Emergent geomorphic-vegetation interactions on a subalpine alluvial fan

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Abstract

Following perturbation, an ecosystem (flora, fauna, soil) should evolve as a function of time at a rate conditioned by external variables (relief, climate, geology). More recently, biogeomorphologists have focused upon the notion of co-development of geomorphic processes with ecosystems over very short through to very long (evolutionary) time-scales. Alpine environments have been a particular focus of this co-development. However, work in this field has tended to adopt a simplified view of the relationship between perturbation and succession, including: how the landform and ecosystem itself conditions the impact of a perturbation to create a complex spatial response impact; and how perturbations are not simply ecosystem destroyers but can be a significant source of ecosystem resources. What this means is that at the within landform scale, there may well be a complex and dynamic topographic and sedimentological template that co-develops with soil, flora and fauna. Here, we present and test a conceptual model of this template for a subalpine alluvial fan. We combine detailed floristic inventory with soil inventory, determination of edaphic variables and analysis of historical aerial imagery. Spatial variation in the probability of perturbation of sites on the fan surface was associated with down fan variability in the across-fan distribution of fan ages, fan surface channel characteristics and fan surface sedimentology. Floristic survey confirmed that these edaphic factors distinguished site floristic richness and plant communities up until the point that the soil-vegetation system was sufficiently developed to sustain plant communities regardless of edaphic conditions. Thus, the primary explanatory variable was the estimated age of each site, which could be tied back into perturbation history and its spatial expression due to the geometry of the fan: distinct plant communities were emergent both across fan and down fan, a distribution maintained by the way in which the fan dissipates potentially perturbing events.

Keywords

Ecosystem, Perturbation, Plant community, Alluvial fan, Emergence, Subalpine

Introduction

The important role that vegetation plays in influencing geomorphic processes has been understood and quantified for many years (see Osterkamp et al. (2012) for review). Research has clearly established that landscape change can only be understood when vegetation impacts are properly represented (e.g. Murray and Fonstad 2007) even if the vegetation cover is sparse (e.g. Osterkamp et al., 2012). Root systems play a critical role in stabilising the land surface (e.g. Schwarz et al., 2010; Stoffel and Wilford, 2012) and in reducing erosion and encouraging sediment retention (e.g. Viles et al., 2008). However, the relationship between vegetation and geomorphic processes is bi-directional and interwoven (Stallins, 2006). The time since the last effective perturbation, which may be a geomorphic perturbation, is a critical parameter in plant succession (e.g. Jones, 1980; Burga et al. 2010; Dickerson et al., 2013). However, whilst perturbation can lead to substantial ecosystem losses if of too high a magnitude, it may also provide crucial ecosystem resources. For instance, if perturbation leads to deposition, it may create substrates more or less favorable to both soil development (e.g. Lacoste and Salanon, 1969; Garcia-Arguire et al., 2007) and plant growth (e.g. Howard and Mitchell, 1985; Dickerson et al., 2013), provided the deposition rate is not too great (e.g. Viles et al., 2008). Roulier (1998) distinguishes between perturbations that rejuvenate, age or destroy ecosystems according to their magnitude. Spatial extent may also be important. A single perturbation at the small scale may allow the local return of conditions favourable to primary colonisers (Johnson and Miyanishi, 2010) at the expense of secondary or tertiary colonisers, who can otherwise out-compete primary colonisers (Cordonnier, 2004) in terms of access to light or other resources (competitive exclusion). If the landscape comprises a large number of such perturbations and they do not all occur at the same time, then the number of ecological niches may be maximized. Thus, whilst the initial impacts of a perturbation might appear to be destructive, the result may be a more complex abiotic environment that can also lead to significant spatial variability in biota.

The focus of this paper is the interactions between perturbations associated with geomorphic processes and floristic diversity on a subalpine alluvial fan. Alluvial fans are an interesting focus because they have a down fan change in the magnitude, frequency and duration of disturbance (e.g. Stoffel et al., 2008) which means that at any one time, any one location on the fan has both a certain time since it was last disturbed by an event of a given magnitude, as well as a local edaphic environment that reflects its depositional and erosional history. In this paper, we develop and evaluate a basic conceptual model for how this might determine the spatial patterns of floristic diversity in a subalpine setting, within the wider conceptual framework that geomorphic processes and ecosystems should be seen as in a state of co-evolution (Corenblit et al., 2008, 2011). The focus of our work is a subalpine alluvial fan, the Larzettes fan, in a regionally protected Nature Reserve, the Vallon de Nant, in the Vaudois Alps, Switzerland.

An a priori model for the co-development of alluvial fan surfaces and plant communities

The aim of this section is to synthesise from literature review an *a priori* model for the co-development of alluvial fan surfaces and plant communities. Alluvial fan surfaces can be considered to be a complex mosaic of topographic and sedimentary environments, largely resulting from processes of erosion and deposition (McAuliffe, 1994; Parker, 1995). The focus of this paper is Type II alluvial fans (Blair and MacPherson, 1994), those formed by water-transported sediments.

Alluvial fans commonly comprise a primary channel fed at the alluvial fan apex (e.g. Figure 1) and what appears to be a network of distributary or secondary channels. However, this appearance can be misleading as closer inspection of fan sedimentology shows that these secondary channels are more likely to reflect relict primary channels rather that constituting a truly diffusive braid network (Blair and MacPherson, 1994). In relation to floristic communities, the fan surface will record the history of the position of the primary channel, and perhaps secondary channels associated with more extreme events, as a series of topographic undulations, with potential variability in sedimentology and local drainage. These channels also have the ability to disturb floristic succession with an impact on plant communities that depends upon the magnitude and frequency of disturbance. As the form of fans is radial, the lateral space that the fan can occupy (here defined as the accommodation space) increases from the fan apex (proximal) to the distal part of the fan. In general, the greater the accommodation space, the less confined the fan channels. This is conceptualized in Figure 1, for three locations A, B and C on the dashed line extending from fan apex to fan base. Close to the fan apex, at point C, the fan is generally either occupied or unoccupied by the active channel, defined here as the one that transports water *and* sediment. This should produce durations of occupation by an active channel that are relatively long, with an associated higher magnitude intensity and greater frequency of within-channel disturbance. Processes operating at C should have implications for location B. When C is 'on' then there is a greater probability that B is occupied. But, because fans are generally dissipative systems, an event at C will only reach B if it is big enough. This translates into a more punctuated on-off regime at B, with both periodic occupation by an active channel and more variable event magnitudes, a process that is magnified further down the fan at A.

This model implies a down fan change in the magnitude and frequency of disturbance (e.g. Stoffel et al., 2008), which should be expressed in floristic communities. In the simplest sense, it will impact the time available for soil development, and hence the conditions required by certain species. But it may also impact upon competitive exclusion, by changing the availability of resources (e.g. light, water availability) necessary for plant growth. Across the fan, for a transect (e.g. C, B, Figure 1), this should translate into a very different range of times since last perturbation with transect C being associated with a bimodal distribution and B a more continual distribution. It follows that the two transects should have very different plant communities including biodiversity. In the literature, there are few observations of this effect, but on an arid environment alluvial fan surface, Dickerson et al. (2013) found that sites in the more frequently disturbed channel zones had similar plant communities that were, in turn, different to those found on older and more stable surfaces.

Figure 1 considers only time since perturbation as the variable that influences the development of plant communities. However, the dissipation of fan surface flows will also lead to a complex surface topography and sedimentology that may also influence the development of plant communities. Generally, there is a transition from the apex to the distal part of the fan in the level of primary (and secondary) channel incision. At the apex, the primary channel is incised. With distance down the fan, the level of incision in this channel decreases to what Hooke (1967) calls the intersection point, the maximum downstream extension of incision. Beyond this point, the fan generally takes the form of a depositional lobe but sometimes dissected by headward-extending gullies (e.g. Blair and Macpherson, 1994). Channel incision exerts an important down fan control on the distribution of flow, notably where flow can become distributed on the fan and supply moisture more widely. Thus, at the fan apex, there is more likely to be two extremes of flow/sediment delivery (an incised channel and a 'high and dry' surface), that evolve down fan to less extreme levels of incision and surface isolation, and a more continuous variation in topography.

Flow and sediment flux within the primary channel, and the secondary channels if active, tends to be concentrated and, if sufficiently concentrated, may form debris flows. Flow on the fan surface tends to be sheet flow, which can lead to exceptional deposition events (e.g. the 'sheet floods' of Blair, 1987) notably if the flow is hyperconcentrated, but sheet flow deposits generally involve thinner accumulations of finer sediment. Blair and MacPherson (1994) argue that alluvial fans are primarily constituted by these two kinds of deposits: channel flow and surface sheet flow; even though secondary processes may rework these deposits (e.g. neotectonics, bioturbation). Typically, because the system is dissipative, total stream power decreases downslope (e.g. Blair and MacPherson, 1994) because of both a reduction in fan surface slope but also because the channel system on the fan surface may be distributary leading to proportionally greater energy losses and lower flow velocities on the distal part of the fan. For instance, downstream hydraulic geometry relationships on alluvial fans have been shown to follow those of rivers except that because the system can be distributary, with distance down fan, the total discharge remains the same but the number of channels increases (e.g. Vincent et al., 2004). The discharge per channel falls, but it does so at a faster rate than the total channel width. This implies a down fan reduction in mean channel velocity and depth and hence reduced capacity to transport sediment. The result can be down fan sediment sorting, with coarser sediments deposited proximally and finer sediments distally (e.g. Blissenbach, 1954). The result of these processes should be spatial variation in surface grain size, notably in the proportion of fine-grained material, between channel and surface zones but also from the apex to distal parts of the fan. Reflecting Figure 1, transect C, the fan apex, is more likely to have a more restricted range of surface sedimentologies, with coarser material more dominant. At transect B, as there is a range of degrees of occupation according to the magnitude of each event, there is also likely to be a wider range of grain sizes deposited along fan surface, creating more complex spatial variability in surface sedimentology.

Surface sedimentology may have important impacts upon moisture retention capacity (e.g. Parker, 1995), and notably the speed with which a vegetation-soil system can develop. Links have been made between channels and vegetation characteristics on fan surfaces, with maximum vegetation cover and density found proximal to fan channels in arid environments (Schwinning et al., 2011). Ishida et al. (2010) showed how the spatial heterogeneity of soil moisture, created by fan topography, significantly increased plant diversity. Parker (1995) showed that this heterogeneity was systematic and could be seen in plant diversity. The form of the fan-diversity relationships should vary between environments. For instance, Parker (1995) observed a down fan decrease in plant diversity related to edaphic factors, attributing it to the fact that in the arid environment of her study, flow distribution on the fan surface means that the distal parts of the fan receive less water and are too dry to sustain certain plant communities. But similar down fan reductions in diversity could also arise from competitive exclusion effects where the increasing accommodation space reduces the magnitude and frequency of perturbations allowing certain species to become dominant. Multivariate analysis (e.g. Dickerson et al., 2013) has helped to disentangle these effects. These authors were able to identify two principle components to explain the spatial variation in floristic diversity on an arid alluvial fan: one related to age of the surface and hence its relative stability; and a second related to local edaphic conditions.

Taken together, we have identified the following hypotheses for testing:

1. that there is a down fan change in the across-fan distribution of fan ages, fan surface channel characteristics and fan surface sedimentology, which can lead to distinct across fan distributions of edaphic factors;
2. that down fan changes in the across fan distribution of age and edaphic factors leads to down fan differences in floristic richness and differentiates distinct plant communities; and
3. that the linkage between (1) and (2) is related to the way in which the fan dissipates potentially perturbing events.

