Observed changes in mountain vegetation of the Alps during the XXth century

Role of climate and land-use changes

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Jeanne BODIN
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Binational doctoral thesis

presented to obtain the Ph.D. degree:

Docteur en Biologie Végétale et Forestière
de l'Université Henri Poincaré, Nancy 1, France
and
Doktorin der Naturwissenschaften
Dr. rer. nat. (*Doctor rerum naturalium*)
der Gottfried Wilhelm Leibniz Universität Hannover, Germany

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Matthias DOBBERTIN, Doctor, WSL, Birmensdorf, Switzerland (Referee)
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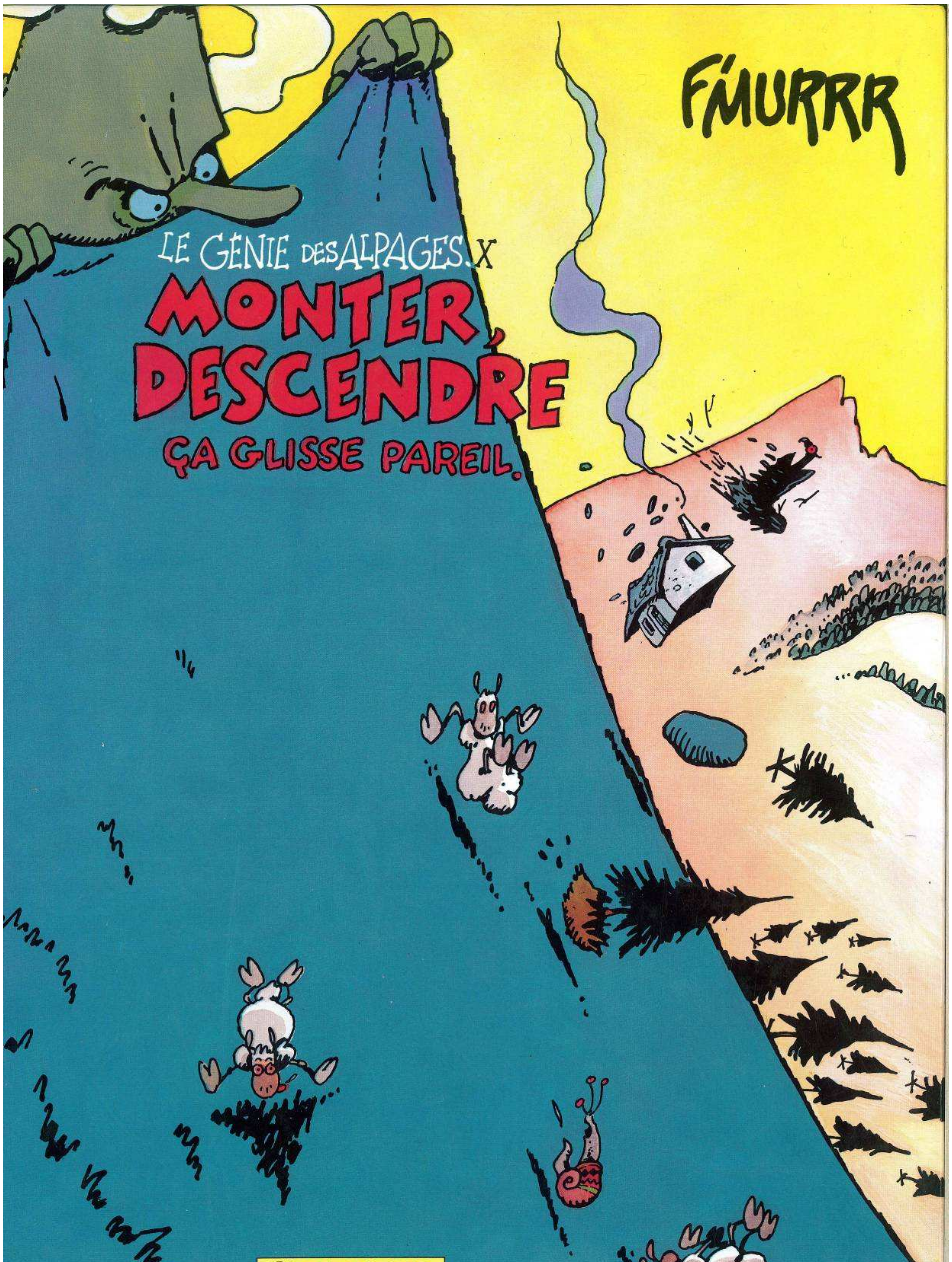

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LE GÉNIE DES ALPAGES. X

MONTER, DESCENDRE

ÇA GLISSE PAREIL.

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Summary

Annexes

Abstracts

I. GENERAL INTRODUCTION

There is an intrinsic interest in studying vegetation because it is an element of biodiversity, as such participating in ecosystems resilience and playing different functional roles in biogeochemical cycles. It contributes to the heritage value of habitats and landscapes. On the other hand, vegetation illustrates the different dynamic stages of plant succession, from pioneer to climax stage.

Moreover, vegetation is a useful indicator of environmental conditions, including both the abiotic (climate, soil…) and biotic conditions (stand characteristics, human impact…). Phytosociologists intensively used this indicator since the beginning of the XXth century for natural and semi-natural site description and classification, in the context of nature and landscape management.

Since a few decades, the interest has shifted from a static assessment of the spatial variations of the environment based on the vegetation, to the study of the dynamic response of vegetation to environmental changes in the context of global change. Several vegetation changes caused by anthropogenic perturbations were emphasized. Changes in the amount and composition of atmospheric deposits, in land-use management and/or in climate, all of them occurring on the long-term and over large areas and showing to have significant impacts on the vegetation. In the following, these main drivers responsible for long-term vegetation changes are presented, and thereafter the work focusing more specifically on the vegetation response to climate warming.

A. WHAT ARE THE CHANGES IN THE ENVIRONMENT THAT PROMOTE CHANGES IN VEGETATION?

1. Eutrophication and acidification due to atmospheric deposition

In vegetation change research, the first phenomenon put in evidence was the response to atmospheric deposition of pollutants. Eutrophication, due to atmospheric deposition of ammonium from agricultural fertilization and nitrate from road traffic, house and industry combustions resulted a higher nitrogen content in soils (Thimonier 1994), and an increasing number of nitrophilous species were observed in temperate forests (Thimonier *et al.* 1992;Thimonier *et al.* 1994; Lameire *et al.* 2000; van Herk *et al.* 2002; Bernhardt-Römermann *et al.* 2007) or Mediterranean regions (Schwabe *et al.* 2007; Pinho *et al.* 2008). This phenomenon could lead to a loss of biodiversity since forest vegetation, and semi-natural ecosystems in general are globally adapted to lower levels of nitrogen availability than other types of ecosystems, especially those more strongly disturbed by man activities, and the spatial heterogeneity of N availability will decrease (Gilliam 2006).

Nitrogen fertilization, together with CO_2 enrichment, have favoured growth increase of forest trees in Europe (Kenk & Fischer 1988; Hättenschwiler *et al.* 1996; De Vries *et al.* 2006). Such an impact of atmospheric changes on growth of understorey species has been seldom studied.

Acidification of vegetation, *i.e.* the increase of relative abundance and frequency of more acid tolerant species versus neutrophilous species was also observed in resampling studies. Sulphur deposition was the main driver of this acidification. Nitrogen deposition, especially in the ammonia form, was also partly responsible. Acidification is also a consequence of nutrient uptake, biomass removal by man and natural leaching accompanying forest maturation. But, whereas acid deposition was high in the seventies, it decreased strongly since the eighties due to political efforts, leading to complex response of vegetation: in Austrian Alps, while N deposition was increasing, the number of basophilous species increased because of decreasing sulphur deposition, whereas only a weak response of nitrophilous species was observed (Hülber *et al.* 2008). On the opposite, while sulphur deposition had decreased in Norway, a decline in abundance of several vascular plants was reported and attributed to a lagged response to previous soil acidification (Økland *et al.* 2004). In northwestern Germany, vegetation responded only weakly to acidification and eutrophication (Diekmann & Dupré 1997).

2. Species loss from habitat fragmentation

Habitat fragmentation could hinder the dispersal of specialist species, leading to their rarefaction or local extinction. The concept of ecological corridors was proposed to facilitate species dispersal thanks to the connectivity of formerly disconnected habitats. In spite of these decisions, losses were already observed in species having a scattered or rare distribution, sometimes at their distribution margin (Lavergne *et al.* 2005, Lavergne *et al.* 2006).

Causes of habitat fragmentation are multiple, and are mainly due to urbanization and transport infrastructures. More generally, these causes result from land-use change and are often linked to other phenomena such as eutrophication. For example, in British chalk grassland, a decline in stress-tolerant species specialists of calcareous soils was observed, while mesotrophic species appeared and Ellenberg fertility value increased. These phenomena were explained by habitat fragmentation and nutrient enrichment (Bennie *et al.* 2006).

3. Forest colonisation after agricultural abandonment and its consequences on vegetation

Rural depopulation has lead to the abandonment of agricultural activities in less accessible or less fertile areas (Tasser & Tappeiner 2002; Gellrich & Zimmermann 2007), more or less continuously over the 20th century, while other agricultural regions were increasingly intensively managed. Abandoned fields and pastures were immediately colonised by shrubby formation and then forests, strongly transforming the local species composition and the landscape organization. Chauchard (2007) gives a list of abandoned lands and types of subsequent reforestation in Europe, as a consequence of land abandonment.

In Mediterranean mountains, forest expansion started at the end of the 19th century mainly with *Pinus sylvestris* colonisation (Tatoni *et al.* 2004), leading to more mature stands during the last decades, and an increase in the abundance of *Fagus sylvatica* and *Abies alba* (Courdier & Dreyfus 2005; Chauchard *et al.* 2007). In the Alps, regeneration and colonisation of tree species above the tree-line has been often attributed to pasture abandonment rather than to climate warming (Penuelas & Boada 2003; Cairns & Moen 2004; Motta *et al.* 2006; Bolli *et al.* 2007; Cairns *et al.* 2007; Gehrig-Fasel *et al.* 2007; Batllori & Gutiérrez 2008), as shown for *Abies alba* by Chauchard *et al.* (submitted), or for *Larix decidua* Didier (2001). As a consequence of forest colonisation, a decline of species diversity due to a homogenization of vegetation cover at the landscape scale was observed in calcareous Alps of Austria (Dullinger *et al.* 2003).

In France, the increase in forest cover over the last decades has been highest in the low elevation mountains of south-eastern France, and especially in the Southern Alps (see figure 1).

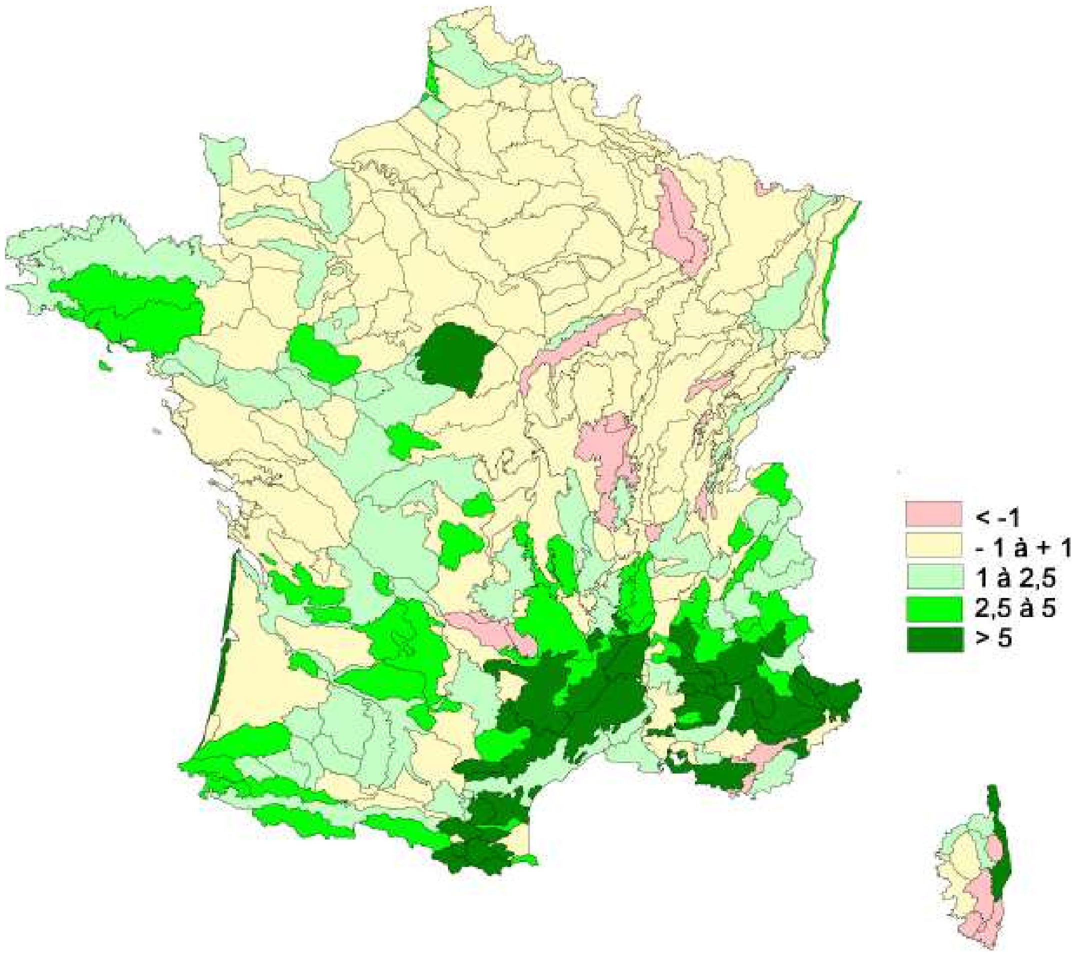

Figure I-1: Change in forest cover in France over the period 1978 to 2004, in percentage of total forest cover in each of the small forest regions of France. Data from the National Forest Inventory.

