high compared to other zones; the CB_*u* subunit revealed the minimum value, with 11 species representing 8.7% of the regional diversity, with zero exclusive species.

To estimate the effectiveness of the survey, "species accumulation curves" (*Mao Tau* function) were fitted (Fig. 4). The curve showing the number of species observed in the plots (per subunit) was logarithmic and did not reach a plateau. These data clearly suggested that regional diversity is not completely revealed in any channel subunit. As an alternative, the Michalis–Menten equation (Colwell et al., 2004) was applied to the data set to estimate the species richness (Table 4). The estimator predicted the maximum value of total species richness in the EBL_*u* subunit (106.8 species) and the next highest value in the Bk_*l* subunit (87.5). The minimum value of total richness was expected in CB_*u* (15.1), with a small difference with respect to the observed number of species (11).

Table 3
(A) Summary of canonical correspondence analysis (CCA) for the 57 most frequent species; (B) environmental variables ordered according to their importance (lambda value, i.e. effectiveness).

Axes	1	2	3	4	Total inertia
(A)					
Eigenvalues	0.525	0.325	0.252	0.146	8.753
Species–environment correlations:	0.929	0.895	0.851	0.745	
Cumulative % variance of species data	6	9.7	12.6	14.3	
Cumulative % variance of species-environment relation:	34.9	56.5	73.2	82.9	
Sum of all eigenvalues					8.753
Sum of all canonical eigenvalues					1.505
(B)					
	Conditional Effects				
Variable	Var. *N*	Lamb	*P*	*F*	
N	6	0.47	0.001	13.59	
F	5	0.28	0.001	8.71	
Alt	1	0.23	0.001	7.4	
D	7	0.23	0.001	6.95	
Horiz × Downch_*d*	4	0.12	0.001	3.6	
Horiz_*d*	2	0.07	0.001	2.54	
Downch_*d*	3	0.1	0.001	3.27	

Table 4
Alpha, beta and gamma diversity (calculated and predicted). Greater diversity values are indicated with an asterisk. Abbreviations: CB_*u*, CB_*m*, CB_*l*=upper, middle, lower channel bed; Bk_*u*, Bk_*m*, Bk_*l*=upper, middle, lower channel bank; EBL_*u*, EBL_*m*, EBL_*l*=upper, middle, lower external bank/levee.

	CB_*u*	**Bk_*u***	**EBL_*u***	**CB_*m***	**Bk_*m***	**EBL_*m***	**CB_*l***	**Bk_*l***	**EBL_*l***
***N*plot**	11	53	26	15	41	28	13	38	20
Empty plot	47	15	6	35	13	2	18	3	3
Alpha diversity (mean)	0.5	3.7	5.1*	1.7	3.6	4.6	1.9	4.9	5.2*
Sd	1.3	2.8	3.8	3.2	2.6	2	2.6	2.5	2.7
Beta diversity (Jaccard)	0.332	0.097	0.067*	0.105	0.104	0.097	0.082*	0.091	0.142
Sd	0.159	0.123	0.102	0.128	0.118	0.120	0.113	0.129	0.136
Gamma diversity	11	57	67*	39	56	48	32	62*	45
Percentage of the regional diversity	8.7	45.2	53.2	31	44.4	38.1	25.4	49.2	35.7
Unique species	0	3	12	5	4	3	1	8	3
Expected gamma diversity (Michaelis–Menten evaluator)	15.1	72.1	106.8*	65	76.8	71.3	59.4	87.5*	67.4