Case study

The focus of this manuscript is a subalpine alluvial fan (Figure 2), just below the current tree line, in the Vallon de Nant, South-West Switzerland. The Vallon de Nant is one of two valleys of the river Avançon, a true right tributary of the Swiss River Rhône. The Vallon is an incised valley (approximately south-north) with a length of 6.5 km and a surface area of 13 km^2, with an elevation range of 1,300 m to 3,100 m. The Vallon has been partially protected from development since 1896, when the Grand Muveran region was established as a zone of protection for fauna (Vittoz and Gmür, 2009). It became a Nature Reserve in 1969, with complete forest protection from human activity. Taken together, this protection has kept the Vallon in a relatively natural state for more than 100 years (Dutoit, 1983; Randin, 2002). Unlike many other similar valleys, there is no flow abstraction or regulation and what grazing that is allowed is communal and has been strictly regulated to a very low intensity.

The climate of the Vallon is typical of the North-West European Alps, but with local modifications due to the effects of surrounding relief on the valley. Rainfall is distributed throughout the year and increased notably by the effects of local relief upon westerly and north-westerly air streams (Vittoz and Gmür, 2009). Given the elevation of the basin, important accumulations of snow can occur between November and April (Dutoit, 1983). Snow cover can be maintained until late spring in the valley bottom due to shading from the surrounding rock walls (east side of the valley). Geologically, the Vallon is located on the inverse flank of a series of folded sedimentary layers (the “Nappe de Morcles de l’Helvétique”) (Badoux, 1971, 1972; Schlup et al., 2009). These are calcareous sedimentary rocks deposited between the Middle Jurassic and the Eocene. Superficially, Quartenary deposits cover the majority of the Nappe.

In terms of vegetation, the Vallon extends from the montane zone through the tree line (~1,900 m) and into the sub-nival and nival zones. The Larzettes alluvial fan, that we focus upon in this study, extends from 1,500 to 1,700 m. The fan located on the right bank of the river that drains the Vallon de Nant, the Avançon de Nant, at the base of the Pointe d’Aufalle (2’725 m) (Figure 2). It is oriented north-west and sits below a series of rock faces, with a surface of about 170’000 m^2. It was chosen to be typical of a small European subalpine alluvial fan system in terms of its spatial scale. During the period of data collection in 2012, the fan (Figure 2) was bounded by an active primary channel and system of secondary channels on the true right of the fan and a recently abandoned and less active channel system on the true left of the fan. Between these two channel systems, notably towards the base of the fan, there was evidence that the fan was more stable with established trees. However, the distribution of the trees does not depend only on stability but also on historical management, as the very base of the fan was, and is still, grazed by some cows.

Methods

Sample sites and selection

Five transects (A to E) were established on the code with E being on the fan apex and A towards the fan base, at the upper limit of grazing (Table 1; Figure 2). Transects B to E had negligible impacts from grazing; transect A had some grazing impacts. A total of 100 1 m^2 sample sites were established, distributed between these five transects. The total number of sites chosen reflects the combined length of transects A to E in relation to the relatively small spatial scale of fan surface variability (e.g. the width of secondary channels) and was commensurate with the approaches of others (e.g. Lacoste and Salanon, 1969). We selected sample sites on the five transects as follows. Transect A was impacted upon by grazing so we restricted the number of sample sites along this transect to un-impacted zones and only 12 sites. For transects D and E, to aid statistical analysis, we set the minimum number of sites at 15. The remaining 58 sites were divided between transects B and C in proportion to the transect length. The five transects were then mapped onto a recent aerial photograph. This allows identification of four basic land covers: (1) bare sediments; (2) early colonizing vegetation; (3) shrubs; and (4) forest and also the length of each land cover on the five transects (Table 1). A pilot field visit showed that the local edaphic and biotic complexity was greater in zones (1) and (2) and so we decided to allocate sampling sites within each transect using an initial, stratified sample weighted towards these two land covers. Hence, if the total land cover length for the five transects is divided by the number of samples for that land cover (Table 1), this gives an average site spacing of 12.25 m and 14.00 m for (1) and (2) and 18.0 m and 18.9 m for (3) and (4). Within each stratified sample within each transect, sample sites were located randomly and the position recorded with a dGPS using as a base station a point that had been corrected into the Swiss co-ordinates system CH-1903 to cm precision. In the forest zone, it was necessary to wait until leaf fall in the early Autumn to measure the points and so the sites were monumented and then reoccupied. At each site a 1 m x 1 m quadrat was positioned with its lower side along the transect line to define the measurement surface.

Floristic composition and cover

At each site, each species present was recorded and species cover was visually estimated in classes: r, <0.1%; +, 0.1-1%; 1, 1-5%; 2a, 6-15%; 2b, 16-25%; 3, 26-50%; 4, 51-75%; 5, >75%. In addition, the percentage covers of trees, shrubs, grasses, mosses/lichen, bare soil and sediment were recorded. Shrubs were defined as individuals between 0.50 and 6.0 m in height; and soil cover was distinguished from sediment cover by having a characteristic diameter less than 2 mm.

Edaphic variables: field measurements and samples

Soils were uniformly young and poorly developed. There was little evidence of soil profile development. Thus, we focused upon bulk characterization of the surface material. The surface granulometry was characterized by measuring the *b* axes for a random sample (random selection of co-ordinate pairs on a 10 x 10 square grid defined by the quadrat extent) of 20 stones, which tests showed sufficient to approximate the median surface grain size. The depth of soil, if present, was measured by randomly sampling 10 locations within the quadrat, by planting vertically a long rod up to the first obstacle (stone). For 97 of the sample sites, a surface soil sample was taken.

Edaphic variables: additional laboratory analyses

The soil samples were analysed to determine both the residual wetness and the loss on ignition. In order to aid initial sieving, all samples were dried for 12 hours at 45°C (Baize, 2000). The samples were then sieved with a 2 mm sieve to obtain “fine earth” (Baize, 2000, 2004). The residual humidity (H_r) is defined as the loss of mass (in proportion) of the fine earth sample between drying at 45°C and drying at 105°C (Baize, 2000). Although H_r can vary with recent rainfall, this parameter generally reflects the presence of clay and organic material (Baize, 2000). Data were also collected during a relatively dry period of the summer meaning that H_r estimates were more reliable. In general, values less than 1% indicate a sandy soil and values greater than 4% soil that is more clay-like (Baize, 2000).

The loss on ignition (*LoI*) was defined as the mass loss by proportion of a sample after combustion for 2 hours at 450°C. This method does not distinguish between mineral and organic carbon (Baize, 2000). In theory, this partition may be estimated, or additional analyses to distinguish between the two types might be possible (e.g. Baize, 2000; Moreno et al., 2001). This was not done in this project because of the relative abundance of the calcareous substrate which should produce relatively homogeneous values of the mineral carbon component.

Additional site characterization using digital elevation data

A digital elevation model obtained by the Canton Vaud in 2002 using airborne laser altimetry was used to provide additional site characterization. This was pre-processed by the Canton to provide a bare earth model with a 1.0 m resolution, comparable with the quadrat area at each sample site. Basic processing was used to determine for each sample site: (1) annually averaged levels of shading; (2) aspect; and (3) local curvature in plan and profile. Plan and profile curvature were calculated using the standard Zevenbergen and Thorne (1987) methodology. As the Zevernbergen and Thorne methodology uses a 3 x 3 grid cell template, these parameters are calculated over a 3 x 3 m^2 area and so characterize a slightly larger area than the quadrat (1 m^2). Further processing was undertaken using the Matlab software TopoToolBox (Schwanghart and Kuhn, 2010) to calculate: (4) local slope; and (5) flow accumulation area (after pits were filled and using multiple flow routing with a coefficient of diffusion of 5, after Quinn *et al.*, 1991), the area upstream of each point which is likely to be able to provide surface runoff to that point. The slope and flow accumulation area were used to calculate the topographic index of wetness (Kirkby, 1975; Gascuel-Odoux et al., 1998). Finally, there is a strong correlation between elevation and accommodation space (-0.996) and so we use elevation as a simple measure of accommodation space, with lower elevations indicating higher accommodation space.

Sample site age

Given the importance of time since last perturbation (Figure 1), we attempted to determine the duration since last major perturbation, what we call the site age. To do this, we make the specific assumption that a perturbation is directly related to the delivery of sediment or local erosion and so a perturbation can be identified by comparing aerial photographs, and identifying sites that change from being vegetated to being sediment covered. Hence, the duration since last perturbation can be determined. Aerial photographs were available for the Vallon de Nant for 1957, 1969, 1980, 1992 and 2004. Here, the maximum time between photographs is 12 years and so we make the assumptions that this is the minimum time required for vegetation re-establishment after perturbation and that perturbations can be identified in vegetation response. These images provided a relatively coarse temporal resolution.

In order to extend the record beyond 1957, a small number of *Larix decidua* trees within the study area were cored. Although research has suggested that the impact of coring upon *Larix decidua* is small (Van Mantgem and Stephenson, 2004; Wunder et al., 2011), the coring has to be subject to an authorization and this limited the number of trees that could be cored to 10. To do this, we focused upon the largest trees along transect B and where there was clearly no sign of disturbance by sediment delivery. The cores were taken close to the soil to avoid under-estimation of the age through unmeasured rings (McCarthy et al., 1991; Desrochers, 1996; Pierson, 2007). These dates indicate the time since tree establishment, which may not be the same as the time since disturbance for two opposing reasons: (1) it may take some time for tree establishment after perturbation, the germination lag time (Pierson, 2007); and (2) trees may survive a subsequent perturbation if they are sufficiently established. In theory, it is possible to correct for the germination lag time: for example, Pierson (2007) calculated the germination lag time for Douglas fir to be about 5 years provided trees were cored close to the ground. Given the difference in tree species in our study, and the possibility that the lag time varies between environments, we do not apply this correction here.

Statistical analysis

Statistical analysis focused upon two elements. In a first step, we sought to generalize both the floristic composition and the edaphic data into variables that could be used for multivariate analysis. For the floristic composition we used a measure of Alpha diversity, the species richness. We were able to visualize the between transect variability in species richness and to assess whether or not there was a statistically significant association between transect (i.e. down fan position) and diversity.

Species richness neither retains information specific to the kinds of environments being studied here, nor considers associations between individual species. Hence, we grouped the site inventories with a hierarchical clustering (Bray-Curtis distance and Ward's minimum variance clustering; Borcard et al., 2011) and extracted indicator species of the groups according to Dufrêne and Legendre (1997). On the basis of these discriminant species, each group was attributed to a phytosociological unit, based upon the Swiss environmental classification (Delarze and Gonseth, 2008).

With these data we were able to undertake simple assessments between individual edaphic variables and both measures of diversity and classifications of sites into units. Non-parametric Kruskal-Wallis analysis of variance was used for this purpose. However, whilst this allows general identification of how edaphic data relate to spatial variability in fan ecology, the edaphic variables are themselves highly inter-correlated. Thus, in a second step, we reduced the 11 edaphic variables, plus sample site age, to a smaller number of factors using a factor analysis. To simplify the interpretation of the resulting factors, and to insure that the factors remained pairwise uncorrelated for subsequent linear modelling, we applied a varimax rotation. We used a minimum cut off of 5% contribution to the original data variance in defining the number of accepted factors.

In a third step, we sought to establish relationships between the edaphic factors and the floristic composition. For the diversity indices, we used an optimizing stepwise regression where factors were added to the model in order of decreasing importance provided that their contribution to the total explanation of the model was significant at $p < 0.05$. For the phytosociological units, and because we could not guarantee normal distributions of factor scores at this level, we undertook non-parametric Kruskal-Wallis analysis of variance.

Results

Down fan changes in Alpha diversity

Figure 3 shows the distribution of the species richness considered in this study. In all three cases, the transect mean diversity increases progressively from the fan top (transect E) to the fan base (transect A). Non-parametric Kruskal-Wallis tests showed a statistically significant ($p < 0.05$) variability between transects for all three measures of diversity. Non parametric pairwise comparison of means (Mann-Whitney U) shows that this arises primarily from differences between transects A/B and C/D/E ($p < 0.05$ for A v B, A v C, A v D, A v E; B v C, B v D, B v E, D v E). Figure 2 visualises the species richness at each sample site as proportional circles superimposed on the orthoimage and shows how the diversity both increases down fan but also varies cross-fan in relation to channel activity.