4. Herbivory

High density of wild herbivores disturbs sapling regeneration in forests. More generally, variations in browsing pressure influence forest understorey or grassland species composition since herbivores are selective grazers (Picard *et al.* 1993; Côté *et al.* 2004; Chauchard *et al.* 2006; Eskelinen & Oksanen 2006; Mayer & Huovinen 2007; Osem *et al.* 2007; Moen & Lagerström 2008; Boulanger *et al.* 2009; Mudrak *et al.* 2009).

5. Land use legacy

Previous land use still has an influence on today vegetation. In France for example, the area covered by forests today is twice the area as it was two centuries ago, involving that at least half of French forests had previously a different land use. Species typical from ancient forests in Europe were identified. These species are rather shade-tolerant, geophyte and hemicryptophyte and have low dispersal ability (Hermy *et al.* 1999; Dupouey *et al.* 2002). Ancient forest species were often absent from recent forests because of their low colonisation rate. As a consequence, lists of typical species for recent forests have also been established.

These legacies of previous land use could persist through time for very long periods. Present diversity of species is still influenced by former Roman land use, even fifteen centuries after abandonment (Dupouey *et al.* 2002; Dambrine *et al.* 2007). Diversity is higher around the ancient buildings (farms) than further away, due to differences in nutrient cycling. The same kind of vegetation persistence was reported on abandoned summer farms in Western Norway (Potthoff 2007).

6. Forest management and forest dynamics

The natural forest regeneration and aging cycle, and forest management, which controls stands density and height, both influence understorey species composition primarily by changing light conditions (Deconchat & Balent 2002; Wild *et al.* 2004; Łysik 2008; Tinya *et al.* 2009; Dölle & Schmidt 2009; Baeten *et al.* 2009). In addition, natural stand aging, as well as wood uptake, both increase soil acidity (Tamm & Hallbäcken 1988), which in turn affects understorey species composition. Species richness was shown to be higher in unmanaged forests, compared to managed forests (Paillet *et al.* 2009), mainly because the oldest stages of the natural regeneration cycle are usually truncated in managed forests, where this cycle is shortened. This phenomenon can affect plant species occurrence, for those preferring the latest stages of forest dynamics.

B. CLIMATIC CHANGE

The general increase of temperature observed in the last century accelerated during the last decades (Trenberth *et al.* 2007), at a global level. Similarly, climate on the French territory had undergone a 0.9°C warming between 1901 and 2000 (Moisselin *et al.* 2002 and figure 2), mainly because of an increase in minimal temperature, and a 0.3°C/decade warming during the last thirty years. In Switzerland, the mean decadal trend reached +0.13°C over the last three decades (Rebetez & Reinhard 2008). This warming trend was stronger in the mountains compared to the lowlands over the last 15 years of the twentieth century (Beniston *et al.* 1997; Beniston 2006). Temperature increase on the overall European Alps was 1.1°C between 1890 and 2000 according to Böhm *et al.* (2001).

1. Expected responses of species and biomes

Ecosystems and species are expected to respond to such an environmental change at different levels (Walther *et al.* 2002), *e.g.* by acclimatation (phenology, growth), migration (distribution range) and genetic adaptation. Climatic envelope models have been used to project future potential distribution of species depending on the climate scenarios established by IPCC. These models expect northward or upward migration of species ranges or biomes (Bakkenes *et al.* 2002, Skov & Svenning 2004, Gaucherel *et al.* 2008), and extinctions risks for the worst (Thomas *et al.* 2004, Thuiller *et al.* 2005). They were later improved by taking into account other factors influencing species distribution, as biotic interactions and dispersal ability (Brooker *et al.* 2007, Morin *et al.* 2008), and land-use change on a more global level (Sala *et al.* 2000, Defries *et al.* 2002, Dirnbock *et al.* 2003, Thuiller *et al.* 2004, Turner *et al.* 2007, Araújo *et al.* 2008). Because the climate already changed during the XXth century, such migrations of species, following the movement of their climatic niche, should have already started. The topic of the present work is the study of the way species distribution follows the shift of their climatic niche.

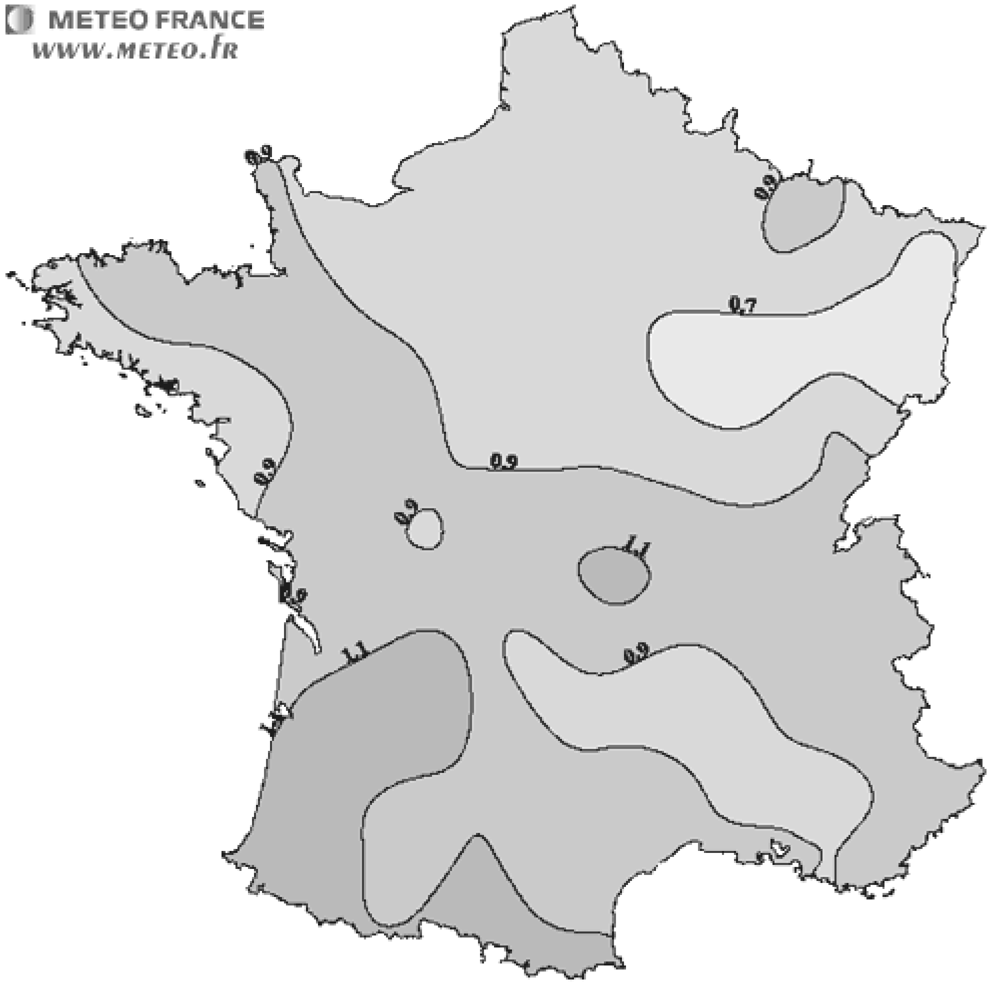

Figure I-2: Trend of mean temperature over the XXth century, Météo France.

2. Particular case of mountains

In mountain, there is a strong decreasing temperature gradient with increasing elevation. It has been estimated to be 0.56°C per 100 m of elevation in the southern Alps based on a synthesis of numerous climate stations (Aimé & Sarrailh 1972), and valuable for all mountain region (Ozenda 1985). This gradient is much steeper than in the lowlands along latitude (Jump *et al.* 2009). Distances between successive isotherms are much smaller in mountains. Thus, species are expected to migrate more rapidly in response to climate change in the mountains than in the lowlands. Moreover, mountains are often less urbanised than lowlands in Europe and include fewer infrastructure and agricultural zones, so that such obstacles should not hinder wild species migration. Thus, models of species migration were established with a finer resolution in mountain regions to take into account microclimatic features of mountain areas (Gottfried *et al.* 1999, Trivedi *et al.* 2008, Randin *et al.* 2009). But observations are needed to verify projections, to check the extent of species responses, and to understand the real triggers and mechanisms of vegetation shifts. In this thesis, the interest is focused on observations of vegetation responses to recent climate change. One of the key questions is: will vegetation belts (collinean, montane, subalpine, alpine and nival belt) migrate as a whole entity, all species within a belt behaving more or less in the same manner, as illustrated be Ozenda & Borel (1995) or will species display independent patterns, leading to a redistribution of species' composition and communities between vegetation belts? Paleoecology and the study of post-glacial migrations in Europe tend to support the idea that species communities are not moving as an entity, but are evolving through independent species' migration patterns (Huntley 1991). The study of the recent vegetation changes, in reaction to the climate warming of the end of the XXth century could bring valuable information about this important question.

C. KNOWLEDGE ON OBSERVED VEGETATION SHIFTS RELATED TO CLIMATE WARMING

Effects of climate warming on species' or community shifts have been observed for animals as well as plants (Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003; Walther 2004) from different types of ecosystems.

Plant species shifts along latitudinal gradients have been documented mainly at high latitude as a frequency increase of herbaceous species (Smith 1994) or increasing shrub abundance (Sturm *et al.* 2001) in arctic or Antarctic tundra. A progress of native evergreen broad-leaved species (the so-called lauriphyllous species) in forests was expected since they should be favoured by an increase in late winter and spring temperatures. While budburst of deciduous trees has not yet started, leaves of these evergreen species should benefit from an increase in early spring temperature. Indeed, a northward shift of *Ilex aquifolium* was reported from northern Europe (Walther *et al.* 2005a). An increase in frequency of this species was also noted within its distribution range, in north-eastern France (Cluzeau *et al.* 2001a; Cluzeau *et al.* 2001b). In Mediterranean area, *Ferula communis* L. subsp. *glauca* was also shown to shift northward (Mandin 1993).

Response of animal species to climate warming was mostly observed for butterflies (Parmesan 1996; Parmesan *et al.* 1999; Parmesan & Yohe 2003; Warren *et al.* 2001; Franco *et al.* 2006) or birds (Thomas & Lennon 1999; Devictor *et al.* 2008), but also for some other taxonomic groups (Hickling *et al.* 2006). Both northern and southern ranges limits were affected.

However, most studies on the climate change impact on species distribution have focused on mountain areas where species are expected to respond more strongly.

1. Observed species shifts in mountain areas

Here we concentrate on plant migration responses to climate warming.

a. Extension at the upper limit of species distribution

First studies focusing on vegetation shifts in mountains were conduced on alpine summits, by reinventory of summit flora. The oldest ones were the reinventory of earlier studies realised by Braun-Blanquet on Piz Languard in Bernina and Piz Linard in Engadin, Switzerland (Braun-Blanquet 1955; Braun-Blanquet 1957, respectively), and although climate warming was not yet highly topical, increase in species richness on these two summits already suggested a signal of climate warming and were seminal for the following studies.