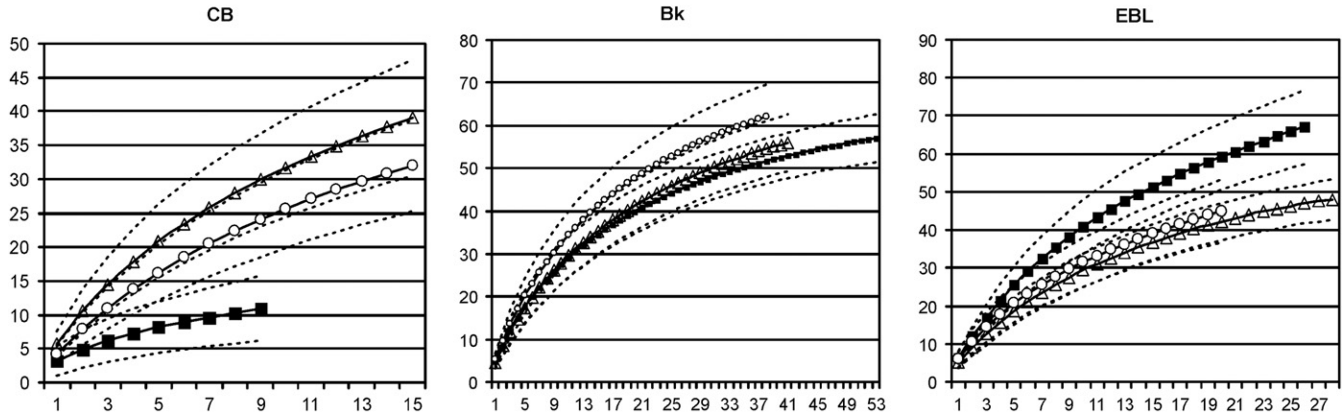

Fig. 4. Accumulation curves for plant species from the nine landform subunits. Dotted lines represent 95% confidence intervals. Symbols: (1) black square: upper channel; (2) white triangle: middle channel; (3) white circle: lower channel.

4. Discussion

Floristic analyses showed that the channels were strongly dominated by few species: *A. schraderana*, *A. viridis*, *L. alpinopilosa*, *R. scutatus* and *P. alpina*. In the whole channel system, *A. schraderana* played the role of the dominant/ubiquitous species with weak relationships with the geomorphologic disturbance: the species was not found only in the CB_*u*, which is the most disturbed subunit.

Nevertheless, our results (both frequency table and CCA) evidenced that the composite channels in the study area showed considerable floristic heterogeneity (126 species in total) and different gradients of biodiversity (alpha, beta and gamma diversities) according to channel niches. The most likely mechanism responsible for such patterns is environmental heterogeneity associated with channel subunits. These are a consequence of the complex interaction occurring between the geomorphologic processes (i.e. disturbance due to debris flow, snow avalanche, running water and rock/debris fall), resulting in a variety of erosive and depositional events (Baroni et al., 2007), and ecological factors (Gould and Walker, 1999). An increase in elevation or greater distance downstream or from the water table can be marked by a change in geomorphological features, followed by changes in nutrient availability and soil moisture with continuum variations in species composition along the channels (van Coller et al., 2000).

4.1. Floristic patterns and ecological gradients

Toward the upper channel and the channel bed (CB_*u*) the geomorphic processes are more active due to high disturbances of running water, snow avalanches and long-lasting snow cover. In such areas vegetation cover is scarce or void with an increase in empty plots (Nakamura et al., 2002). In the upper channel bed, only plant species can grow that are well adapted to very poor (i.e. scarcity of nutrient) and humid soils (*F*) and able to resist mechanical disturbance. In this unfavorable environment, plants can be found with ruderal character, adopting pioneer strategies, and successfully colonizing unstable/mobile debris (Caccianiga et al., 2006). These include in particular *Adenostyles leucophylla*, *D. clusii*, *Leucanthemopsis alpina* and *O. digyna*.

Debris flow and water turbulence periodically remove alluvium, soil patches and vegetation along corridors inducing, local or large-scale revegetational succession (Harris and Gustafson, 1993).