Ecological characterization of the sample sites

For the 100 sample locations, 91 had at least two species and could be classified. A total of 107 species were observed more than once with the most common species identified being *Petasites paradoxus* (75% of sites), *Calamagrostis varia* (68% of sites) and *Carex sempervirens* (60% of sites). Around 53% of species were found in fewer than 10% of sites. The classification of sample sites identified seven groups plus an eighth group of sites without vegetation (Figure 4b). Based upon their indicator species, these could be attributed to one of the units of Delarze and Gonseth (2008). The species richness of samples in each unit was determined (Figure 4a). The lowest levels of species richness are associated with two groups attributed to *Epilobion* *fleischeri* and one to *Petasition paradoxi*, the pioneer vegetation on alluvial deposits (Figure 4b), but these groups are distinguished in the classification by the greater richness at sites labeled *E. fleischeri (1)*, and the presence of species like *Hieracium staticifolium*. *E. fleischeri (2)* sites were typical of the very earliest stages of colonization. The *Petasition paradoxi* had no clear indicator species but was dominated by *Leontodon hispidus*, *Petasites paradoxus* and *Gypsophila repens*. Two units labeled *Caricion firmae* and *Seslerion* were both typical of the secondary states of plant succession, with higher plant cover. The *C. firmae* sites contained commonly *Carex ferruginea*, *Dryas octopetala*, *Carex sempervirens* and *Saxifraga paniculata*, most of them typical of rocky environments. The *Seslerion* is already closer of a grassland, represented by sites commonly with *Sesleria caerulea* and *Hieracium villosum*. One unit was attributed to the subalpine coniferous forests (*Abieti-Piceion)*, with a relatively high diversity in sample sites and the presence of species like *Abies alba*, *Vaccinium myrtillus*, *Aposeris foetida* and *Sorbus aucuparia*. The most diverse sites are labeled *Polygono-Trisetion,* corresponding to eutrophic grasslands, containing species like *Campanula rhomboidalis*, *Trollius europaeus* et *Crepis pyrenaica*.

These units are mapped onto the species richness values superimposed in the orthoimage in Figure 2 and it shows clear structuring of sample sites with distance from the fan apex to the fan base. As the transects lengthen, the number of associations present increases to its maximum (7 in both transects B and C).

Environmental characterization of sample sites and their linkages to species associations

Figure 5 summarises key environmental data by transect. By comparing transects, this allows down fan changes in environmental characteristics to be described. Kruskal Wallis H tests are used to assess if there is significant variability between transects. Figure 5a shows that the slopes associated with each transect decline down fan ($p < 0.001$), suggesting that the fan is concave downward. At the same time, the plan curvature increases down fan (Figure 5b, $p = 0.025$). Figure 5c suggests little clear trend in the topographic index of wetness ($p > 0.05$), and Figure 5d similarly an absence of trend for the flow accumulation area ($p > 0.05$), although flow accumulation areas have an increased range with distance down fan until the fourth transect (B) where the range starts to diminish quite rapidly. It follows from initial increases in upslope contributing area for sites in the main channel with distance down the fan until changes in the curvature and slope begin, encouraging more diffusive flow, and hence a reduction in the largest values of the flow accumulation area. The median grain-size appears to decrease down fan (Figure 5e), but this trend is not statistically significant ($p > 0.05$). For two of the three indicators of soil development (residual humidity, Figure 5g and loss on ignition, Figure 5h) a significant variability between transects ($p = 0.023$ and $p = 0.013$ respectively) was identified. Both indicators suggest a greater level of soil development in general in the lower transects, notably B and A.

Table 2 summarises the environmental data for the sites associated with each unit. Data are plotted in Figure 6, along with the species richness data for comparison. These have also been subject to a Kruskal Wallis test. First, Table 2 suggests some association with elevation ($p < 0.001$): unvegetated sites are more likely to be at higher elevations, along with the *C. firmae and E. flesicheri (1)*. The *Polygono-Trisetion,* which has the highest species richness, tends to be found at a restricted range of lower elevations, along with the *Abieti-Piceion*. The remaining units are associated with intermediate elevations. Given the restricted elevation range and as elevation is inversely correlated with accommodation space, this suggests some association between accommodation space and the unit found, and hence different regimes of magnitude and frequency of geomorphic perturbations. We use elevation as a surrogate for accommodation space in subsequent analysis.

Reflecting the concave cone geometry, slope and elevation are positively correlated (r = 0.481, $p < 0.05$) and so it is not surprising that Figure 6c shows patterns similar to elevation in Figure 6b, although the differences are less marked ($p = 0.030$). The topographic index of wetness flags the *E. flesicheri (2)* sites as most likely to be wet (Figure 6d), and the latter commonly have lower slopes and larger flow accumulation areas (Figure 6e). It corresponds to the most active river beds. In contrast, the *Polygono-Trisetion* sites are commonly drier (Figure 6d) and have smaller flow accumulation areas (Figure 6e). When all units are considered, there is no significant variability ($p > 0.05$) between wetness or flow accumulation area and unit. Grain sizes varies between units ($p = 0.004$). *P. paradoxi* and the two sets of *E. flesicheri* sites seem to be associated with coarser grains. However, differences between units in the range of median grain sizes found are also evident, with much greater ranges for *Seslerion* and somewhat greater for *Abieti-Piceion* than the other units.

The three indices of soil development, depth (Figure 6h), residual humidity (Figure 6i) and loss on ignition (Figure 6j) all vary by unit ($p = 0.019$, $p < 0.001$ and $p < 0.001$ respectively). The shallowest soils appear to be associated with the two *E. flesicheri*, and to some extent with *C. firmae*.

Sample site dating

The aerial photographs for 1957, 1969, 1980, 1992 and 2004 allowed the recent history of the fan to be established (Figure 7). It shows that the range of ages present on the fan increases with distance down fan, with two main zones of more recent fan activity on the fan left and the fan right. The currently most active channel is found on the fan right. The diagram also shows an older channel that penetrated the middle of the fan between 30 and 50 years ago. The photograph ages have been supported by the available tree core data. These suggest that the oldest tree is greater than 100 years old, with four trees between 84 and 96 years old in the same area. One tree core on the left hand side of the fan showed some deformation 13 years before the sample was taken (i.e. 1999) and which is thought to be related to Storm Lothar that had a particularly important impact in this valley. This storm falls within the 9-20 year age range according to the photographs and suggests that the event was significant enough to activate the left hand side of the fan but not to record itself in the older trees sampled in the middle of the fan. Globally, a chi-squared test on the distribution of age classes by transect is significant ($p<0.05$) and Figure 8 shows the distribution of sites by age class and transect. A down fan transition from proportionately greater representation in the younger age classes at the fan head (classes 1 and 2, < 20 years, in transect E) towards over representation in the older age classes towards the fan base is evident. A greater bimodality at the fan head is evident, reflected in the fact that transects D and E contribute 56.7% of the chi-square estimate and only have 30.4% of the intermediate age classes 3, 4 and 5 (21-55 years).

Figure 9 shows the relationship between estimated site age and phytosocioligical units. This shows the role that time plays in influencing plant community composition: the pioneer, less-vegetated sites, the *Patasition paradoxi* and *E. fleischeri* (2) are associated with younger ages. *E. fleischeri* (1) is slightly older, followed by *C. firmae*, *Seslerion* and eventually *Abieti-Piceion*. *Polygono-Trisetion* sites are limited to the oldest and most stable sites, as confirmed by the dendrochronology which suggests that the ages of trees may be substantially longer than measured in the imagery. What is interesting is the presence of some younger ages in the *Abieti-Piceion*. Field observations often showed gravel deposits around certain trees. This may be related to the more limited impact of perturbations once forest cover develops and trees are able to survive more extreme events provided that the latter are neither too great in amplitude nor too frequent. Similarly, some less vegetated sites seem to have been abandoned for more than 20 years, suggesting that factors other than just time influence the vegetation process.

Factor analysis and relationship to floristic characteristics.

The factor analysis identified seven factors that explained 73.2% of the original edaphic/age dataset (Table 3). Application of stepwise regression to assess the extent to which these factors explained species richness identified four factors. The total level of adjusted explanation was relatively high (65.6%).

The most important factor identified was the one that contributed least to the total variability in the original edaphic/age data in the regression analysis (Factor 7, Table 3). Factor 7 predominantly represents variability in age, but also has some, albeit much weaker, significant correlations with elevation and hence accommodation space and granulometry: thus high scores on Factor 7 indicate older sites, possibly also with greater accommodation space and with finer surface material. Given the signs of the regression coefficient in Table 4, it suggests that older sites, where there is more accommodation space and finer surface material, have higher species richness.

Consistently, the second most important factor identified in explaining alpha diversity was Factor 1 (Table 4). Factor 1 explained the highest percentage of the variance in the original age/edaphic data (Table 3) and is very highly correlated with residual humidity and loss on ignition, that is the measured wetness of sites and their organic matter content. Taken together, and given evidence of some correlation with age, this is likely to represent a soil development factor, high scores on this factor indicating a higher degree of soil development. It does not seem to associate with soil depth, suggesting that the soil development here is not associated with the development of a deeper weathered layer, but rather soil development through organic matter accumulation. Given the sign of the regression coefficient (Table 4) and the associated loadings (Table 3), it suggests that wetter sites with more organic matter, and a more developed soil, have higher species richness.

Again consistently, the third most important factor identified in explaining species richness was Factor 5 (Table 4). The factor scores are greater for sites that are commonly more shaded but also with a higher elevation and hence smaller accommodation space (Table 3). Given the sign of the regression coefficient (Table 4), this suggests that sites with a larger accommodation space and less shading have more species.

Finally, a fourth factor, Factor 2, was added into the model (Table 4). The factor scores for Factor 2 are more positive at higher elevation (i.e. lower accommodation space) sites, that are also steeper, have a lower value of the topographic index of wetness (i.e. that are drier) and which have a slight tendency to a coarser grain size. Given the sign of the regression coefficient (Table 4), this suggests that sites with a higher accommodation space, that are less steep and that have a higher topographic index of wetness and a lower grain size have a higher species richness. But this is the weakest factor in the regression analysis. Factor 2 does not pick up residual humidity, in the same way that Factor 1 does not pick up the topographic index of wetness. Thus, there may be a decoupling on the fan surface between: the wetness of sites as might be theoretically expected given the surface topography of the fan and subsequent flow routing; and local controls on wetness which appear to be related to the ability of accumulated organic matter to increase moisture retention.

It is perhaps surprising that the factors that explain most of the original variance in the edaphic/age data (i.e. the factor analysis) are not those that are uniformly the most important in the regression analysis. The factor analysis also shows a relatively distributed contribution to this variance across the seven factors identified. This may reflect the fact that the edaphic data in particular contain significant amounts of noise that is hard to generalize across sites. Equally, some elements of the edaphic data that might be expected to explain spatial patterns of biodiversity do not appear as important in the regression modeling.

Table 5 extends this analysis to the phytosociological units, by evaluating the extent to which each factor varies between the seven units identified. The results reflect very clearly the species richness results for the stepwise regression with a clear and significant variability between units for the factor scores of Factors 1, 2 and 7. Figure 10 shows where this variability comes from: *P. paradoxi* and the two sets of *E. fleischeri* have markedly lower scores on Factors 1 and 7, suggesting that (Table 3) they are associated with sites with lower accommodation space (i.e. higher elevation), that are younger with a less developed soil. The seven units partition Factor 2 more continuously but also in a way that is different to Factors 1 and 7: the *E. fleischeri (1)* and *C. firmae* have somewhat higher Factor 2 scores, although the range for the latter is much greater than for the former, suggesting that these are found on sites with lower accommodation space, steeper slope, coarser grains and lower values of the topographic index of wetness (i.e. topographically 'drier'). *Seslerion* and *E. fleischeri (2)* have typically much lower scores on this Factor, and so are found in sites with higher accommodation space, lower slope, higher topographic wetness and finer surface grain size.