Later, based on the same kind of phytogeographical monograph of a region (*e.g.* Rübel 1912), series of summits were reinventoried in the Alps (Hofer 1992; Grabherr *et al.* 1994; Grabherr *et al.* 1995). Species newly recorded at the summits were considered to have migrated from lower elevation, responding to a global temperature increase. This was confirmed by more recent studies in the same area (Walther *et al.* 2005b; Walther *et al.* 2005c; Holzinger *et al.* 2008). According to Jurasinski & Kreyling (2007), this upward shift led to an increase in homogeneity among summits. Homogenization process could also have occurred in Norwegian mountain since species with wide altitudinal and ecological ranges were both increasing in abundance and shifting upward, while more specialist species declined (Klanderud & Birks 2003). The same kind of increase in species richness was observed along an elevation gradient in Italy, in front of the valleys previously studied by Braun-Blanquet in Switzerland (Parolo & Rossi 2008). Additionally, species which were already present at lower elevation along the transect at the first sampling date were recorded at higher elevation during the resampling study, confirming the observed trend of upward species shift. In order to get results homogenised on a worldwide scale, a project of long-term summits monitoring and reinventory has been designed with a homogeneous methodology. First results are consistent with other summits reinventory, and show that new species from lower belts have colonised the summits (Pauli *et al.* 2007; Erschbamer *et al.* 2009). In arctic mountains, only an increase in the abundance of one shrub and two herbaceous species was reported, but no global upward shift (Wilson & Nilsson 2009), whereas an upslope expansion was reported on a sub-Antarctic Island (le Roux & McGeoch 2008).

Within forest belts, anthropogenic disturbances other than climate change could be at a lower level than in above-forest areas, mainly because livestock and pasturing are most often more intense above than below the treeline. The pine mistletoe was monitored along a transect at its upper range limit, and displayed an upward shift, seemingly caused by climate warming (Dobbertin *et al.* 2005).

b. Treeline and ecotones

In addition to herbaceous and understorey species mentioned in the previous paragraph, the advance of tree species in mountain areas have been also often studied. Since detection of the altitudinal tree limit is relatively easy, in comparison of the mapping of herbaceous species distribution, and because the mechanisms underlying the determination of treeline have been of interest for a long time (Broll & Keplin 2005), altitudinal tree limit has been used as a study model of forest ecosystem response to climate warming. However, because the position of the treeline was shown to be controlled as much by anthropogenic pressure as it is by climate (Bader & Ruijten 2008), effect of climate warming on its advance has been debated. The consensus is that current advance of treeline has been mostly triggered by pasture abandonment above treeline, but that climate warming also favoured tree regeneration and growth (Penuelas & Boada 2003; Cairns & Moen 2004; Motta *et al.* 2006; Bolli *et al.* 2007; Cairns *et al.* 2007; Gehrig-Fasel *et al.* 2007; Batllori & Gutiérrez 2008). However, treeline advance was not expected when it was already at its potential highest limit, *i.e.* its climatic limit (Ninot *et al.* 2008). Only few authors proposed climate change as the only cause of treeline advance (Kullman 2002; Sanz-Elorza *et al.* 2003; Beckage *et al.* 2008; Wieser *et al.* 2009),

c. Retraction at lower limits of species distribution

Whereas cold temperatures seem to represent a real constraint on the development of species at their northern or upper distribution range, warm temperatures seem not to be the decisive factor at southern or lower limits (Vetaas 2002). Other factors such as habitat replacement by species shifting at their colder limit, habitat fragmentation or other anthropogenic disturbances could influence the species response (contraction, extinction) to temperature increase at their lower/warmer limits, making its interpretation difficult. Thus, partly because of the scattered species presence at lower margins compared to upper margins and, consequently, partly because their more difficult detection, very few studies were undergone on plant species at their lower limits. As expected, a decline of species at their lower limits was observed, either based on their reproductive performances (García-Camacho & Escudero 2009) on their abundance, frequency or growth (Klanderud & Birks 2003; Lesica & McCune 2004; Mitzunaga *et al.* 2005; Pauli *et al.* 2007; Erschbamer *et al.* 2009) preceding a probable extinction.

d. Shift of the species distribution optimum

For the moment, few studies have focused on the whole range of species distribution of mountain plants, because not enough complete datasets were available at two different dates. This kind of method should detect as well extinction or migration at each range limit, as a change in species frequency at the lower or upper elevations within the original range. Thus, optimum or mean elevation of a species is an interesting information because it integrates the presence of the species over its whole distribution range. Only three studies reported changes in species elevation using such an approach. The first one reported an upward shift of mean elevation of 316 species in the southern French Alps (Dupouey *et al.* 1998). Another one described a significant mean shift of 171 species optimum in French mountain forests (Lenoir *et al.* 2008), and others showed the increase of the averaged cover-weighted mean elevation of ten widely distributed species along a transect in Californian mountains (Kelly & Goulden 2008). All these three studies attributed the observed shift to climate warming.

e. Changes in community composition

When it is not possible to consider the whole range of species, for example when the number of plots is not large enough, it can be still interesting to study changes at the level of the entire plant community. Communities integrate ecological parameters of the environment. Parallel to the development of phytosociology discipline in the seventies, different authors have proposed indicator values of plant species for different factors of the environment, for the species pool of temperate central Europe (Ellenberg 1974) and Switzerland (Landolt 1977). These indicator values were used as such in other countries of Europe, or were completed or modified (*e.g.* for Italy by Pignatti *et al.* 2001). More recently, indicators were constructed for French forest species based on a coupled statistical analysis of floristic and environmental data from the Ecoplant database (Gégout *et al.* 2005). For example, such indicator values can be averaged at the community level, and their change over time monitored, without a precise knowledge of the movements of each species belonging to the community. Such an approach can be used when the number of plots resampled is low, or when the total area sampled is small. Based on such calculations at the community level, Keller *et al.* (2000) showed that climate warming had provoked a change in community composition towards a more thermophilous vegetation.

2. Which phenomena influencing species distribution could interact with climate warming

Often, in previously quoted studies, vegetation not only reacted to climate warming, but also to some other direct or indirect anthropogenic disturbances. In some cases, the response to climate change has been considered as being independent from the response to these other anthropogenic disturbances (*e.g.* eutrophication). But, such other anthropogenic disturbances could also reinforced the impact of climate change: habitat fragmentation at the southern margins of species associated to climate warming favoured species loss (Lavergne *et al.* 2005; Lavergne *et al.* 2006), whereas pasture abandonment triggered the upward shift of subalpine or woody species favoured by temperature increase (Vittoz *et al.* 2009).

The species shifts already observed could be also the consequence of a slow re-colonisation process triggered by temperature increase since the end of the Little Ice age, *i.e.* around 1850 (Kammer *et al.* 2007), rising the question of inertia of species response.

D. WHERE AND HOW TO DETECT VEGETATION CHANGES AND SPECIES MIGRATION? GENERAL METHODOLOGY

The study of vegetation changes under anthropogenic disturbances implies to have repeated inventories over years at one's disposal, or at least to find historical monitoring data for reinventory. These ancient studies should provide information on species presence together with either an accurate geolocalisation or a detailed ecological description of the environment (elevation, exposition, soil type, pH, habitat…). The record of species in each plot should be as exhaustive as possible.

1. Different approaches

a. Different methodologies

Authors of ancient studies did not always take care of the exact localisation of the plots they studied because their goal was often a static description of the vegetation in a region, or the study of an ecological question at one point in time, without any plan to come back later. Reinventories on permanent plots can only be based on fine localised plots, either on several plots with restricted area, or on fewer plots but with extended area. However, there are methods which can be used in case of resampling studies of non permanent plots. In this latter case, instead of studying changes in the appearance, disappearance or abundance of species at one or several locations exactly relocated and resampled, one can build a model of the relationship between species presence or abundance and environmental factors as elevation or aspect, and study the changes in this model over time. Such a method no longer needs permanent plots, but is instead relying on an appropriate global sampling scheme of vegetation at different dates. This method can be applied to the study of single species niche as well as to community changes, as long as environmental factors have been recorded together with vegetation data.

Another advantage of resampling in non-permanent plots is that it can more easily avoid the problem of intrinsic stand ageing between each inventory observed on permanent plot. When resampling a limited set of permanent plots, the first factor that will influence vegetation dynamics is the ageing and maturation of the stands at each plot (canopy closure, tree ageing, litter accumulation, progressive soil acidification…). It is usually difficult to separate such a maturation effect from other impacts. In non-permanent plot designs, one can rebuild a representative sample of the area under study at each date of sampling, not affected by stand ageing by an appropriate selection of plots according to their degree of maturation.

In resampling studies, two different cases should be distinguished: those where the initial sampling campaign was designed in order to be redone later, and those where it was not planned to do any later resampling. The first case includes the monitoring networks launched in France and Europe during the last decades. Such networks usually provide homogeneous vegetation data over space and time. In these networks, the sampling is often designed in order to be representative of the vegetation in the area under study at a given date. In comparison with studies not initially designed to be resampled, monitoring networks most often cover larger areas (region- or nation-wide) whereas the former are restricted to a selected area. In monitoring networks, planned for repeated inventories, protocols of vegetation recording are most often available, and the quality of vegetation censuses is usually better, as well as their exhaustiveness.

b. Which part of species range to observe?

i. Species range limits

Historically, studies have mostly focused on species' shifts at the upper limits, and the lower limits for animals mainly.

An expansion at the upper limit is expected under effect of climate warming. Hence, migration should be put in evidence by recording an arrival of species above their previous upper limit. It could be determined by recording new species arriving into a delimited area, for example a mountain summit. The shift is measured as the difference with the last recorded upper elevation known.

At lower limits, a retraction of the range is expected under climate warming. Method consists in a careful search and check of species presence at delimited localities known as the previous lower limit of the species, and a record of the today lower elevation of the species.

These methods usually focus on very restricted areas because the exhaustive search for upper or lower limits can be very long. It raises the question of the sampling intensity. Indeed, the extinction or arrival of a species at a locality could be the result of a species move within its distribution range, without any true change in upper or lower limits. Such a change will be confused with a change in elevation if the sampling intensity is too low.

More important is the problem of frequency increase because of an increasing exhaustiveness along the successive inventories (Archaux *et al.* 2006, Archaux *et al.* 2008, Vittoz & Guisan 2007). It is a very general observation that the number of species observed on a given area increase along time due to an improvement of observers exhaustiveness, either because they are better trained, or because they use previous lists of recorded species in the field when recording the new list. This is especially relevant for designs that were not planned to be resampled from the beginning.

One advantage of the method is that only few data are necessary, such as a list of localities for lower or upper limits of species, or a record of species found on a mountain summit. Such kind of data is available in a large number of ancient publications.

ii. Species optimum

The position of species optima along the elevation gradient can shift due to a homogeneous upslope movement of the whole species range, or an extinction or colonisation at one of the range limits. Simple models can be used to estimate the position of this optimum, such as the classical Gaussian logit model. This implies that the species displays a continuous and not-fragmented distribution in order to fit the model on the observed species frequency. Hence it is necessary to work with sufficiently frequent and not scattered species. The calculated optimum is usually not sensitive to a homogeneous increase of species frequency along the entire studied gradient. Thus, the position of the optimum does not depend on the exhaustiveness of the plant censuses, which is an interesting property of this indicator.

However, a lot of presence/absence observations are needed for each species in order to fit the distribution model, implying the availability of rather large data sets.

iii. Species communities

When not enough data are available to model the distribution of species according to elevation, it is still possible to test if vegetation has moved. One can use external information available for each species on its ecological requirements (*e.g.* life traits, Ellenberg's or Landolt's indicator values) and integrate this information at the whole plant community level, by averaging or other procedures. For example, temperature indicator values are available for most of the plant species of the Alps. Using these indicator values averaged at each plot, it is possible to test if vegetation has shifted towards a more thermophilous or cryophilous state between two inventories.

Such indicator values are not very sensitive to the presence or absence of a given species, nor sensitive to the plant census exhaustiveness. Thus, they are not much influenced by the quality of the vegetation census. Because they use a priori information, calibrated in other, previous, studies, such indicator values can be calculated without a precise knowledge of the distribution of species in the area under study, contrary to the modeling of the niche optimum, which needs to gather presence/absence data in a large number of plots.