The disturbances progressively decreased going down the channel and levee, providing more favorable microsites for vegetation colonization. As a result, the vegetation cover tended to increase in these sites (Lyon and Gross, 2005). In particular, Landolt's nutrient indicator and the (Horizontal × Down-channel) distances appear to be correlated. Shrub and megaforb species, such as *S. appendiculata* and *E. angustifolium*, tended to grow preferentially in the lower channel (i.e. at lower altitude) and in lateral/external positions, in the absence of water turbulence and in the presence of soils with an enhanced sandy matrix (*D*) and rich in nutrients (*N*). Their presence is related to the delayed snow melting (after July), which favors the accumulation of fine sediments retained in the snow cover (Butler, 2001).

At lower altitude, the shrub species (*A. viridis*, *S. appendiculata* and *S. helvetica*) contributed to creating microenvironments for herbaceous species and to increasing diversity in these habitats. Moreover, isolated individuals of ruderal pioneer species could grow in microhabitats between masses in EBL_*u* and EBL_*m*. On the other hand, some shrub species (*A. viridis* and *S. appendiculata*) acted as pioneer species in the lower portion of the channels and close to the streams.

More thermophilous species (*Galium anisophyllum*, *Rhodiola rosea* and *T. serpyllum* s.l.) grew preferably toward the highest values of the horizontal distance on the EBL subunits.

Anemochory was the main method of dispersal in the context of the channels. The "Am" dispersal strategy (anemochory-meteorochory, i.e. seeds with hairy appendages or fly structures) was ubiquitous in the context studied herein. Our results suggest that this strategy seems to be partially substituted by the "Ab" strategy (anemochory-boleochory, small seeds without particular features are spread when the fruit is shaken by wind) in areas with lower nutrient availability and towards upper altitudes. By this way seeds are generally dispersed only over short distances (Soons and Ozinga, 2005). This trend appears to be in accordance with Erschbamer et al. (2001) and Caccianiga et al. (2006). A lot of pioneer species, mainly colonizing the upper channel, displays strong ruderal characteristics and arrived there probably via short-distance anemochory. However, in this geomorphological structures flood (hydrochory) and debris flow are also very important seed dispersal factors (Jentsch and Beyschlag, 2003; Watterson and Jones, 2006), and snow avalanches and rock fall events play a role for plant propagation as well. Seeds, spores and seedlings are transferred through water flow or snow movements, deposited on mass (rock fall) surfaces downstream the course of a channel (Butler, 2001). Seed dispersal by geomorphological processes, scarcely considered in most of the seed dispersal studies in alpine environments, favor probably mainly the colonization spread of high alpine species which generally grow in the glacial foreland at lower altitudes, for instance *L. alpina*, *L. alpino-pilosa*, *O. digyna*, *P. laxa*, *Ranunculus glacialis S. bryoides*, and *S. oppositifolia* (Caccianiga and Andreis, 2004; Raffl et al., 2006). Therefore, composite channels in the alpine regions act as biological corridors that connect alpine, subalpine and often high mountain areas, and act as conduits for many species, because locally long-lasting snow cover at low altitude, following avalanches, reduces reasonably the growing season (Baroni et al., 2007).

In fact, a large portion of the alpine flora of the Alps is restricted to azonal habitats, especially rocks, scree and snowbeds, which represent abnormal habitats created by disturbances (Grabherr et al., 1995; Keller et al., 2005). We deem that a great variety of such plant habitats are concentrated within composite channels: (a) due to the presence of debris deposits with heterogeneous sedimentological characteristics: masses and boulders, blocks, sands, soil patches, etc., that create micro-topographical niches; (b) for the presence of channel areas with different snow cover duration (longer in the upper zones); (c) for strong differences in the soil moisture (higher in the CB). According to Gottfried et al. (1998) high-altitude specialist plants (like *Androsace alpina*), if widespread are able to reach such habitats as refugia. On the other hand, rare/uncommon species more probably may become extinct on some mountains following climatic changes (Keller et al., 2005).