Discussion

Down fan variability in the across-fan distribution of fan surface ages, fan surface channel characteristics and fan surface sedimentology

Figure 7 shows a down fan variability in the distribution of fan ages within each transect. This sustains the basic hypothesis shown in Figure 1 that, with distance down the fan, the range of ages present increases to provide a more continuous age distribution. The proportion of the fan that is active decreases down fan (Figure 7). Proportionally more younger surface ages are found at the fan head. By the fan base, a more continuous distribution of ages is found (Figure 8). This more continuous age distribution arises because of: (1) the increasing accommodation space towards the fan base; and (2) the diffusive nature of the fan surface. With distance down fan, larger accommodation space will reduce the frequency of perturbation and the diffusive nature of the fan surface will reduce the magnitude of perturbation. Thus, the fan geometry, through its effects upon frequency and magnitude, impacts upon the time available for soil development and so upon both plant colonization and succession. As Blair and Macpherson (1994) noted, the apparent complexity of fan surface topography (relief shaded DEM, Figure 2) can be misleading as the age data in Figure 7 confirms that over the time period studied in this research, the flow appears to disturb the fan surface, and hence occupy significantly only a small proportion of the fan width. The fan appears to be relatively stable. Some research has suggested the progressive stabilization of Alpine alluvial fans since the end of the Little Ice Age, following climatic amelioration (e.g. Lewis and Birnie, 2001; Stoffel and Beniston, 2006; Colombera and Bersezio, 2011), although this may be more related to changes in the frequency of rainfall triggering events than temperature rise (Bollschweiler and Stoffel, 2010).

In turn, some association between transects and basic channel characteristics and surface sedimentology was found: the fan structures edaphic variables (Figure 5). For instance, down fan, the flow accumulation area decreases (Figure 5d), the median grain-size decreases (Figure 5e) and the range of soil depths (and hence the level of soil development) increases, except for transect A where the range decreases (Figure 5f). Both the measured flow accumulation and granulometry changes down fan reflect the basic models of fan geomorphology established for some time (e.g. Blissenbach, 1954; Hooke, 1967; Blair and Macpherson, 1994; Vincent *et al.*, 2004). Thus, the growing accommodation space down fan, and the associated more diffusive flow, also impact upon edaphic parameters more generally. We are able to confirm the first basic hypothesis that there is a down fan variability in the across-fan distribution of fan ages, fan surface channel characteristics and fan surface sedimentology, which can lead to distinct across fan distributions of edaphic factors.

Fan surface age, edaphic factors and floristic diversity and community development

If we look at the floristic composition just in terms of alpha diversity, then it was possible to explain a relatively high proportion of species richness using three or four of the seven factors identified in a factor analysis. Two of the factors related strongly to the age since the last significant perturbation at the site. Sites with more species tended to be older, with greater organic matter accumulation, finer grain size and better developed soils. Distinguishing cause and effect here is a little difficult because the presence of organic matter and finer grain sizes may both improve local conditions for plant growth (e.g. through improving water retention). However, they may also be a response to plant growth (organic matter accumulation, trapping of fine sediment, perhaps enhanced weathering rates). For locations on the fan that are older and less perturbed, there is a co-development of soil and vegetation. Where there is perturbation, and sites are younger, it is more likely that variability in local edaphic conditions will be determining vegetation development. Thus, we can envisage two states on the fan surface: (1) those of younger sites, where local variability in edaphic conditions causes variability between sites in terms of the plant species that can develop and their rates of growth (e.g. Burga *et al.*, 2010); and (2) those of older sites, which are influenced partly by edaphic conditions, but also the history of vegetation and soil development. The latter modifies the local environment such that plant colonization and growth is less dependent on edaphic conditions.

As would be expected, age and soil development were also able to distinguish the type of vegetation found and resulted in the emergence of certain phytosociological units as dominant in certain zones of the fan (Figure 2, Figure 6). The main trend is related to vegetation dynamics, with a succession from pioneer communities (*E. fleischeri*) towards more stable forest communities (*Abieti-Piceion*). The effects of the fan upon the distribution of edaphic factors (Figure 7) were less clear than age and soil development effects, but age did not explain the spatial differentiation of units completely (Figure 9). Further, the factor analysis revealed the importance of grain size, slope and the topographic index of wetness in explaining a much smaller part of the spatial variation in diversity (Table 3, Table 4) and distinguishing between different units (Table 3, Table 5). In this case, in relation to the second hypothesis, down fan changes in the across fan distribution of edaphic factors lead to down fan differences in floristic richness and dominant plant community, but these effects are less important than age and its implications for soil development.

For age and soil development to be important, a key variable will be the time since last perturbation. Our age data do not resolve the full history of all possible perturbations on the fan surface: rather they resolve the major perturbations, those that are associated largely with the primary channel migration at the fan apex. Yet, age still appears as a dominant variable in the analyses (Table 3, Table 4). Alongside age is the importance of elevation which we used here as a surrogate for accommodation space. Figure 7 shows that these are closely related: older sites tend to be those associated with lower elevation and greater accommodation space. Figure 8 shows how site age is distributed within each section. This confirms one of the basic ideas in Figure 1. The highest sites, in section E with the lowest accommodation space, tend to have an ‘on-off’ characteristic: they are either very young or very old. Given the relative stability of this fan, it appears possible to have very old sites even at the fan apex. But, with distance down the fan, and as the accommodation space increases, the distribution of age ranges also increases to its most distributed in section C. In section B, the oldest trees become dominant until at section A where the sites are generally older ones. Thus, also as indicated in Figure 1, there appears to be a down fan reduction in the ability of events to perturb the system, which translates into a growing diversity of site ages. In the most distal parts of the fan, the only disturbance is related to much less frequent shifts in the position of the primary channel. An intermediate zone on the fan surface (sections C and B) has the greatest range of ages present (Figure 8). Because the range of ages present associates with elevation, and hence accommodation space, this explains why Factor 7 (Table 3) implies only a weak association between elevation and age; sites are generally older in the lower parts of the fan, where the accommodation space is greater, because the proportion of the section that is perturbed by the primary fan channel, and hence the number of sites, is reduced.

Conclusion

Figure 1 presented a basic conceptual model for the magnitude and frequency of perturbation on an alluvial fan surface that arises from the way in which an alluvial fan dissipates potentially perturbing events. Central to this model is the growing accommodation space from the fan apex to the fan base, which in turn reduces channel confinement and drives diffusive fan surface flow. Close to the fan apex, points on the fan surface should be 'on-off', that is they should be either occupied or unoccupied by an active channel that transports water and sediment. If occupied by an active channel, the magnitude of processes operating in the channel should be high. With distance down the fan, and growing accommodation space, occupation of points on the fan surface should become less frequent and, because fans are diffusive systems, the intensity of processes operating in active channels should be lower. For any one across-fan transect, there will be a relatively small length of active channels, and a relatively longer length of abandoned channels. The latter should contain a range of ages since perturbation. We were able to confirm this basic model for a subalpine alluvial fan: the apex of the fan had a more bimodal distribution of fan surface ages than transects lower down the fan which had a more continuous distribution of fan ages. Further, we were able to show how the distribution of edaphic variables on the fan surface also reflected this conceptual model with systematic decreases in flow accumulation area, grain-size and slope.

In turn, we were able to link site age and site edaphic factors directly to the results of a floristic survey. Age on the fan surface, measured here as the time since last visual disturbance, was shown to be the primary variable that: (a) influences floristic richness; and (b) discriminates different plant communities. Given the direct link between fan surface ages and the conceptual model of the magnitude and frequency of fan surface disturbance, we have demonstrated a direct link between the distinct plant communities emergent both across fan and down fan and the way in which the fan dissipates potentially perturbing events.

The effects of other edaphic factors were less clear, although finer surface grain size, lower local slope (i.e. less well drained) and higher values of the topographic index of wetness (i.e. wetter) sites were identified as secondary factors in explaining the spatial variation in diversity and in distinguishing between different plant communities. These secondary variables could also be associated to systematic increases in accommodation space from the fan apex to the fan base. However, we were also able to show that older sites had a more developed soil, with greater organic matter content and residual humidity. We related this to the progressive development of vegetation with age and envisaged two states on the fan surface: (1) younger sites, where perturbation leads to spatial variability in edaphic conditions, and variability between sites in terms of the plant species that can develop and their rates of growth; and (2) autogenically controlled older sites, where the co-development of vegetation and soil makes plant communities less sensitive to perturbation-driven edaphic conditions. We argue that this is a primary reason why relationships between plant communities and edaphic conditions are less evident at the scale of the entire fan. In turn, the existence of these two states can be linked to the conceptual model of fan surface perturbation (Figure 1). With distance down fan, as the accommodation space increases and there is a reduction in perturbation frequency and magnitude, so sites can become older and autogenic processes can become dominant.

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Table 1. Sample sites by transect and cover type

Transect	Number of sample sites	Length of transect (m)	Average site spacing (m)	Bare sediments		Early colonizing vegetation		Shrubs		Forest	
				N sites	Length of cover (m)	N sites	Length of cover (m)	N sites	Length of cover (m)	N sites	Length of cover (m)
A	12	550	45.8	1	70	2	120	9	360	0	0
B	32	470	14.7	4	50	10	170	8	80	10	170
C	26	350	13.5	6	90	9	110	11	150	0	0
D	15	125	8.3	5	15	5	50	5	60	0	0
E	15	70	4.7	4	20	9	40	2	10	0	0
Total	100	1 565		20	245	35	490	35	660	10	170
Average lengths (m)					12.25		14.00		18.9		17.0

Table 2. The maximum, median and minimum of environmental data for each phytosociological unit. Units (columns) are ordered in terms of expected successional stage.

Group		**7**	**5**	**6**	**2**	**3**	**1**	**4**
Unit		***E. fleischeri (2)***	***P. paradoxi***	***E. fleischeri (1)***	***C. firmae***	***Seslerion***	***Polygono-Trisetion***	***Abieti-Piceion***
Elevation [m]	Min	1550.5	1542.0	1543.3	1543.4	1528.8	1539.5	1536.7
	Med	1590.5	1588.9	1612.5	1637.2	1597.3	1553.3	1566.9
	Max	1632.7	1664.3	1665.8	1666.8	1641.3	1576.9	1608.1
Aspect [°]	Min	5.7	12.8	1.1	13.9	0.7	20.1	15.9
	Med	322.8	291.5	297.7	310.4	309.9	270.9	315.8
	Max	350.2	341.9	355.7	349.6	353.9	347.0	336.2
Curvature [/100]	Min	-0.2	-0.33	-1.7	-0.86	-1.1	-0.6	-0.3
	Med	-0.03	-0.05	-0.06	-0.08	-0.05	0.3	0.1
	Max	0.41	0.74	0.29	0.5	0.37	0.9	0.5
Shading	Min	190	192	174	171	191	171	179
	Med	210.5	210.5	208	215	210	201	211
	Max	228	220	233	250	243	216	230
Median grain size [cm]	Min	6.0	5.5	4.0	2.0	0.0	0.0	0.0
	Med	7.8	9.0	7.0	5.5	5.0	4.0	5.0
	Max	11.0	13.0	13.5	9.0	22.0	8.5	13
Soil depth [cm]	Min	0.0	4.0	0.0	0.0	5.0	4.8	5.7
	Med	4.8	8.8	6.1	6.6	7.0	9.8	8.5
	Max	8.7	27.5	16.5	12.2	17.5	14.5	18.5
% loss on ignition at 450°C	Min	0	0.4	0.0	0.7	2.1	21.8	8.8
	Med	0.4	0.5	1.2	11.5	24.7	26.1	35.0
	Max	0.7	2.9	7.7	49.0	45.5	47.8	72.2
Topographic index of wetness [log m^2/gradient]	Min	3.2	0.4	0.5	0.2	0.1	0.5	0.0
	Med	7.8	3.7	3.2	2.5	3.7	2.1	4.2
	Max	10.5	6.9	12.0	10.1	8.5	5.5	8.6
Flow accumulation area [m^2]	Min	10.6	1.0	1.0	1.0	1.0	1.2	1.0
	Med	753.4	31.6	11.1	8.1	19.5	3.3	27.6
	Max	16226.0	374.7	39320.0	8640.1	1431.4	77.1	2844.2
Slope [gradient]	Min	0.2	0.4	0.3	0.2	0.1	0.3	0.3
	Med	0.4	0.6	0.7	0.7	0.4	0.4	0.5
	Max	0.5	0.8	1.2	1.0	1.0	0.8	1.3
Residual humidity [%]	Min	0.0	0.2	0.0	0.2	0.4	3.3	1.4
	Med	0.2	0.2	0.4	1.9	3.3	4.1	4.8
	Max	0.3	0.7	1.4	8.9	7.4	6.6	8.5