When data are resampled in permanent plots, the simple comparison of these community indicators between successive dates provides information about the shift in vegetation. In case of non-permanent plots, shifts of vegetation must be identified through the study of the shifts in the relationship between the indicator values and elevation. For example, we will study in such cases (non-permanent plots) the relationship between Landolt's mean indicator value for temperature and elevation and the shift in this relationship between dates. A shift in this relationship implies that vegetation has moved.

c. Different spatial scales

Depending on the extent of the studied area, the significance of the results will differ. Working on small areas is, of course, easier but the results cannot be generalized. Methods based on the detection of changes in the species lower and upper limits, and methods based on the resampling of permanent plots can be used in small areas, because they do not require large datasets. Methods modeling the whole distribution range of a species, such as those used in non-permanent networks, require many plots along the studied environmental gradients and consequently larger study areas.

d. Different temporal scales

There is a trade-off between the time interval over which vegetation changes can be observed and the quality and reliability of the data available. Historical data are often old enough to observe vegetation changes on a long time scale, until a century in Europe. But the quality of old data is questionable, with unclear methodology of vegetation census, low accuracy of plots location, low exhaustiveness. At the opposite, homogeneous and high quality vegetation databases built from current monitoring networks only offer a short time period of study, because they were established only relatively recently. In this latter case, the observed response of species to environmental changes could be weak due to a too short period of observation.

e. Different habitats

Response of plant species to climate changes could depend on the habitat type they belong to (forest or meadows, subalpine or alpine belts…). Moreover, environmental changes other than climate change could have more marked effects in some habitats, relatively to others. Some habitats are prone to specific bias in the detection of long-term changes in vegetation composition. For example, studies based on forest permanent plots are prone to the stand ageing bias (see above). On the other hand, reinventories above the treeline are strongly influenced by pasture abandonment. It is important to avoid or control such confounding factors when studying effects of other environmental changes such as climate change. For example, reinventory in forests could avoid the stand ageing bias by using non permanent plots, carefully selected in order to get an equal average stand age at each sampled date. When working in the alpine belts, the choice of the study area should be made far above the treeline.

In forests of Western Europe, which are nearly all managed, the species composition of the tree stratum is mainly the historical result of the choices made by forest managers. Due to this strong and direct anthropogenic control, it is a biased indicator of environmental changes. Thus, that is the reason why we focused mainly on the understorey vegetation.

2. Description of the thesis chapters

The focus of this thesis is on the response of mountain plant species to climate warming over the Alps (figure 3). Three different aspects are highlighted, that were rarely studied so far: (i) dynamics of lower limits, (ii) changes in species optimum and (iii) changes in indicator values at the community level. Two of the studies are based on large scale sampling schemes. In these two large-scale studies, a new methodology of analysis is applied that is adapted for samples collected in non-permanent plots.

In this study, particular attention is paid to the detection and separation of climate change effects from other anthropogenic changes, especially land-use change, which is one of the main drivers of environmental changes in the montane belt of southern Europe.

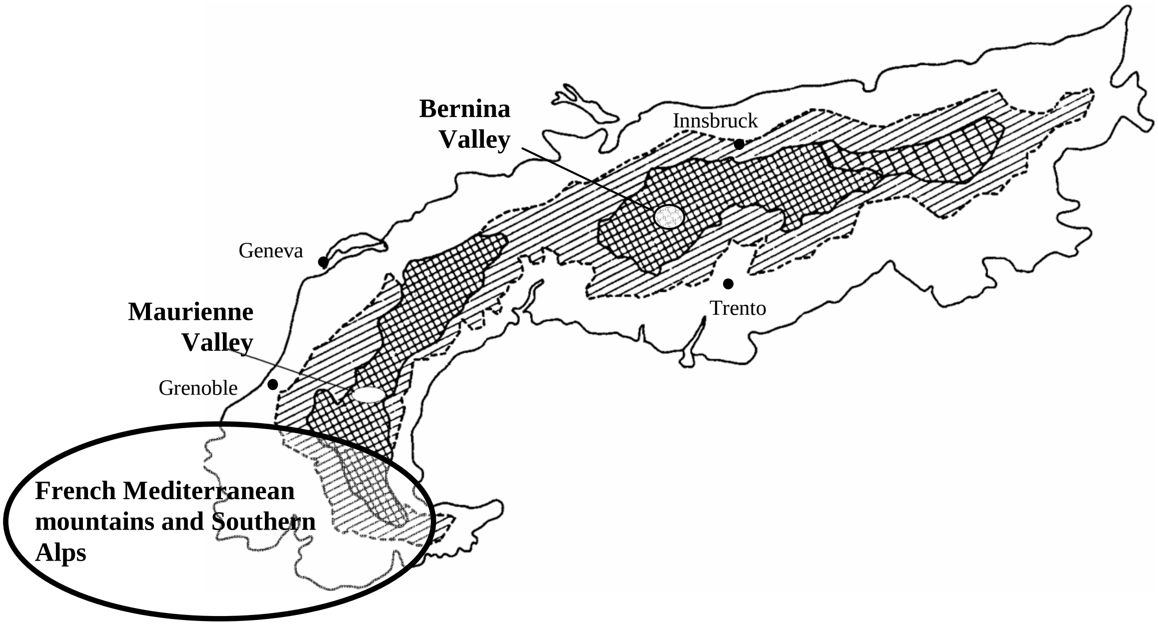

Figure I-3: Zonation of the Alps according to the main bioclimatic division: external Alps (in white), intermediate Alps (light grey hatching) and internal Alps (dark grey hatching). The three study areas of the present thesis are pointed: French Mediterranean mountains and Southern Alps, Maurienne Valley (France), and Bernina Valley (Switzerland, where two studies were made).

Hypotheses:

In case of climate warming, an upward shift of species and communities should be observed. The lower limit of species could also shift, whereas reasons of their limit distribution are not only controlled by climate. The rate of this movement should be quantified in meter per decade and compared to the equivalent shift of temperature. A potential inertia in species response could be expected.

Depending on time and space scale, response of species is able to vary. In addition, methodology used and studied habitat could also induce different species response.

The observed shifts are expected to be related to climate warming. However, knowing the broad distribution of other anthropogenic disturbance, species are potentially able to respond to changes of other environmental factors. If the main driver of vegetation change is climate warming, a spatially homogeneous response of vegetation should be expected because climate warming has been globally homogeneous over the study area. The observed trend should not depend on the methodology used to study it, as well.

The goal of this thesis is to address these questions through four case studies implemented at various time and spatial scales, and with various methodologies (table 1).

The first two studies took place in the mountain forest belt, where the effects of abandonment of pasturing are absent. These first two studies were based on the reinventory of non-permanent plots. An appropriate method of analysis is developed that suits such sampling designs, to test and quantify the shift in species-environment relationships.

In the first study, the vegetation data collected by the French National Forest Inventory (NFI) in the Mediterranean French mountains is analysed. Two successive inventories, separated by 14 years, and with more than 15 000 plots each were compared. This large dataset allowed to model the distribution of a selection of species at each inventory, thanks to logistic regression modelling. The shift in the optimum elevation of each species between the two sampling dates was tested and quantified. Thanks to the dendrometric and stand characteristics collected by the NFI together with vegetation data, it was possible to analyse the role of forest stand dynamics on vegetation shift. The interesting features of this first study are its broad sampling area (all the southeastern part of France), the high sampling intensity (one plot for 130 ha of forest), and the homogeneous methodology maintained through the successive inventories by NFI.

In the second study, a similar approach was applied, also studying the shift in a model of vegetation distribution along the altitudinal gradient, to the forests of an internal alpine valley, the Maurienne Valley. However, not each species was modelled individually, because the number of samples available was not high enough. Instead, the relationship between ecological indicator values of the plant community as a whole (mean Landolt and mean Ellenberg indicator values) and the altitudinal gradient was modelled, which then allowed to study the shift in this model between two successive inventories.

The third study focused on a rarely studied feature of vegetation distribution: the lower limit of species. It was tested if the response of species was similar at their lower limits in comparison with literature results describing the shifts at their upper limit. Old vegetation data, collected one century ago in the Bernina area in the Swiss Alps, served as baseline data for the localization of the lower limits for a number of species, which then was checked for the current occurrence of these species and potential shifts in their lower limit.

Finally, a more localized study of vegetation change is presented, in a small area of the alpine zone of Bernina. The interest of this study consists in the isolation of the area by natural physical barriers that protect the study area from other anthropogenic factors possibly influencing vegetation changes. The focus was on the identity of the new arriving species and the lost ones, in order to help understand the causes of the observed vegetation changes.

Table I-1: The different studies of the thesis.

	Country	Time span (years)	Habitat	Plot number	Sampling method	Analysis method: seek the shift of
French National Forest Inventory	France (South-East)	14	Forest	30,985	Non-permanent plots	Calculated elevation optimum of species
Maurienne Valley	France	47	Forest	475	Non-permanent plots	Community indicator values
Lower limits	Switzerland (Bernina)	100	Forest/Alpine	46	Permanent plots	Lower limits of species
Nunatak	Switzerland (Bernina)	100	Alpine	1	Permanent area	Vegetation composition

E. REFERENCES

Aimé S, Sarrailh JM (1972) Etude comparative du bilan hydrique de quelques bassins des Alpes du Sud. Première partie: Le bilan hydrique selon Thornwaite. *Annales du Museum d'Histoire naturelle de Nice*, **1**, 57-75.

Araújo MB, Nogués-Bravo D, Reginster I, Rounsevell M, Whittaker RJ (2008) Exposure of European biodiversity to changes in human-induced pressures. *Environmental Science \& Policy*, **11**, 38-45.

Archaux F, Gosselin F, Bergès L, Chevalier R (2006) Effects of sampling time, species richness and observer on the exhaustiveness of plant censuses. *Journal of Vegetation Science*, **17**, 299-306.

Archaux F, Camaret S, Dupouey J, Ulrich E, Corcket E, Bourjot L, Brêthes A, Chevalier R *et al.* (2008) Can we reliably estimate species richness with large plots? an assessment through calibration training. *Plant Ecology*, **203**, 303-315.

Bader MY, Ruijten JJA (2008) A topography-based model of forest cover at the alpine tree line in the tropical Andes. *Journal of Biogeography*, **35**, 711-723.

Baeten L, Bauwens B, De Schrijver A, De Keersmaeker L, Van Calster H, Vandekerkhove K, Roelandt B, Beeckman H *et al.* (2009) Herb layer changes (1954-2000) related to the conversion of coppice-with-standards forest and soil acidification. *Applied Vegetation Science*, **12**, 187-197.

Bakkenes M, Alkemade JRM, Ihle F, Leemans R, Latour JB (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology*, **8**, 390-407.

Batllori E, Gutiérrez E (2008) Regional tree line dynamics in response to global change in Pyrenees. *Journal of Ecology*, **96**, 1275-1288.

Beckage B, Osborne B, Gavin DG, Pucko C, Siccama T, Perkins T (2008) A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 4197-4202.

Beniston M, Diaz HF, Bradley RS (1997) Climatic change at high elevation sites: an overview. *Climatic Change*, **36**, 133-251.

Beniston M (2006) Mountain weather and climate: A general overview and a focuson climatic change in the Alps. *Hydrobiologia*, **562**, 3–16.

Bennie J, Hill M, Baxter R, Huntley B (2006) Influence of slope and aspect on long-term vegetation change in British chalk grasslands. *Journal of Ecology*, **94**, 355-368.

Bernhardt-Römermann M, Kudernatsch T, Pfadenhauer J, Kirchner M, Jakobi G, Fischer A (2007) Long-term effects of nitrogen deposition on vegetation in a deciduous forest near Munich, Germany. *Applied Vegetation Science*, **10**, 399-406.

Bolli JC, Rigling A, Bugmann H (2007) The influence of changes in climate and land-use on regeneration dynamics of Norway spruce at the treeline in the Swiss Alps. *Silva Fennica*, **41**, 55-70.

Boulanger V, Baltzinger C, Saïd S, Ballon P, Picard J, Dupouey J (2009) Ranking temperate woody species along a gradient of browsing by deer. *Forest Ecology and Management*.

Braun-Blanquet J (1955) Die Vegetation des Piz Languard, ein Masstab für Klimaänderungen. *Svensk Botanisk Tidskrift, 49, 1-9.* , **49**, 1-9.

Braun-Blanquet J (1957) Ein Jahrhundert Florenwandel am Piz Linard (3414 m). *Bulletin du Jardin Botanique Etat Bruxelles, Volume jubilaire Walter Robyns*, **137**, 221-232.

Broll G, Keplin B (2005) *Mountain Ecosystems. Studies in Treeline Ecology*. Springer, Heidelberg.