4.2. *Biodiversity*

The alpha diversity (richness) increased downstream from upper to lower channel parts in two different manners: (a) progressively along the CB subunit (Table 4) and (b) with a minimum value in the middle sector along Bk and EBL. This tendency probably reflects the general feature of alpha diversity to decrease along an altitudinal gradient in high mountain environments (Norgués-Bravo et al., 2008) and accordingly to follow an improvement of environmental conditions and deposit stability. Nevertheless, the considerable presence of a sandy matrix among clasts and blocks in the Bk_*u* and EBL_*u* compared to Bk_*m* and EBL_*m* probably favors the colonization by a higher number of species in the upper sector (Baroni et al., 2007), partially going against this general tendency. A positive trend in the species richness along the channel sections was observed from CB to EBL ($CB < Bk < EBL$). This suggests a more stable condition along the EBL and Bk subunits than the CB subunit.

The beta diversity according to Jaccard's indexes (intra-habitat variability) did follow neither a longitudinal down-channel nor a transversal trend from CB to EBL. Spatial factors in composite channels can support the reciprocal exchange of species at the boundary among habitats (i.e. geomorphological units and subunits), thereby enhancing the beta diversity (Gould and Walker, 1999). In fact, the highest values of Jaccard's index, found in the EBL_*u* and CB_*l* subunits, are located in subunits at the border between different landforms. Moreover, EBL_*u* is located among channel banks, rocky walls above cone-heads, bedrock gullies above the channel and in deposits of composite alpine debris cones (Baroni et al., 2007). This area is enriched by alpine grassland species that occurred only in one relevé plot, like *Achillea distans*, *Gentiana lutea*, *L. spicata* and *Trifolium alpinum*.

The observed gamma diversity (regional diversity) did follow neither a longitudinal down-channel nor a transversal trend from CB to EBL, as expected. On the contrary, the expected gamma diversity did follow a trend similar to the alpha diversity. This indicates that channels may potentially contain further diversity, as evidenced by the species accumulation curves. Our results revealed that EBL_*u* had the highest values of diversity, the highest number of unique species and more than 50% of the gamma local diversity (Table 4).

As described by previous authors (van Coller et al., 2000), the heterogeneity in species composition among channel subunits probably depends on a combination of environmental variables, such as the spatial position of a subunit, elevation with respect to the water table, variation in grain size, presence of refuge areas and soil patches and increasing landform age. Similarly to what happens in the avalanche tracks, geomorphological disturbance within composite channels can exert an important influence on the biodiversity of subalpine environments and provide important habitats (Rixen et al., 2007).

In conclusion, the composite channels in alpine ecosystems play a crucial role in the rearrangement of plant species between nival and high mountain belts. Our results suggest that in the context of the composite channels, the elevation gradient and partially the dispersal strategies control the distribution of species at the macroscale (landscape) level (Vittoz et al., 2009). The geomorphological disturbance regimes control the alternation of species at the mesoscale level, according to the landform subunits and through their effect upon the spatial distribution of erosion–deposition areas. Continuous variations in species composition, at the microsite level, seem to be governed by environmental gradients, such as nutrients, soil moisture and grain size.

The relationships between channel processes (disturbance) along the channels and microhabitat differences contribute to ecological complexity and to regional biodiversity. Diversity characteristics depend in this environment both on stability (alpha and gamma) and on heterogeneity (beta). So we are sure that composite channels could play an important refuge–habitat function both for uncommon and widely distributed species during the widely accepted current trend of global warming. Indeed, according to experimental studies and models developed, the arctic-alpine and orophytic elements are moving under this influence and will continue to move upward in elevation (Parolo and Rossi, 2008), and alpine channels can function as migration corridors. Because of their unique attributes and structure, composite channels should be constantly monitored in the future also for their role as refugia for high mountain plant diversity, as bioindicators of climatic changes, and as sites where alpine plant species can find protection and conservation.

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