Table 3. Loadings of each original variable on each factor. Data in bold, italic, show significant loadings ($p < 0.05$)

Factor	1	2	3	4	5	6	7
Elevation	0.001	***0.610***	0.136	***-0.215***	***0.505***	***-0.445***	***-0.224***
Cosine of aspect	-0.014	0.096	-0.244	***0.947***	0.131	-0.015	-0.110
Curvature	0.137	-0.114	0.039	0.114	0.074	***0.688***	0.040
Shading	-0.041	-0.016	-0.087	0.109	***0.773***	0.014	0.077
Slope	-0.125	***0.732***	-0.107	0.091	0.021	-0.104	-0.001
Topographic Index of wetness	-0.140	***-0.577***	***0.587***	-0.129	0.213	-0.132	-0.142
Flow accumulation area	-0.120	-0.063	***0.899***	-0.204	-0.180	-0.100	-0.054
Granulometry	-0.122	***0.245***	0.010	***0.226***	-0.072	0.012	***-0.285***
Soil depth	0.049	0.008	-0.201	-0.168	-0.090	***0.405***	-0.005
Residual humidity	***0.970***	-0.072	-0.078	-0.024	-0.028	0.133	0.154
% loss on ignition at 450°C	***0.950***	-0.098	-0.093	-0.019	-0.045	0.105	0.167
Age class	***0.565***	0.096	-0.142	-0.082	0.057	0.094	***0.792***
Explained variance	**18.8**	**11.3**	**11.1**	**9.3**	**8.1**	**7.6**	**7.1**

Table 4. Results of the application of the factor analysis in Table 3 to stepwise regression using species richness as the dependent variable.

Step	Factor added	Coefficient	*p*
1	7	0.611	0.000
2	1	0.473	0.000
3	5	-0.160	0.005
4	2	-0.126	0.028
Total adjusted R^2(%)	65.6		

Table 5. Results of the application of Kruskal-Wallis analysis of variance to each factor, grouping data for each test by association. Bold indicates $p < 0.05$.

Factor	*p*
1	**0.000**
2	**0.047**
3	0.222
4	0.759
5	0.093
6	0.097
7	**0.000**

Figures

Figure 1. A conceptual model of down fan variability in the magnitude and frequency of perturbations on an alluvial fan surface.

Figure 2. An aerial orthoimage (©SwissTopo 2004) and relief shaded Digital Elevation Model (DEM) of the Larzettes cone. Superimposed on the aerial orthoimage are spatial patterns of species richness (dot size) and the associated environmental classification in phytosociological units. The number of plots in each unit are given on the left. The sample locations are also shown on the relief-shaded DEM. Note the two primary channels at the fan apex. The right hand side fan was the most frequently active in 2012.

Figure 3. Box plots of species richness for each section from E (fan apex) to A (fan base) (see Figure 2). The upper and lower box margins mark the 75th (Q_{75}) and the 25th (Q_{25}) quartiles respectively, with the mid box line showing the median. The whiskers show the extremes of the data (maximum and minimum) except for situations where outliers are present, defined as either $Q_{75}+1.5(Q_{75}- Q_{25})$ for the maximum and $Q_{25}-1.5(Q_{75}- Q_{25})$ for the minimum.

Figure 4. Box plots of the species richness (4a) and example images of the their associated classified units (4b). The upper and lower box margins mark the 75th (Q_{75}) and the 25th (Q_{25}) quartiles respectively, with the mid box line showing the median. The whiskers show the extremes of the data (maximum and minimum) except for situations where outliers are present, defined as either $Q_{75}+1.5(Q_{75}- Q_{25})$ for the maximum and $Q_{25}-1.5(Q_{75}- Q_{25})$ for the minimum.

Figure 5. Box plots of edaphic variables for each section from E (fan apex) to A (fan base). The upper and lower box margins mark the 75th (Q_{75}) and the 25th (Q_{25}) quartiles respectively, with the mid box line showing the median. The whiskers show the extremes of the data (maximum and minimum) except for situations where outliers are present, defined as either $Q_{75}+1.5(Q_{75}- Q_{25})$ for the maximum and $Q_{25}-1.5(Q_{75}- Q_{25})$ for the minimum.

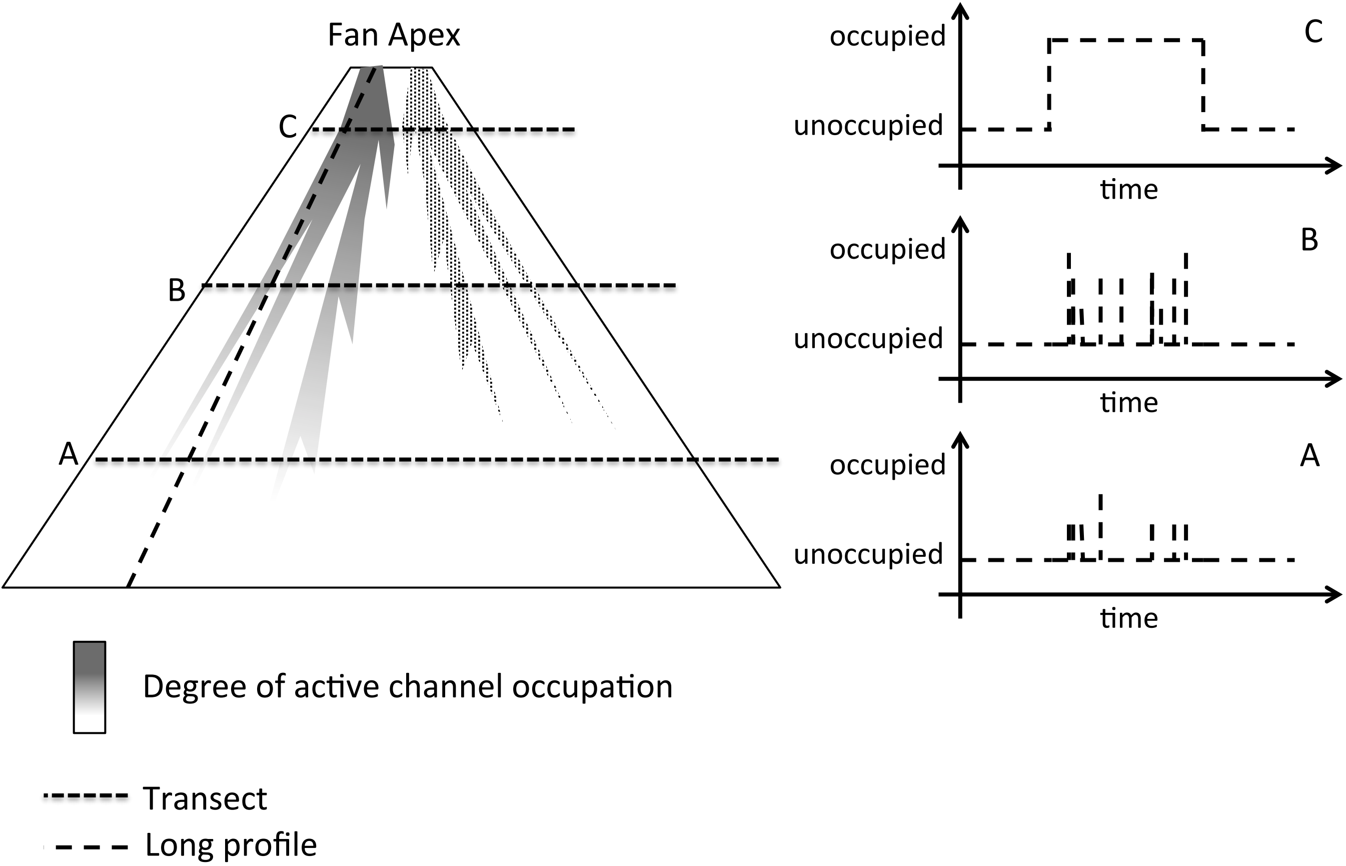
Figure 6. Box plots of edaphic variables sorted by phytosociological units. Species richness and elevation are also shown. The upper and lower box margins mark the 75th (Q_{75}) and the 25th (Q_{25}) quartiles respectively, with the mid box line showing the median. The whiskers show the extremes of the data (maximum and minimum) except for situations where outliers are present, defined as either $Q_{75}+1.5(Q_{75}- Q_{25})$ for the maximum and $Q_{25}-1.5(Q_{75}- Q_{25})$ for the minimum.

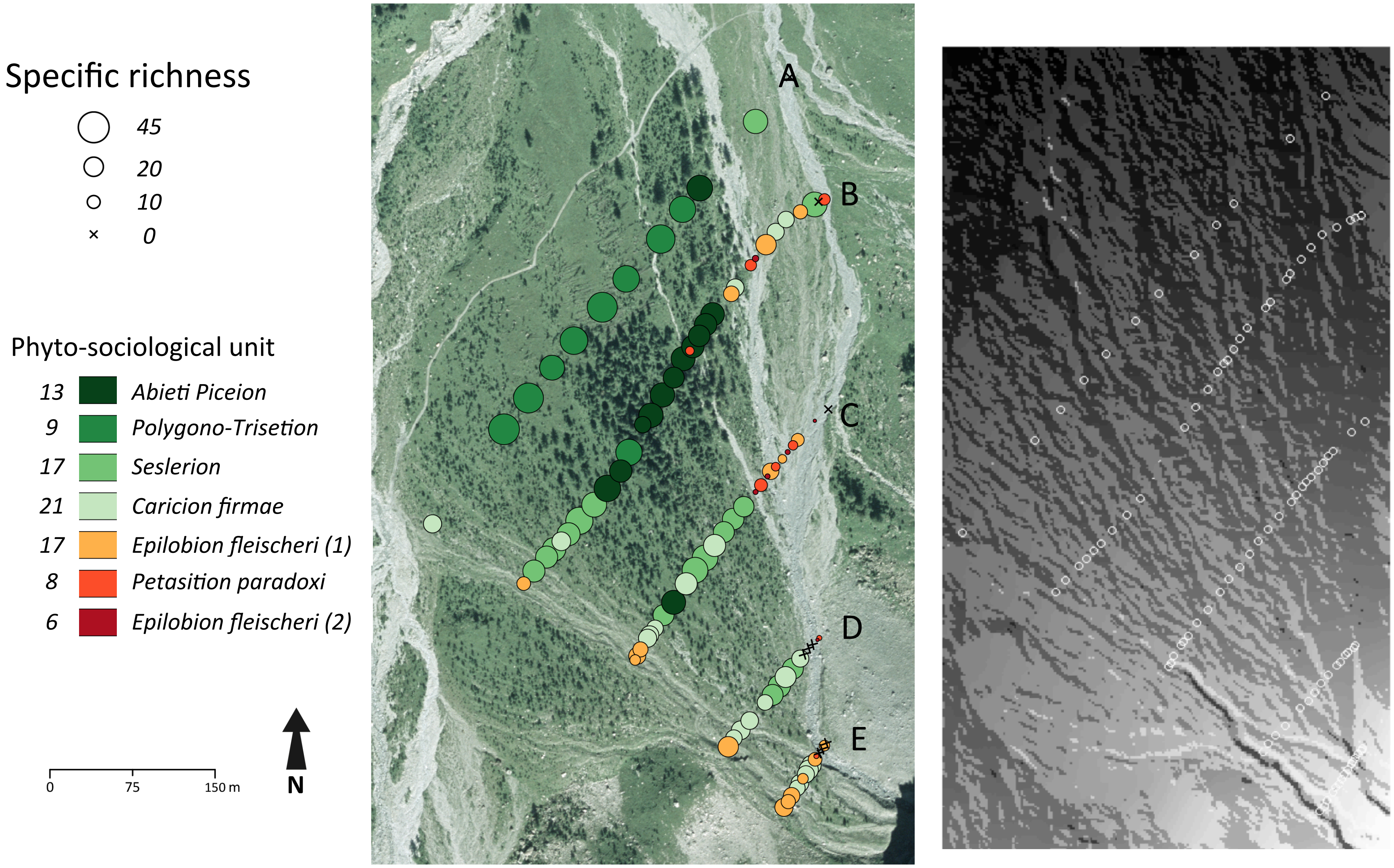
Figure 7. Fan surface ages measured using dendrochronology and orthophotographs.