Brooker RW, Travis JM, Clark EJ, Dythamd C (2007) Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of Theoretical Biology*, **245**, 59–65.

Böhm R, Auer I, Brunetti M, Maugeri M, Nanni T, Schöner W (2001) Regional temperature variability in the european Alps : 1760-1998 from homogenized instrumental time series. *International Journal of Climatology*, **21**, 1779-1801.

Cairns DM, Moen J (2004) Herbivory influences tree lines. *Journal of Ecology*, **92**, 1019-1024.

Cairns DM, Lafon C, Moen J, Young A (2007) Influences of animal activity on treeline position and pattern: Implications for treeline responses to climate change. *Physical Geography*, **28**, 419-433.

Chauchard S, Pille G, Carcaillet C (2006) Large herbivores control the invasive potential of nonnative Austrian black pine in a mixed deciduous Mediterranean forest. *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestiere*, **36**, 1047-1053.

Chauchard S, Carcaillet C, Guibal F (2007) Patterns of land-use abandonment control tree-recruitment and forest dynamics in Mediterranean mountains. *Ecosystems*, **10**, 936-948.

Chauchard S (2007) *Dynamique d'une forêt de montagne méditérranéenne dans un monde changeant*. Unpublished PhD thesis, Université Montpellier II, Science et Techniques du Languedoc, .

Chauchard S, Beilhe F, Carcaillet C (submitted) Elevation of the upper tree-limit of silver fir (*Abies alba* Mill.) in the Alps since the middle-20th century: a land-use change phenomenon.

Cluzeau C, Drapier J, Virion R, Dupouey J (2001) Changements à long terme de la végétation forestière : apport des données de l'IFN. Rapport projet GIP-ECOFOR «Forêt et Modifications de l'Environnement ».

Cluzeau C, Dupouey J, Drapier J, Virion R (2001) Etude des modifications à long terme de la végétation forestière à partir des données de l'IFN. *Revue Forestière Française*, **53**, 413-419.

Courdier JM, Dreyfus P (2005) Retour du hêtre et du sapin dans les pineraies de l'arrière pays méditerranéen. Conséquences pour la gestion et la biodiversité - Return of beech and fir in pioneer coniferous stands in the Mediterranean region. Consequences for management and biodiversity. *Rendez-Vous Techniques*, 56-62.

Côté SD, Rooney TP, Tremblay J, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 113-147.

Dambrine E, Dupouey J, Laüt L, Humbert L, Thinon M, Beaufils T, Richard H (2007) Present forest biodiversity patterns in France related to former Roman agriculture. *Ecology*, **88**, 1430-1439.

De Vries W, Reinds GJ, Gundersen P, Starba H (2006) The impact of nitrogen deposition on carbon sequestration in European forests and forest soils. *Global Change Biology*, **12**, 1151–1173.

Deconchat M, Balent G (2002) Effets de la sylviculture et de l'exploitation forestière sur la diversité végétale. *Revue Forestière Française*, **LIV**, 559-566.

Defries RS, Bounoua L, Collatz GJ (2002) Human modification of the landscape and surface climate in the next fifty years. *Global Change Biology*, **8**, 438-458.

Devictor V, Julliard R, Couvet D, Jiguet F (2008) Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society B-Biological Sciences,* **275**, 2743-2748.

Didier L (2001) Invasion patterns of European larch and Swiss stone pine in subalpine pastures in the French Alps. *Forest Ecology and Management,* **145**, 67-77.

Diekmann M, Dupré C (1997) Acidification and eutrophication of deciduous forests in northwestern Germany demonstrated by indicator species analysis. *Journal of Vegetation Science,* **8**, 855-864.

Dirnbock T, Dullinger S, Grabherr G (2003) A regional impact assessment of climate and land-use change on alpine vegetation. *Journal of Biogeography*, **30**, 401-417.

Dobbertin M, Hilker N, Rebetez M, Zimmermann NE, Wohlgemuth T, Rigling A (2005) The upward shift in altitude of pine mistletoe (*Viscum album* ssp. *austriacum*) in Switzerland—the result of climate warming?. *International Journal Biometeorology,* **50**, 40-47.

Dölle M, Schmidt W (2009) Impact of tree species on nutrient and light availability: evidence from a permanent plot study of old-field succession. *Plant Ecology,* **203**, 273-287.

Dullinger S, Dirnbock T, Greimler J, Grabherr G (2003) A resampling approach for evaluating effects of pasture abandonment on subalpine plant species diversity. *Journal of Vegetation Science,* **14**, 243-252.

Dupouey J, Becker M, Bert D, Cadel G, Lefèvre Y, Picard J, Thimonier A (1998) Évolution récente des sols, de la végétation et de la productivité des forêts de montagne françaises. *Écologie*, **29**, 341-349.

Dupouey JL, Dambrine E, Laffite JD, Moares C (2002) Irreversible impact of past land use on forest soils and biodiversity. *Ecology,* **83**, 2978–2984.

Dupouey J, Sciamma D, Koerner W, Dambrine E, Rameau J (2002) La végétation des forêts anciennes. *Revue Forestière Française*, **LIV**, 521-531.

Ellenberg H (1974) *Zeigerwerte der Gefäßpflanzen Mitteleuropas*. Erich Goltze KG, Göttingen.

Erschbamer B, Kiebacher T, Mallaun M, Unterluggauer P (2009) Short-term signals of climate change along an altitudinal gradient in the South Alps. *Plant Ecology*, **202**, 79-89.

Eskelinen A, Oksanen J (2006) Changes in the abundance, composition and species richness of mountain vegetation in relation to summer grazing by reindeer. *Journal of Vegetation Science*, **17**, 245-254.

Franco AMA, Hill JK, Kitschke C, Collingham YC, Roy DB, Fox R, Huntley B, Thomas CD (2006) Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology*, **12**, 1545-1553.

García-Camacho R, Escudero A (2009) Reproduction of an early-flowering Mediterranean mountain narrow endemic (*Armeria caespitosa*) in a contracting mountain island. *Plant Biology,* **11**, 515-524.

Gaucherel C, Guiot J, Misson L (2008) Changes of the potential distribution area of French Mediterranean forests under global warming. *Biogeosciences*, **5**, 1493-1504.

Gégout J, Coudun C, Bailly G, Jabiol B (2005) EcoPlant: A forest site database linking floristic data with soil and climate variables. *Journal of Vegetation Science*, **16**, 257-260.

Gehrig-Fasel J, Guisan A, Zimmermann NE (2007) Tree line shifts in the Swiss Alps: Climate change or land abandonment?. *Journal of Vegetation Science*, **18**, 571-582.

Gellrich M, Zimmermann NE (2007) Investigating the regional-scale pattern of agricultural land abandonment in the Swiss mountains: A spatial statistical modelling approach. *Landscape and Urban Planning*, **79**, 65-76.

Gilliam FS (2006) Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *Journal of Ecology,* **94**, 1176-1191.

Gottfried M, Pauli H, Reiter K, Grabherr G, Richardson DM (1999) A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming. *Diversity & Distributions*, **5**, 241-251.

Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. *Nature*, **369**, 448.

Grabherr G, Gottfried M, Gruber A, Pauli H (1995) Patterns and current changes in alpine plant diversity. In: *Ecological Studies* (eds Chapin, Körner), pp. 167-181. Springer-Verlag Berlin Heidelberg.

Hermy M, Honnay O, Firbank L, Grashof-Bokdam C, Lawesson J (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation*, **91**, 9-22.

Hickling R, Roy DB, Hill JK, Fox R, Tomhas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450-455.

Hofer HR (1992) Veränderungen in der Vegetation von 14 Gipfeln des Berninagebietes zwischen 1905 und 1985 - Changes in the vegetation on 14 peaks of the Bernina area between 1905 and 1985. *Berichte des Geobotanischen Instituts ETH, Stiftung Rübel, Zürich*, **58**, 39-54.

Holzinger B, Hulber K, Camenisch M, Grabherr G (2008) Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates. *Plant Ecology*, **195**, 179-196.

Hülber K, Dirnböck T, Kleinbauer I, Willner W, Dullinger S, Karrer G, Mirtl M (2008) Long-term impacts of nitrogen and sulphur deposition on forest floor vegetation in the Northern limestone Alps, Austria. *Applied Vegetation Science*, **11**, 395-404.

Huntley B (1991) How plants respond to climate change: Migration rates, individualism and the consequences for plant communities. *Annals of Botany*, **67**, 15-22.

Hättenschwiler S, Schweingruber FH, Körner C (1996) Tree ring responses to elevated CO2 and increased N deposition in *Picea abies*. *Plant, Cell and Environment*, **19**, 1369-1378.

Jump AS, Mátyás C, Peñuelas J (2009) The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology and Evolution*, **24**, 694-701.

Jurasinski G, Kreyling J (2007) Upward shift of alpine plants increases floristic similarity of mountain summits. *Journal of Vegetation Science*, **18**, 711-718.

Kammer PM, Schöb C, Choler P (2007) Increasing species richness on mountain summits: Upward migration due to anthropogenic climate change or re-colonisation? *Journal of Vegetation Science*, **18**, 301-306.

Keller F, Kienast F, Beniston M (2000) Evidence of response of vegetation to climatic change on high-elevation sites in the Swiss Alps. *Regional Environmental Change*, **2**, 70-77.

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11823-11826.

Kenk G, Fischer H (1988) Evidence from nitrogen fertilisation in the forests of Germany. *Environmental Pollution*, **54**, 199-218.

Klanderud K, Birks H (2003) Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *The Holocene*, **13**, 1-6.

Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, **90**, 68-77.

Lameire S, Hermy M, Honnay O (2000) Two decades of change in the ground vegetation of a mixed deciduous forest in an agricultural landscape. *Journal of Vegetation Science*, **11**, 695-704.

Landolt E (1977) *Ökologische Zeigerwerte zur Schweizer Flora*. Stiftung Rübel, Zürich.

Lavergne S, Thuiller W, Molina J, Debussche M (2005) Environmental and human factors influencing rare plant local occurrence, extinction and persistence: a 115-year study in the Mediterranean region. *Journal of Biogeography,* **32**, 799-811.

Lavergne S, Molina J, Debussche M (2006) Fingerprints of environmental change on the raremediterranean flora: a 115-year study. *Global Change Biology*, **12**, 1466–1478.

Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science,* **320**, 1768-1771.

Lesica P, McCune B (2004) Decline of arctic-alpine plants at the southern margin of their range following a decade of climate warming. *Journal of Vegetation Science,* **15**, 679-690.

Łysik M (2008) Ten years of change in ground-layer vegetation of European beech forest in the protected area (Ojców National Park, South Poland). *Polish Journal of Ecology*, **56**, 17-31.

Mandin J (1993) Progression actuelle d'espèces méditerranéennes vers le nord. Le cas de *Ferula communis* (L.) Rouy et Camus en Ardèche (France). *Acta botanica Gallica*, **140**, 81-90.

Mayer AC, Huovinen C (2007) Silvopastoralism in the Alps: Native plant species selection under different grazing pressure. *Ecological Engineering*, **29**, 372-381.

Mitzunaga H, Sako S, Nakao Y, Shimono Y (2005) Factors affecting the dynamics of the population of *Fagus crenata* in the Takakum Mountains, the southern limit of its distribution area. *Journal of Forest Research*, **10**, 481-486.

Moen J, Lagerström A (2008) High species turnover and decreasing plant species richness on mountain summits in Sweden: Reindeer grazing overrides climate change?. *Arctic Antarctic and Alpine Research,* **40**, 382-395.

Moisselin J, Schneider M, Canellas C, Mestre O (2002) Les changements climatiques en France au XXe siècle. Étude des longues séries homogénéisées de données de température et de précipitations. *La Météorologie*, **38**, 45-56.

Morin X, Viner D, Chuine I (2008) Tree species range shifts at a continental scale: new predictive insights from a process-based model. *Journal of Ecology*, **96**, 784-794.

Motta R, Morales M, Nola P (2006) Human land-use, forest dynamics and tree growth at the treeline in the Western Italian Alps. *Annals of Forest Science*, **63**, 739-747.

Mudrak E, Johnson S, Waller D (2009) Forty-seven Year Changes in Vegetation at the Apostle Islands: Effects of Deer on the Forest understory. *Natural Areas Journal*, **29**, 167-176.

Ninot JM, Batllori E, Carrillo E, Carreras J, Ferré A, Gutiérrez E (2008) Timberline structure and limited tree recruitment in the Catalan Pyrenees. *Plant Ecology & Diversity*, **1**, 47-57.