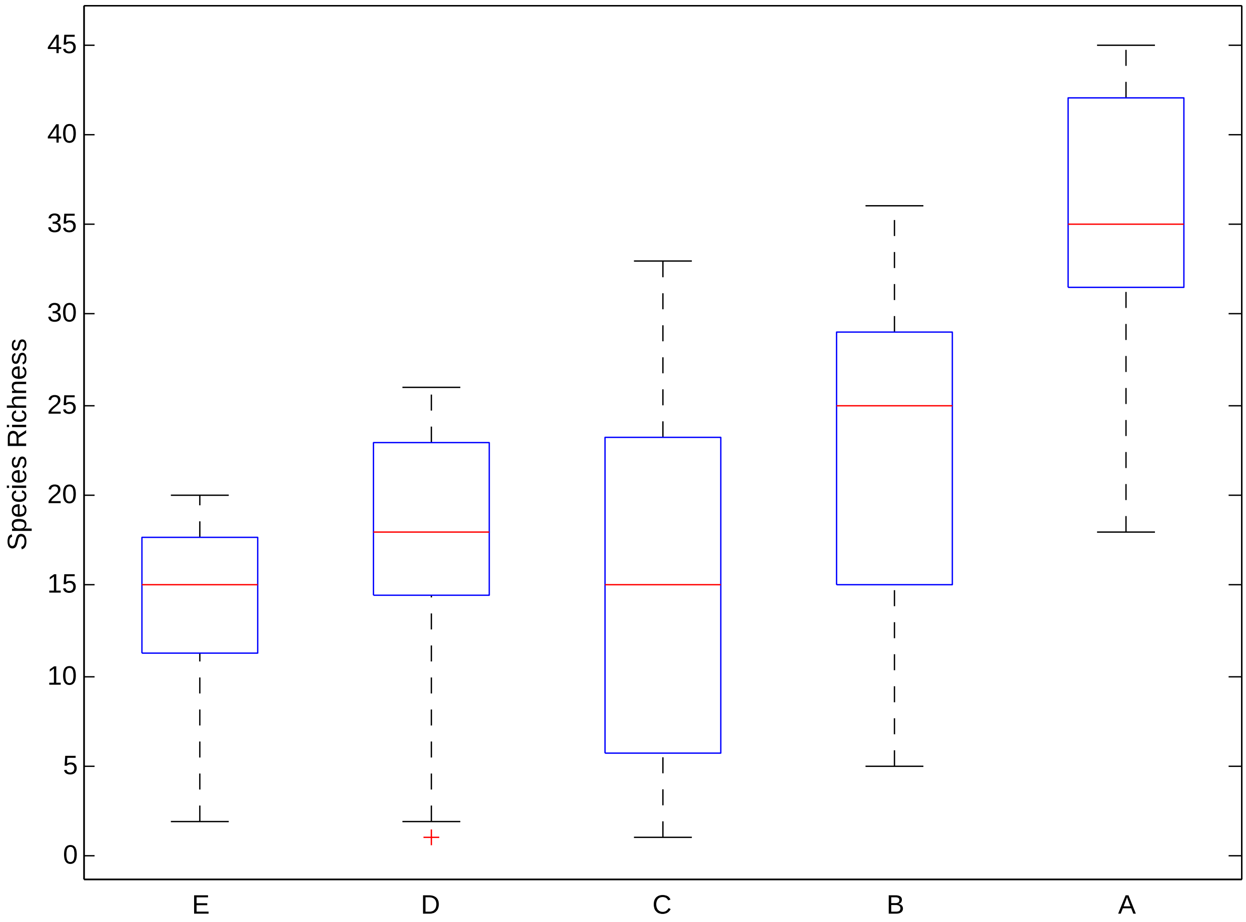
Figure 8. Frequency of each age class within each section, shown as proportional circles.

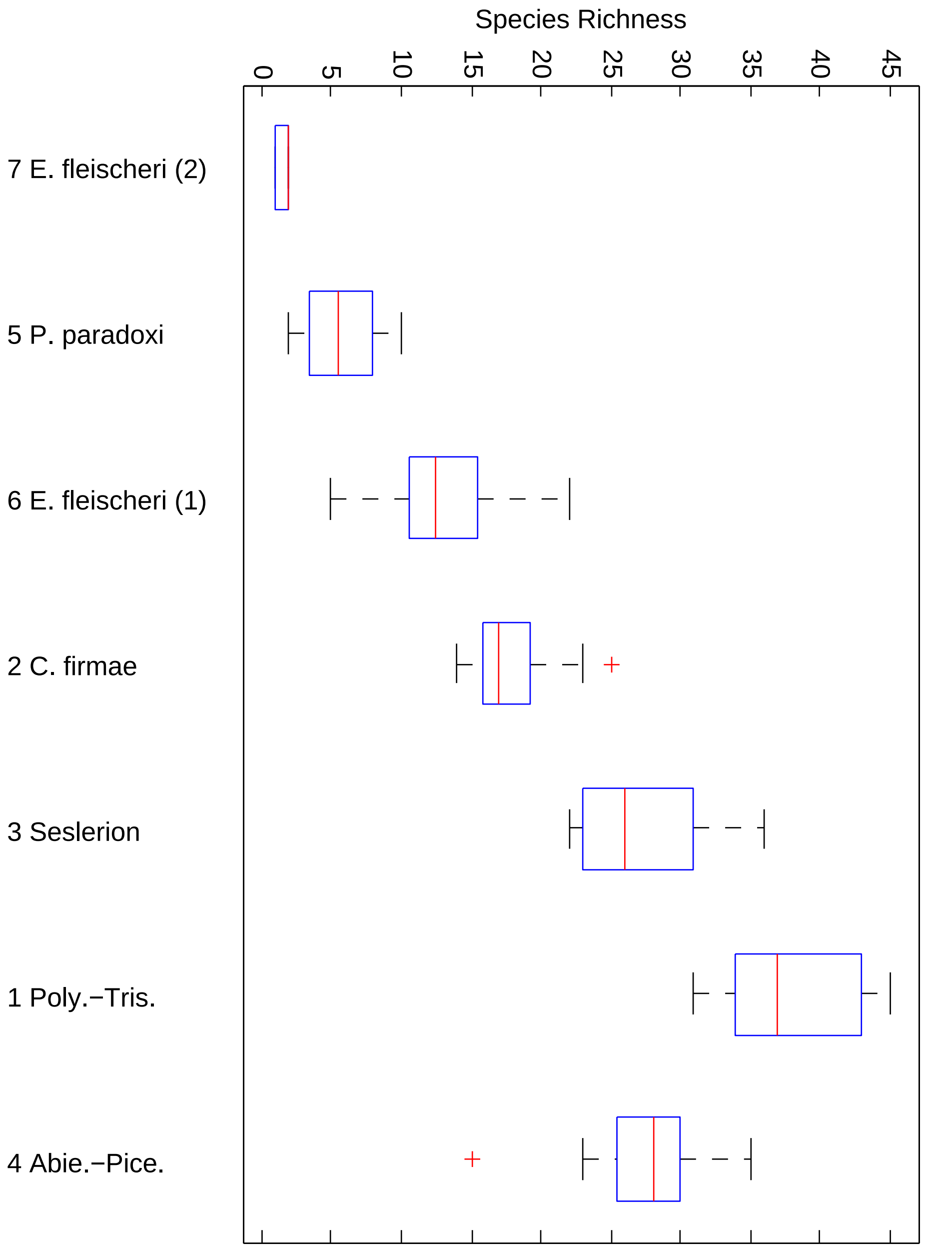
Figure 9. The relationship between estimated age and the sample sites classified as phytosociological units.

Figure 10. Box plots of factor scores (Factors 1, 2 and 7) sorted by units. The upper and lower box margins mark the 75th (Q_{75}) and the 25th (Q_{25}) quartiles respectively, with the mid box line showing the median. The whiskers show the extremes of the data (maximum and minimum) except for situations where outliers are present, defined as either $Q_{75}+1.5(Q_{75}- Q_{25})$ for the maximum and $Q_{25}-1.5(Q_{75}- Q_{25})$ for the minimum.


Fan Apex
C
B
A
occupied
unoccupied
time
C
occupied
unoccupied
time
B
occupied
unoccupied
time
A
Degree of active channel occupation
Transect
Long profile


Specific richness
45
20
10
0
Phyto-sociological unit
13 Abieti Piceion
9 Polygono-Trisetion
17 Seslerion
21 Caricion firmae
17 Epilobion fleischeri (1)
8 Petasition paradoxi
6 Epilobion fleischeri (2)
0
75
150 m
N
A
B
C
D
E


45
40
35
30
25
20
15
10
5
0
Species Richness
E
D
C
B
A


Species Richness
0
5
10
15
20
25
30
35
40
45
7 E. fleischeri (2)
5 P. paradoxi
6 E. fleischeri (1)
2 C. firmae
3 Seslerion
1 Poly.−Tris.
4 Abie.−Pice.