Økland T, Bakkestuen V, Økland RH, Eilertsen O (2004) Changes in forest understorey vegetation in Norway related to long-term soil acidification and climate change. *Journal of Vegetation Science,* **15**, 437-448.

Osem Y, Perevolotsky A, Kigel J (2007) Interactive effects of grazing and shrubs on the annual plant community in semi-arid Mediterranean shrublands. *Journal of Vegetation Science,* **18**, 869-878.

Ozenda P (1985) *La végétation de la chaîne alpine dans l'espace montagnard européen*. Masson, Paris.

Ozenda P, Borel J (1995) Possible responses of mountain vegetation to a global climatic change: The case of the Western Alps. In: *Potential ecological impacts of climate change in the Alps and Fennoscandian mountains* (eds Guisan A, Holten JI, Spichiger R, Tessier L), pp. 137-144. Conservatoire et Jardin Botaniques de Genève.

Paillet Y, Bergès L, Hjältén J, Ódor P, Avon C, Bernhardt-Römermann M, Bijlsma R, De Bruyn L *et al.* (2009) Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. *Conservation Biology*.

Parmesan C (1996) Climate and species' range. *Nature*, **382**, 765-766.

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579-583.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37-42.

Parolo G, Rossi G (2008) Upward migration of vascular plants following a climate warming trend in the Alps. *Basic and Applied Ecology*, **9**, 100-107.

Pauli H, Gottfried M, Reiter K, Klettner C, Grabherr G (2007) Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994-2004) at the GLORIA*master site Schrankogel, Tyrol, Austria. *Global Change Biology*, **13**, 147-156.

Penuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biology*, **9**, 131-140.

Picard J, Boisaubert B, Maillard D, Maire M (1993) Dynamique de l'abroutissement dû au chevreuil (*Capreolus capreolus* L.) dans une hêtraie-chênaie calcicole (Forêt de Haye, Meurthe-et-Moselle). *Revue Forestière Française*, **XLV**, 525-538.

Pignatti S, Bianco P, Fanelli G, Guarino R, Petersen J, Tescarollo P (2001) Reliability and effectiveness of Ellenberg's indices in checking flora and vegetation changes induced by climatic variations. In: *''Fingerprints'' of Climate Change* (eds Walther G, Burga CA, Edwards PJ), pp. 281-301. Kluwer, New York and London.

Pinho P, Augusto S, Martins-Loucao MA, Pereira MJ, Soares A, Maguas C, Branquinho C (2008) Causes of change in nitrophytic and oligotrophic lichen species in a Mediterranean climate: Impact of land cover and atmospheric pollutants. *Environmental Pollution*, **154**, 380-389.

Potthoff K (2007) Persistence of alpine grass-dominated vegetation on abandoned mountain summer farms in Western Norway. *Norsk Geografisk Tidsskrift-Norwegian Journal of Geography*, **61**, 192-206.

Randin C, Engler R, Normand S, Zappa M, Zimmermann N, Pearman P, Vittoz P, Thuiller W *et al.* (2009) Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology*, **15**, 1557-1569.

Rebetez M, Reinhard M (2008) Monthly air temperature trends in Switzerland 1901-2000 and 1975-2004. *Theoretical and Applied Climatology*, **91**, 27-34.

Root T, Price J, Hall K, Schneider S, Rosenzweig C, Pounds J (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57-60.

Rübel E (1912) *Pflanzengeographische Monographie des Berninagebietes*. Engelmann, Wilhelm, Leipzig.

Sala OE, Chapin III FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF *et al.* (2000) Global Biodiversity Scenarios for the Year 2100. *Science*, **287**, 1770-1774.

Sanz-Elorza M, Dana ED, Gonzalez A, Sobrino E (2003) Changes in the high-mountain vegetation of the Central Iberian Peninsula as a probable sign of global warming. *Annals of Botany*, **92**, 273-280.

Schwabe A, Kratochwil A, Pignatti S (2007) Plant indicator values of a high-phytodiversity country (Italy) and their evidence, exemplified for model areas with climatic gradients in the southern inner Alps. *Flora*, **202**, 339-349.

Skov F, Svenning J (2004) Potential impact of climatic change on the distribution of forest herbs in Europe. *Ecography*, **27**, 366-380.

Smith RIL (1994) Vascular plants as bioindicators of regionla warming in Antarctica. *Oecologia*, **99**, 322-328.

Sturm M, Racine C, Tape K (2001) Increasing shrub abundance in the Arctic. *Nature*, **411**, 546-547.

Tamm CO, Hallbäcken L (1988) Changes in soil acidity in two forest areas with different acid deposition: 1920s to 1980s. *Ambio*, **17**, 56-61.

Tasser E, Tappeiner U (2002) Impact of land use changes on mountain vegetation. *Applied Vegetation Science*, **5**, 173-184.

Tatoni T, Roche P, Médail F and Barbero M (2004) The impact of changes in land use on ecological patterns in Provence (Mediterranean France). In: *Recent dynamics of Mediterranean vegetation and landscape* (eds Mazzoleni S, Di Pascale G, Di Martino P, Rego F, Mulligan M) pp 107-120. John Wiley & Sons, London

Thimonier A, Dupouey J, Timbal J (1992) Floristic changes in the herb-layer vegetation of a deciduous forest in the Lorraine plain under the influence of atmospheric deposition. *Forest Ecology and Managment*, **55**, 149-167.

Thimonier A. (1994) Changements de la végétation et des sols en forêt tempérée européenne au cours de la période 1970-1990 Rôle possible des apports atmosphériques. Université Paris XI Orsay en Sciences de la Vie.

Thimonier A, Dupouey J, Bost F, Becker M (1994) Simultaneous eutrophication and acidification of a forest ecosystem in northeast France. *New Phytologist*, **126**, 533-539.

Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. *Nature*, **399**, 213.

Thomas C, Cameron A, Green R, Bakkenes M, Beaumont L, Collingham Y, Erasmus B, de Siqueira M *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145-148.

Thuiller W, Araujo MB, Lavorel S (2004) Do we need land-cover data to model species distributions in Europe? *Journal of Biogeography*, **31**, 353-361.

Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 8245–8250.

Tinya F, Márialigeti S, Király I, Németh B, Ódor P (2009) The effect of light conditions on herbs, bryophytes and seedlings of temperate mixed forests in Őrség, Western Hungary. *Plant Ecology*, **204**, 69-81.

Trenberth K, Jones P, Ambenje P, Bojariu R, Easterling D, Klein Tank A, Parker D, Rahimzadeh F *et al.* (2007) Observations: Surface and Atmospheric Climate Change. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL), pp. 235-336. Cambridge University Press, Cambridge, United .

Trivedi MR, Berry PM, Morecroft MD, Dawson TP (2008) Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. *Global Change Biology*, **14**, 1089-1103.

Turner BL, Lambin EF, Reenberg A (2007) The emergence of land change science for global environmental change and sustainability. *Proceedings of The National Academy Of Sciences Of The United States Of America*, **104**, 20666-20671.

Vetaas OR (2002) Realized and potential climate niches: a comparison of four Rhododendron tree species. *Journal of Biogeography*, **29**, 545-554.

Vittoz P, Guisan A (2007) How reliable is the monitoring of permanent vegetation plots? A test with multiple observers. *Journal of Vegetation Science*, **18**, 413-422.

Vittoz P, Randin C, Dutoit A, Bonnet F, Hegg O (2009) Low impact of climate change on subalpine grasslands in the Swiss Northern Alps. *Global Change Biology*, **15**, 209-220.

Walther G, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J, Hoegh-Guldberg O *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389-395.

Walther G (2004) Plants in a warmer world. *Perspectives in Plant Ecology, Evolution and Systematics,* **6**, 169-185.

Walther G, Beißner S, Burga CA (2005) Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, **16**, 541-548.

Walther G, Beißner S, Pott R (2005) Climate change and high mountain vegetation shifts. In: *Mountain Ecosystems – Studies in Treeline Ecology* (eds Broll G, Keplin B), pp. 77-96. Springer, Heidelberg.

Walther G, Berger S, Sykes MT (2005) An ecological 'footprint' of climate change. *Proceedings of the Royal Society B*, **272**, 1427–1432.

Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG *et al.* (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65-69.

Wieser G, Matyssek R, Luzian R, Zwerger P, Pindur P, Oberhuber W, Gruber A (2009) Effects of atmospheric and climate change at the timberline of the Central European Alps. *Annals of Forest Science*, **66**.

Wild J, Neuhäuslová Z, Sofron J (2004) Changes of plant species composition in the Šumava spruce forests, SW Bohemia, since the 1970s. *Forest Ecology and Management,* **187**, 117–132.

Wilson SD, Nilsson C (2009) Arctic alpine vegetation change over 20 years. *Global Change Biology*, **15**, 1676-1684.

le Roux PC, McGeoch MA (2008) Rapid range expansion and community reorganization in response to warming. *Global Change Biology*, **14**, 2950-2962.

van Herk C, Aptroot A, van Dobben H (2002) Long-term monitoring in the Netherlands suggests that lichens respond to global warming. *Lichenologist*, **34**, 141-154.

II. SHIFT OF MOUNTAIN VEGETATION IN FORESTS OF THE SOUTHERN ALPS: CLIMATE OR LAND-USE CHANGE?

Running title: Species shift in Mediterranean mountains

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A. ABSTRACT

Present vegetation changes in mountain areas are often explained by climate warming. However, more direct anthropogenic impacts, such as recolonisation of abandoned pastures by forest, above the current tree line, are difficult to separate from the effects of climate change because they affect large areas and occur over a long time span, as climate change does. Even within forest belts where such confounding factors should be reduced, long-term stand dynamics could confound the climate signal. Here, we evaluated the direction and rate of plant species elevation shifts in mountain forests of the Southern Alps. In order to assess the effect of changes in stand dynamics, we compared what occurred in the whole set of stands with closed stands only. We used floristic data from the French National Forest Inventory, collected in 1985 and 1999. They provided a large scale (30985 plots) and

representative sample of vegetation between 0 and 2500 m a.s.l.. Species response curves along the elevation and exposure gradients were fitted in a logistic regression model. 62 species shifted downward whereas 113 shifted upward, resulting in a significant upward median shift of 19.2 m. Upward shifting species were preferentially woody and heliophilous, suggesting a role for forest closure and maturation in the observed changes. Excluding all open forest stages from analyses, the upward trend became weaker (9.5 m) and not significant. Forests of the study area have undergone closure and maturation, more strongly at lower altitudes than at higher ones, thus creating an apparent shift of vegetation. In the Southern Alps, land-use change is the main driver of the upslope movement of forest vegetation. Since the trend of forest maturation exists on large areas over Europe, forest dynamics should be better taken into account, among the causes of vegetation changes, before concluding at any effect of climate change.

B. INTRODUCTION

Mountain regions have been identified as remarkable area to test ecological and evolutionary responses of biota to geophysical influences (Körner 2007) and thus to study the impact of global warming on vegetation. Compared to lowlands, mountains are characterised by a steep gradient of temperature and fewer obstacles to plant migration such as infrastructure or agricultural fields. Thus, species should have to move over smaller distances and in a homogeneous matrix to follow their temperature range, allowing mountain plants to migrate more rapidly when climate changes. Indeed, mountain areas were amongst the earliest systems to detect effects of recent climate change (Grabherr *et al.* 1994). Because of this high sensitivity to temperature increase, and the high diversity and rate of endemism of mountain ecosystems (Körner 2002), the potential impact of climate change on biodiversity in mountain is particularly alarming, as underlined by the IPCC (Fischlin *et al.* 2007). Bioclimatic models project extreme migrations and serious risk of extinctions in montane areas (Thomas *et al.* 2004).

Observed impact of climate change on species distribution ranges suggests that species response is already obvious (Walther *et al.* 2002; Parmesan 2006). In high mountains, most studies focused on small areas, such as the flora of summits in the Swiss and Austrian Alps. Grabherr *et al.* (1994), Walther *et al.* (2005a, 2005b) and Holzinger *et al.* (2008) observed an increase in species richness on these summits. Pauli *et al.* (2007) monitored an alpine-nival ecotone in the Austrian Alps and showed an expansion of alpine species at their upper limit, while some nival species decreased in cover at their lower limit. Community changes towards higher temperature demanding species were shown by Carraro *et al.* (1999), Keller *et al.* (2000), and Walther & Grundmann (2001) . Similarly, the reinventory of a Swiss nunatak revealed that species from the lower vegetation belt migrated to a glacier island (Vittoz *et al.* 2008). Few studies have focused on the whole distribution range to measure shift in the observed mean altitude of a species (Kelly & Goulden 2008) or in its modelled elevation optimum (Lenoir *et al.* 2008).

The drivers and causes of these vegetation shifts are still debated. Current climate change is often considered as the main factor. According to Kammer *et al.* (2007), upward shift on mountain summits could alternatively be explained by the re-colonisation since Little Ice Age (*i.e.* about 1850). Until now, most of vegetation responses attributed to climate warming were observed above forest belts, where direct anthropogenic effects in relation to land use changes could also play an important role. Vegetation shift in subalpine grasslands could be promoted by climate warming, but should be, in addition, linked to pasture abandonment that have widely occurred during the last century (Vittoz *et al.* 2009). Many studies have focused on forest- or tree-line ecotones, showing an upward shift during the last decades (Kullman 2002; Walther 2004; Beckage *et al.* 2008). However, original climatic tree line was largely lowered by historical human activities (Bartoli 1966; Holtmeier & Broll 2007; Bader & Ruijten 2008). Consequently, the current tree-line advance in the Alps is at least triggered, if not entirely controlled, by the decrease in management and grazing intensity during the last decades (Didier 2001; Motta *et al.* 2006; Bolli *et al.* 2007; Gehrig-Fasel *et al.* 2007; Albert *et al.* 2008; Vittoz *et al.* 2009).

Forest belts, under the tree line, offer several advantages for the detection of the impact of climatic change on plant species distribution. They should be less prone to the previous confounding effects of decrease in pasturing and subsequent forest recolonisation. In addition, studies at the tree line have often concentrated on changes in tree species only, not considering understorey species. Yet, the lower strata of forest ecosystems are less influenced by changes in forest management than the tree stratum itself, which composition is strongly controlled by the choice of target species. Thus, understorey species could be more reliable indicators of climatic change than species of the tree canopy only. Despite these advantages, few studies addressed vegetation shifts within mountain forest belts (Carraro *et al.* 1999; Dobbertin *et al.* 2005; Lenoir *et al.* 2008).

However, even within the forest belts, human activities and natural dynamics not linked to climate change could induce vegetation changes. Agricultural abandonment at lower altitudes widely occurred in European mountains during the last centuries (MacDonald *et al.* 2000; Gellrich & Zimmermann 2007). As a consequence, lower elevation forests are still biased towards early stages of the forest succession. Moreover, Western European forests show a general trend of increasing wood stock, due to an increasing lag between forest growth and wood uptake (Dupouey *et al.* 2009). This is especially relevant in mountain forests, where poor accessibility to the stands limits their exploitation. These phenomena could involve a slow maturation and closure of forest (Walther & Grundmann 2001), leading to long-term changes in vegetation communities. Limited sets of permanent plots, which are mostly used in long-term vegetation studies, are especially prone to such bias because they are often not representative of the entire range of forest successional stages. In these datasets, it appears difficult to disentangle the effects of stand ageing from those of other environmental changes, as they are confounded, both developing in the meantime (Thimonier *et al.* 1994). Large samples of non permanent vegetation plots allow a better account of these forest stand changes, under the condition that they are controlled as a part of the sampling scheme at each sampling date. National forest inventories, when they collect vegetation data, offer such advantages. Samples are drawn in order to be statistically representative of large areas, methods of vegetation sampling are well documented and remain consistent over space or time.

1. Objectives of the study

Here we analysed vegetation changes between two successive samples of the French National Forest Inventory covering the southwestern Alps, collected between the eighties and the nineties during a period of strong warming (0.5°C/decade) and using a stratified sampling protocol.

Our first objective was to identify the direction and quantify the rate of forest species shift along the elevation gradient in the French Mediterranean mountains. For that purpose, species presence was modelled according to elevation, exposure and sampling date. Then, we tried to identify the causes of the observed shifts by two ways. First, we analysed life traits associated with upwarding or downwarding species. It has been previously shown that the upward movement of thermophilous, light-seed, evergreen and short life-cycle (herbaceous) species should be favoured by climate warming. Secondly, we looked for the impact of stand dynamics processes by comparing the observed shift in the whole forest area on the one hand with that measured in closed forests only, on the other hand. The impact of forest dynamics should be lessened in closed forests and climate change effects highlighted.

C. MATERIAL AND METHODS

1. Study area

The study region covers an area of 60 000 km^2 in the South East of France (2°32’37” to 7°42’05”E and 42°59’03” to 45°21’37”N) and in the southern half of Corsica Island (8°37’09” to 9°23’41”E and 41°23’37” to 42°20’22”N) (figure 1), from sea level to 4100 m a.s.l.. We chose such a large region because even small truncations of the altitudinal gradient can lead to strong bias in the study of plant diversity patterns (Nogués-Bravo *et al.* 2008).

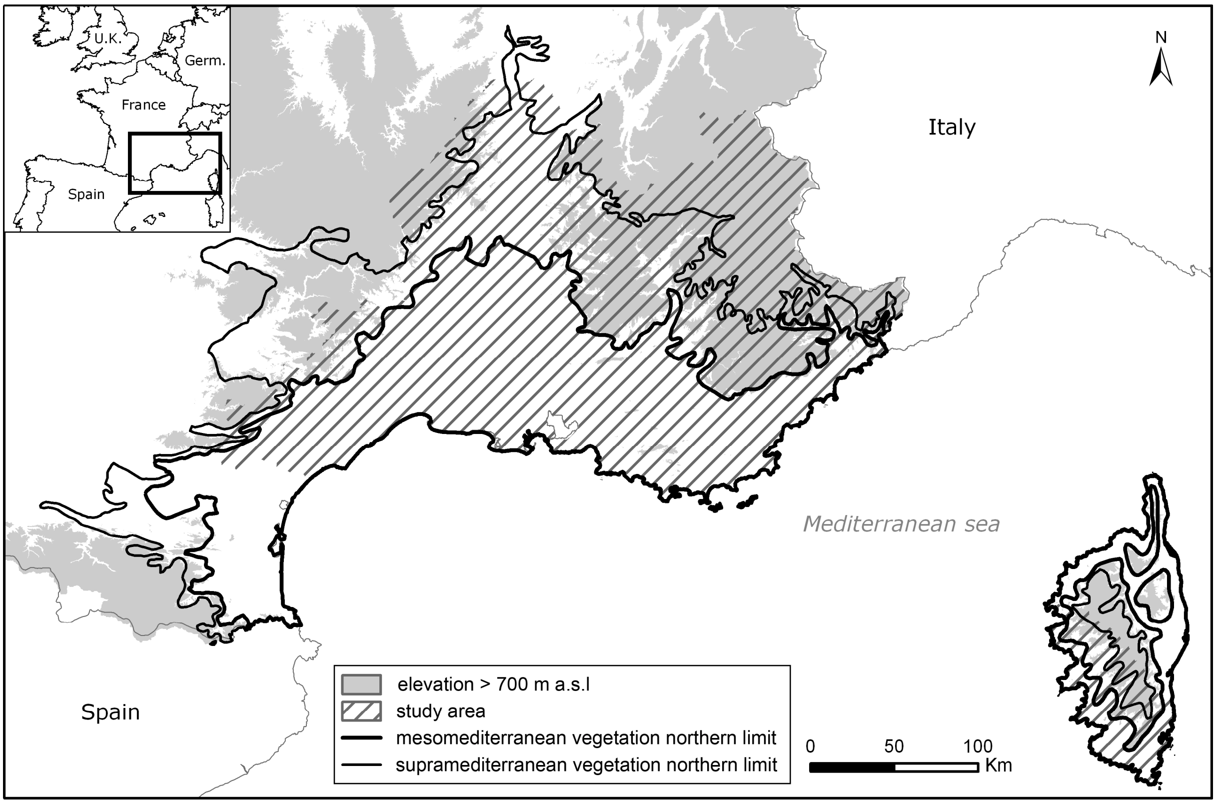

Figure II-1: Study area with relief and vegetation type. Bioclimatic limits according to the Council of Europe and Commission of the European Communities (1987).

The study area was inventoried twice by the French National Forest Inventory (NFI) between 1981 and 2004. The first inventory was conducted between 1981 and 1989 (mean inventory year, weighted per area sampled each month: 1984.7). The second inventory cycle took place between 1992 and 2004 (mean weighted inventory year: 1998.8).

Forest covered 33% of the area at the first inventory and 36% at the second one, from sea level to 2250 m a.s.l. Indeed, forest cover had started to increase since the 19th century. In 1878, it was only 19% (Douguédroit 1981).

A strong and concomitant elevation gradient of climate (Quézel & Médail 2003) and succession of forest vegetation belts (Ozenda & Lucas 1987) has been early recognised and characterised by biogeographers: thermomediterranean climate restricted to the eastern part of the study area near sea-level, mesomediterranean, and supramediterranean climates at intermediate elevation, with mean annual temperature higher than 8°C and dominated by *Quercus ilex*, *Quercus suber*, *Quercus pubescens*, *Castanea sativa*, *Pinus halepensis*, *Pinus pinaster* or *Pinus sylvestris*, mountain and subalpine belts at the highest elevations, dominated by *Fagus sylvatica*, *Abies alba*, *Pinus sylvestris*, *Picea abies*, *Larix decidua*, *Pinus uncinata* and *Pinus cembra*.

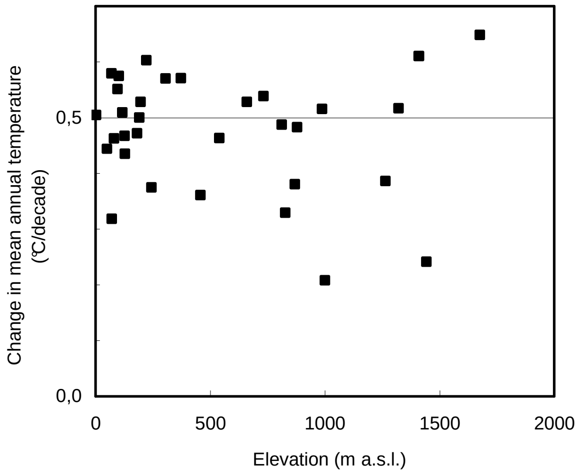

Figure II-2: Mean annual temperature increase over the 1971-2000 period as a function of elevation at 32 meteorological stations located in the study area.

The observed annual thermal gradient is 0.56°C per 100 m, according to Aimé & Sarrailh (1972). The warming trend in the study region over the 1971-2000 period was 0.5°C/decade for mean annual temperature. A careful study of 71 meteorological stations in our study region, of which 32 only were retained after exclusion of dubious series following the filtering procedure of Caussinus & Mestre (2004) showed no variations in this warming trend with elevation (figure 2) between sea level and 1675 m a.s.l. Minimal and maximal temperature trends both displayed the same lack of tendency with elevation.

2. Vegetation dataset

For each of the two successive inventories, an independent sample was drawn. The sample was stratified by ecological regions, forest types, administrative divisions and ownership type (Drapier & Cluzeau 2001), *i.e.*:

(i) ecological regions: the area was divided into 66 small forest ecological regions, delineated according to geological and climatic criteria.

(ii) forest types: based on an aerial photography analysis, the zone was stratified according to the main tree species and forest structure (coppice, high stand, coppice with standards, young plantation or open stand, including woody heathland, and scattered or sparse woodlands).

(iii) administrative divisions: inventories were conducted independently in each of the 11 French departments, and stratified as a function of ownership type (private, communal and state forest).

In each sampling stratum, plots were randomly selected on a regular grid in order to reach a theoretical sampling effort of one plot per 130 ha of forest on average. This objective was globally reached, with an observed sampling intensity of one plot every 127.3 ha at the first inventory (15 754 plots spread over 2 005 998 ha) and 141.2 ha at the second one (15 231 plots spread over 2 150 261 ha). In the following analyses, each of the 30 985 plots was given a weight equal to the total area of the stratum it belonged to, divided by the total number of plots belonging to this stratum. The plots were distributed between 0 and 2250 m a.s.l. (99.9 weighted percentile of the elevation distribution) at the first inventory and 0 and 2240 m a.s.l. at the second one. The distribution of forest cover along the elevational gradient was very similar among the two sampling periods. Weighted average elevations of the plots were not significantly different between the two inventories (693.8 m a.s.l. and 701.6 m a.s.l. at the first and second inventories, respectively) according to a Student's t-test (p=0.14). However, at the second inventory, sampling pressure had decreased in high altitude forests leading to larger weights for the corresponding plots.