Bare deposits

Epilobion fleischeri (1)

Petasition paradoxi

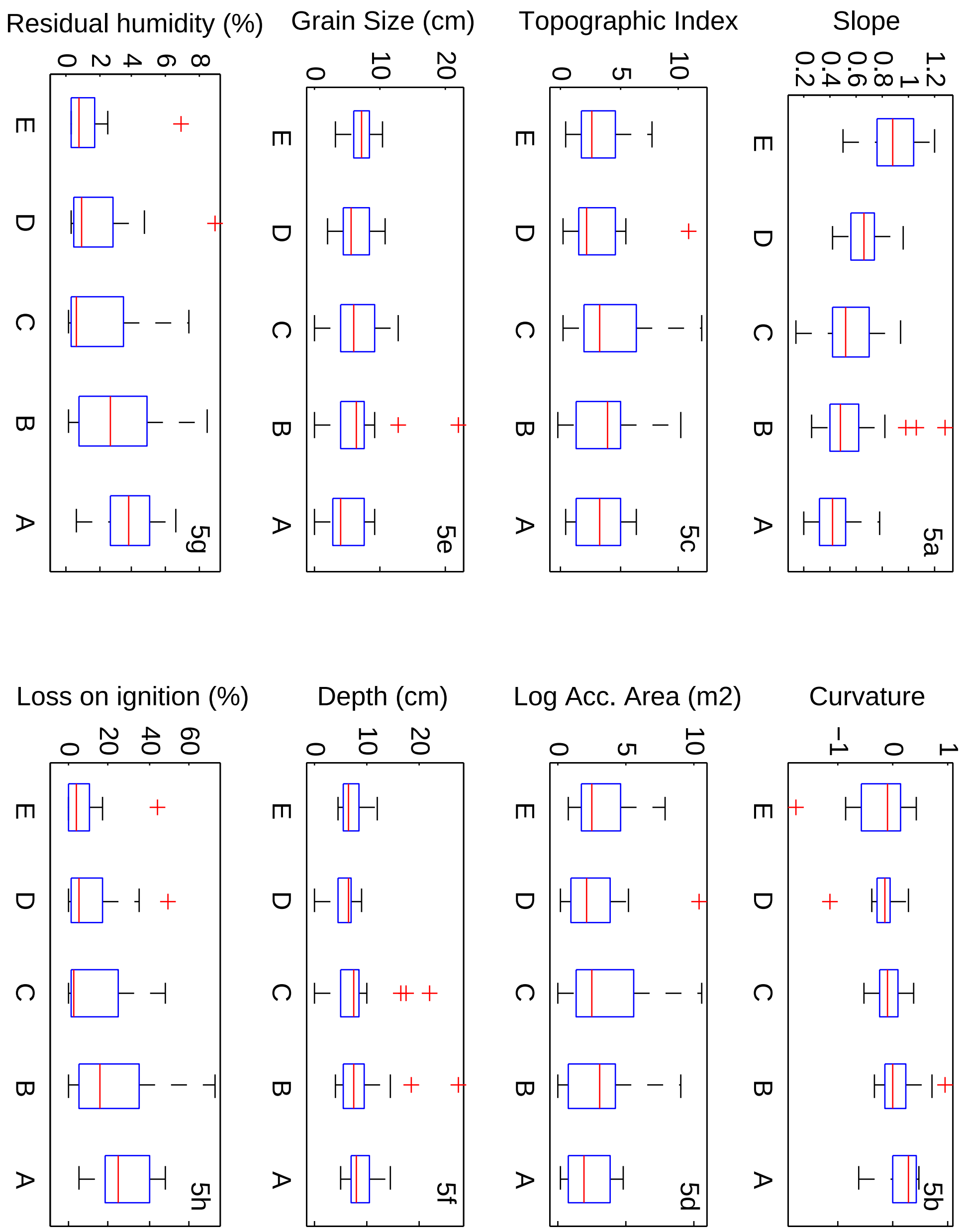
Epilobion fleischeri (2)

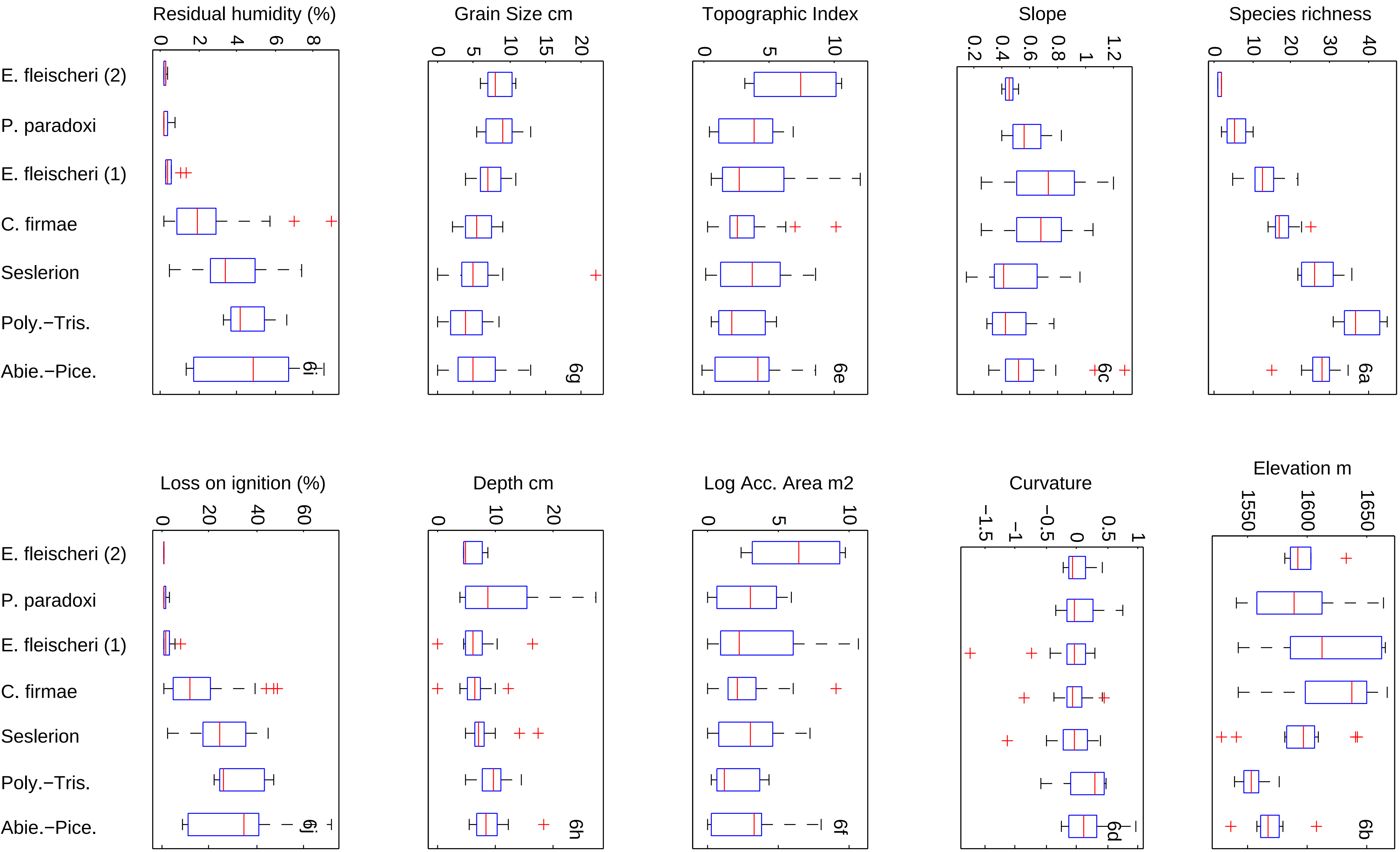
Caricion firmae

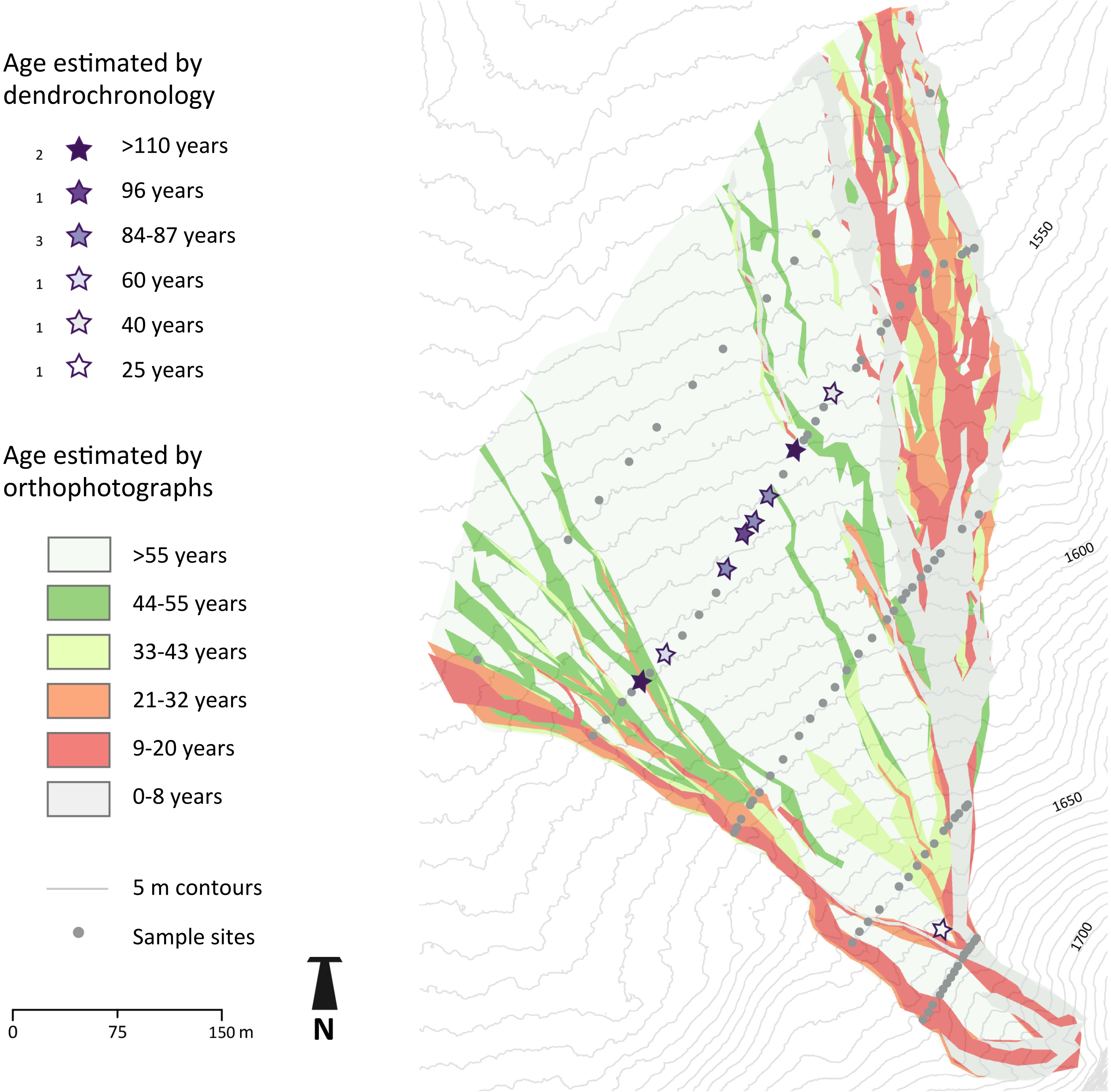
Seslerion

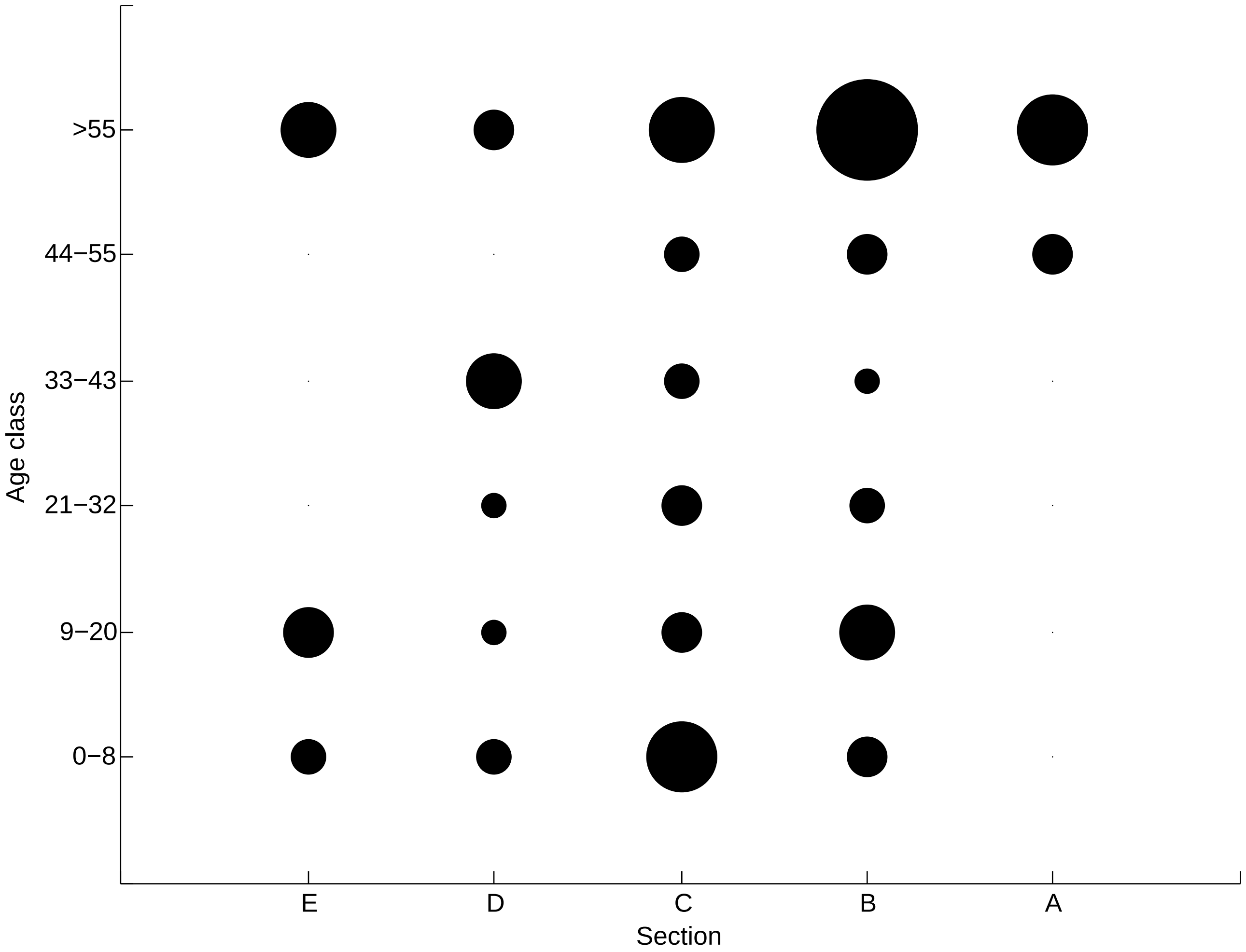
Polygono-Trisetion

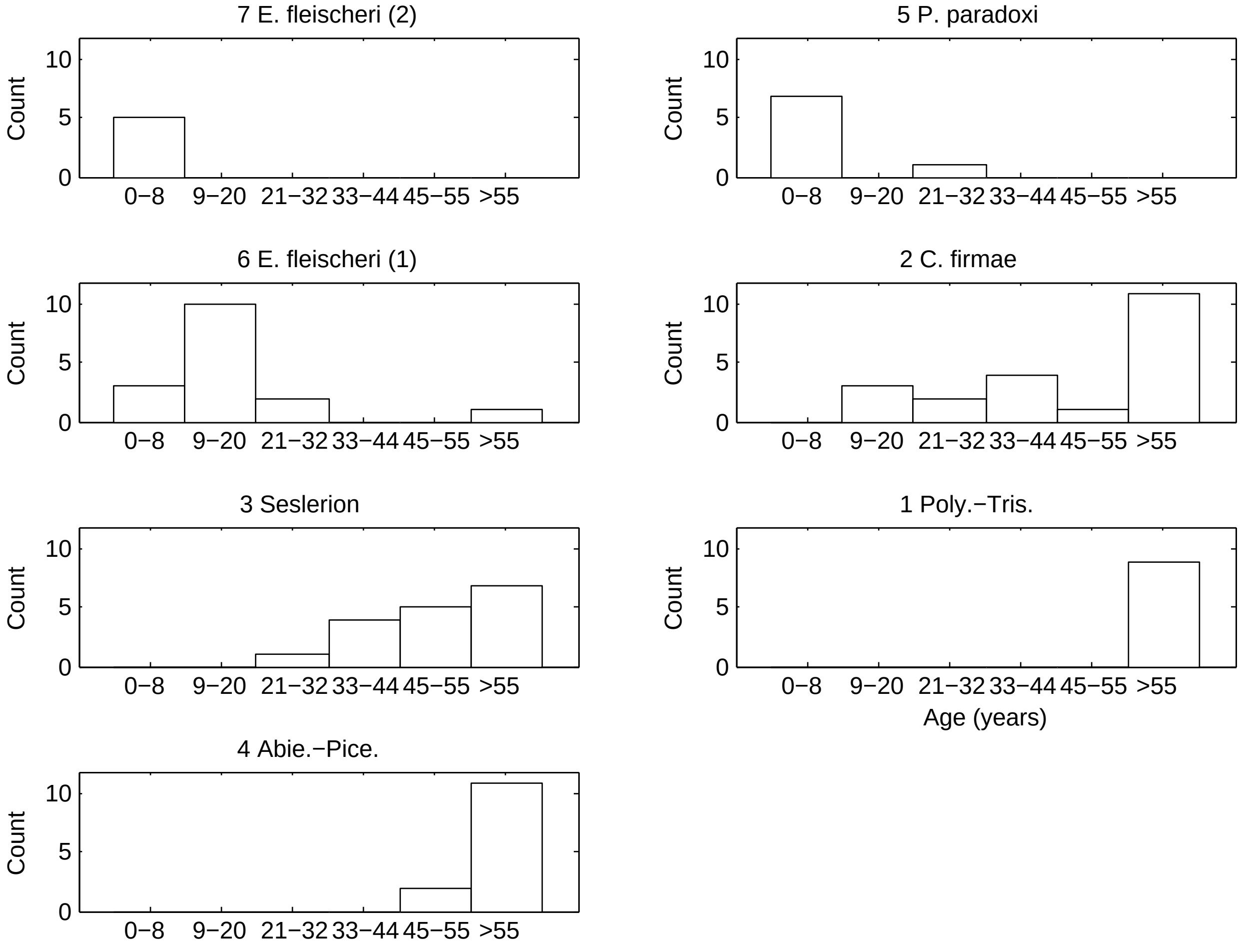
Abieti-Piceion


Slope
0.2
0.4
0.6
0.8
1
1.2
5a
Curvature
-1
0
1
5b
Topographic Index
0
5
10
5c
Log Acc. Area (m2)
0
5
10
5d
Grain Size (cm)
0
10
20
5e
Depth (cm)
0
10
20
5f
Residual humidity (%)
0
2
4
6
8
5g
Loss on ignition (%)
0
20
40
60
5h
E
D
C
B
A


Residual humidity (%)
0
2
4
6
8
6i
Grain Size cm
0
5
10
15
20
6g
Topographic Index
0
5
10
6e
Slope
0.2
0.4
0.6
0.8
1
1.2
6c
Species richness
0
10
20
30
40
6a
E. fleischeri (2)
P. paradoxi
E. fleischeri (1)
C. firmae
Seslerion
Poly.−Tris.
Abie.−Pice.
Loss on ignition (%)
0
20
40
60
6j
Depth cm
0
10
20
6h
Log Acc. Area m2
0
5
10
6f
Curvature
−1.5
−1
−0.5
0
0.5
1
6d
Elevation m
1550
1600
1650
6b
E. fleischeri (2)
P. paradoxi
E. fleischeri (1)
C. firmae
Seslerion
Poly.−Tris.
Abie.−Pice.


Age estimated by dendrochronology
2 ★ >110 years
1 ★ 96 years
3 ★ 84-87 years
1 ☆ 60 years
1 ☆ 40 years
1 ☆ 25 years
Age estimated by orthophotographs
>55 years
44-55 years
33-43 years
21-32 years
9-20 years
0-8 years
5 m contours
Sample sites
0
75
150 m
N
1550
1600
1650
1700


>55
44−55
33−43
21−32
9−20
0−8
Age class
E
D
C
B
A
Section



7 E. fleischeri (2)

5 P. paradoxi

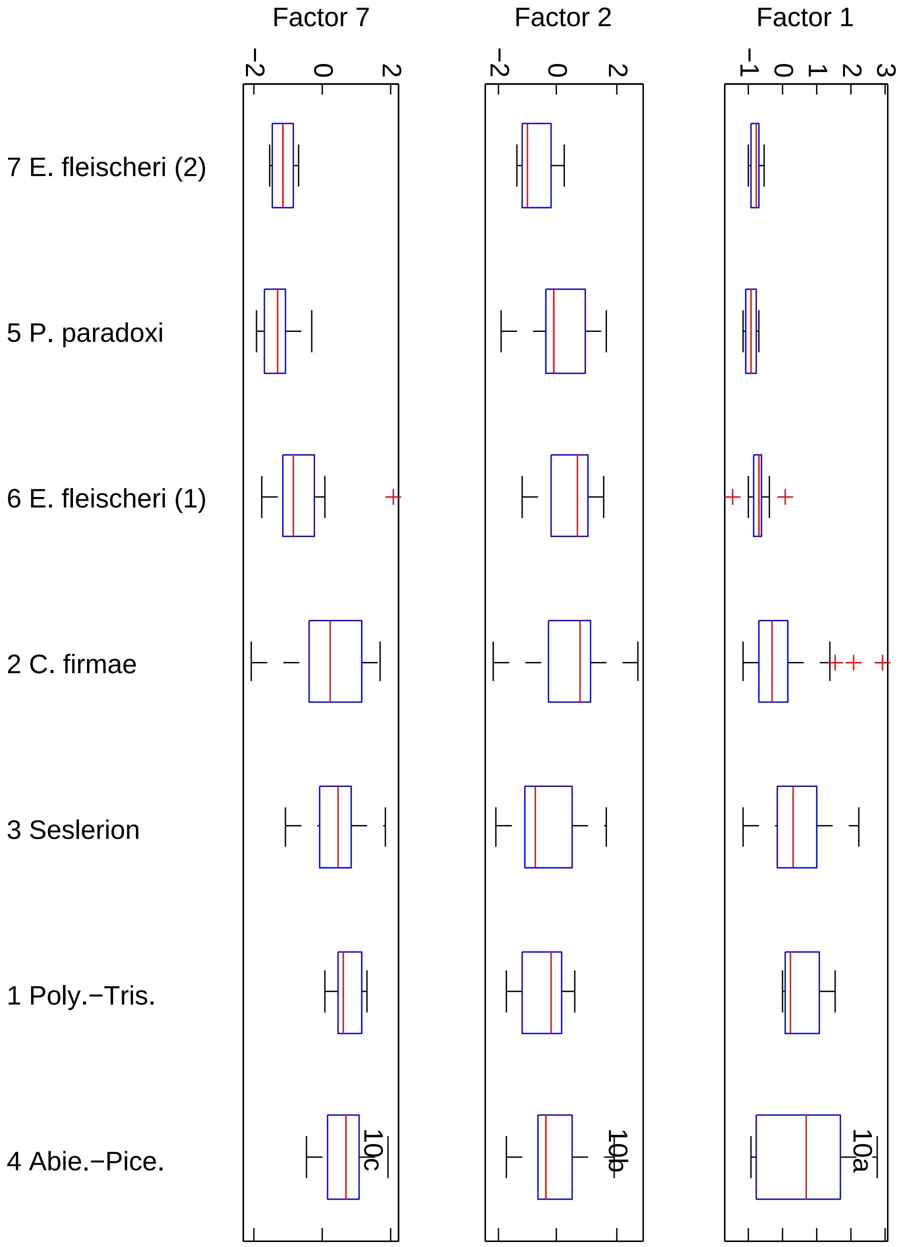
6 E. fleischeri (1)

2 C. firmae

3 Seslerion

1 Poly.−Tris.

4 Abie.−Pice.


Factor 7
Factor 2
Factor 1
−2
0
2
−2
0
2
−1
0
1
2
3
7 E. fleischeri (2)
5 P. paradoxi
6 E. fleischeri (1)
2 C. firmae
3 Seslerion
1 Poly.−Tris.
4 Abie.−Pice.
10c
10b
10a