At each plot, several dendrometric and ecological variables were recorded (Drapier & Cluzeau 2001). Among them, we used for the present study: geographical coordinates, date of sampling, elevation, exposure, botanical observations consisting of a list of all vascular species and terricolous bryophytes. At the first inventory, vegetation was recorded in a 6 m radius circle and in a 15 m radius circle at the second one. A total of 1945 taxa were observed in the whole sample (1536 and 1546 taxa at the first and second sampling inventories, respectively), among which 1137 were common to both samples. 88.9% of the overall occurrences of taxa were identified at the species level or more precisely at the first inventory, and 90.2% at the second one. All taxa were assigned an identification reliability code of high, intermediate or low by NFI observers (respectively 45%, 23% and 32% of the taxa, at the second inventory). Nomenclature follows *Flora Europaea* (Tutin *et al.* 1968-1993). There were 264 604 total observations at the first inventory and 383 744 at the second one, resulting in a mean number of species per plot of 16.6 in 1985, increasing to 25.3 in 1999 because of a higher sampling plot area and, probably, a higher exhaustiveness of plant censuses due to a better training of observers.

3. Data analyses

a. Estimation of species shifts

Contrary to studies conducted in permanent-plot networks, where the variation in mean elevation of a species can be used as an indicator of its altitudinal shift, the observed mean elevation can not be used in a non-permanent plot network because samples do not have exactly the same altitudinal distribution at each date. Thus, in a first step, we modelled the species response to the elevational and exposure gradients and, in a second step, we studied the shift between the two sampling dates of the optimum position provided by the model.

Variations of plant census exhaustiveness between observers has been recognised as a recurrent bias in vegetation monitoring (Archaux *et al.* 2006, 2008; Vittoz & Guisan 2007). Here, several strategies were used in order to minimise the effects of such a bias between the two sampling dates. First, we only retained the taxa that had been noted in 50 plots at least at both dates (386 taxa). This threshold frequency has also been suggested as a general minimum value to derive acceptable ecological response curves with logistic regression (Coudun & Gégout 2006). Among these 386 taxa, we only selected those identified at the species level at least (341 species) and noted by NFI observers with a ‘high’ identification reliability code (252 species). Finally, we studied only changes in the position of the optimum of species, not dealing with changes in global frequency or distribution range which both depend on census exhaustiveness. For each of the 252 species, a quadratic logistic regression model was fitted to presence-absence data. The sampling weight previously defined was used to adjust for representativeness of each plot:

$$logit(p) = a*elevation^2 + b*elevation + c*elevation*period + d*ns^2 + e*ns + f*ns*period + g + h*period + \varepsilon$$

with p: probability of species presence,
elevation: elevation of the plot where the species was recorded
ns: cosine of the exposure of the plot,
period: first or second inventory period
ε: error.

After elevation, exposure is the second most important factor of the local climate in mountains influencing presence-absence of species (Stage & Salas 2007; Ashcroft *et al.* 2008). It was introduced in our model as the cosine of the aspect measured from north in the field (north: ns=1, east and west: ns=0, south: ns=-1) because the north-south gradient has the strongest effect on vegetation. Below a 6% slope, the exposure was not recorded in the field. In this case, a more spatially extended exposure was extracted from a digital elevation model using Arc View 9.2, based on the 8 closest neighbours in a 50 x 50 m grid.

The binary variable ’period’ was introduced in the model both in interaction with elevation and exposure, in order to test for changes in the optimum of each species, and alone, in order to control for variations of the global frequency of species from one inventory to the other.

Among the 252 species which distribution was modelled, we only retained those responding to the following criteria:

1. species displaying a significant global model ($p<0.001$). The global significance of the model was assessed by the likelihood ratio test (Collett 1991). A low threshold value of probability was used because of the large number of tests made.
2. species responding to elevation with a bell-shaped curve, *i.e.* with parameter a for square elevation both negative and significantly different from zero at the 0.05 level (likelihood-based confidence interval).
3. species having an optimum elevation in the altitudinal range of our study area (0-2200 m a.s.l.) at both inventories. This constraint avoided to extrapolate optimum positions outside the sampled range. For each species, the elevation optimum of the bell-shaped curve is given by:

$$Opt_{elev} = - [b + c] / 2*a \qquad \textit{(with c depending on the inventory period)}$$

Then, for each retained species, we calculated the altitudinal shift as the difference between the optimum elevations at the two successive inventories (second minus first). Species displaying a positive or negative shift are hereafter called ascending and descending species, respectively. We tested significance of this shift in a type III test of the c parameter, comparing the full model with the same model without the elevation*period interaction ($p<0.05$).

Finally, the global rate of vegetation change along the altitudinal gradient was estimated as the mean or median elevation shifts of all species selected in steps 1 to 3, divided by the average time elapsed between the two sampling periods (14.1 years). The difference of the mean from zero was tested using a t-test. This average rate was also calculated over those species displaying a significant shift only.

The same procedure (steps 2 and 3) was applied to select species responding to exposure with a bell-shaped curve ($d<0$, $p<0.05$) and an optimum within the -1 to 1 range. Exposure optimum was calculated as:

$$Opt_{ns} = - [e + f] / 2*d \qquad \textit{(with f depending on the inventory period)}$$

We tested significance of the exposure shift in a type III test of the f parameter ($p<0.05$).

b. Species shifts and plant traits

We looked for species life traits associated with species shift, testing which life traits were differently distributed between downward and upward shifting species. We studied Landolt’s indicator values (Landolt 1977) for light (L), temperature (T), continentality (K), soil reaction (R), nitrogen availability (N), soil moisture (F), soil dispersion (D) and humus content (H). Landolt’s indicator values were preferred to Ellenberg’s ones because they were established in a nearest region (Switzerland) of our study area. Then we analysed Raunkiaer’s life forms, divided in deciduous phanerophytes, evergreen phanerophytes, deciduous nanophanerophytes, evergreen nanophanerophytes, woody chamephytes, herbaceous chamephytes, hemicryptophytes, geophytes and therophytes. Previous growth forms were also grouped into simpler categories: woody *versus* herbaceous and evergreen *versus* deciduous. Woody species were classified into tall trees (more than 12 m in height) or low trees and shrubs (less than 12 m), based on the maximum height to which they can grow (Becker *et al.*

1982). We extracted the following traits from the French Mediterranean forest flora (Rameau *et al.* 2008): 1) pioneer species or not, 2) species which can be found in immature stages of the vegetation dynamics or not. Immature stages included fallows, heaths and scrubs, thickets, 3) light requirement (light demanding species *versus* shade tolerant species) and 4) seed dispersal mode (by gravity, seed projection, wind, ants, birds or other animals). Mean seed masses were downloaded from the online Leda Traitbase (Kleyer *et al.* 2008) and log-transformed.

For quantitative traits, we tested the difference in the means between upward and downward shifting species using a t-test. For categorical traits, we tested whether the trait was randomly distributed among descending and ascending species by a Fisher's exact test of association. For each trait and each category, we calculated the mean and median elevation shifts. We looked at which categories were more linked to species shift by calculating their odds ratio:

odds ratio of a given trait category = (u / (1-u)) / (d / (1-d))
with: u: proportion, among ascending species, of species belonging to the given trait category
d: proportion, among descending species, of species belonging to the given trait category

Species with missing values for a given trait were excluded from the calculation of *u* and *d* for all categories of this trait. An odds ratio larger than 1 for a given trait category means that this category is composed of more ascending than descending species relatively to the other categories of the same trait, and conversely for odds ratio smaller than one.

c. Species shifts and successional dynamics

Because French forests are undergoing both an expansion due to previous agricultural abandonment and a maturation due to a delay in forest renewal, the balance between forest succession stages have changed between the two dates of inventories. Overall, percentage area of open forests (including woody heathland, and scattered or sparse woodlands) considered as pioneer stage, decreased from 37% to 19% of the region. We characterised these changes by calculating the percentage area of open forests, the mean basal area and the mean forest age per 100 m elevation classes at each inventory. Stand age was available in even-aged forests only, *i.e.* 78% of the total sample. Open forests had been defined during the aerial photography analysis (see above). To analyse the interaction between successional dynamics and observed altitudinal vegetation shifts, all previous analyses were separately run on two different datasets: the whole sample on the one hand, including all forest type sampled by NFI, and closed forests only on the other hand (including coppices, high stands, coppices with standards and young plantations), considered as established forest habitat. In case of no effect of successional dynamics, the same altitudinal shift should be observed in both the entire sample and closed forests only.

All statistical calculations were made using the SAS software, version 9.1.

D. RESULTS

1. Estimation of species shifts

Out of the 252 species with an occurrence greater than 50 at each inventory and with a good identification reliability, 251 displayed a significant global model of distribution ($p<0.001$). Among them, 175 exhibited both a unimodal (bell-shaped) response curve along the altitudinal gradient (a different from zero at the $p<0.05$ level and a negative) and a calculated optimum, Opt_{elev}, between 0 and 2200 m a.s.l.. 74 out of these 175 species showed a significant shift of the optimum elevation (table 1a and annex 1). By way of illustration, two examples of observed and modelled data are presented in figure 3, one of an ascending species and the second of a descending species. Along the exposure gradient, 45 species displayed both a bell-shaped distribution (d different from zero at the $p<0.05$ level and d negative) and a calculated optimum, Opt_{ns}, between -1 and 1, of which 9 only showed a significant shift of their exposure optimum (table 1a).

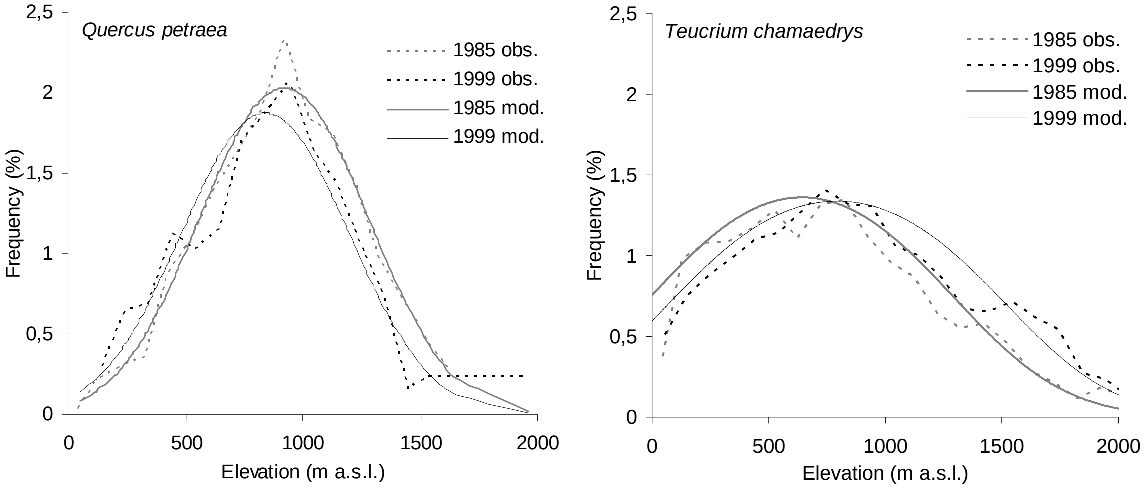

Figure II-3: Observed frequency distribution (dotted line) and modelled probability of presence (full line) at each inventory (1985 in grey and 1999 in black) along the elevation gradient for two selected species: one shifting downward (*Quercus petraea*, left) and one shifting upward (*Teucrium chamaedrys*, right). The modelled probability of presence was calculated using the observed average value of exposure for each species at each inventory.

The total number of ascending species was 1.8 times higher than that of descending species (113 and 62 species, respectively). When considering significant shifts only, 3 times more species displayed an upward shift than a downward one (56 and 18 species, respectively, table 1a and figure 4a).

Over the 175 species responding to elevation in a unimodal way, the mean altitudinal shift was positive and significantly different from zero (+17.9 m, $p<0.05$). The median shift was +19.2 m. Interestingly, species with an optimum below 1300 m a.s.l. displayed, on average, a much larger shift (n=113 species, median=+30.8 m, figure 4a) than those having their optimum above 1300 m a.s.l. (n=62, median=-2.0 m, mean not significantly different from zero). When considering the 74 species shifting significantly only, the mean shift was +47.3 m (significantly different from zero, $p=0.02$) and the median shift +80.8 m.

There were few species shifting significantly northward or southward (table 1a) and the mean exposure shift was not significantly different from zero.

Table II-1: Number of species responding to elevation and exposure in a quadratic logistic model and displaying an altitudinal or exposure shift between the last two national forest inventories a) in the entire sample and b) in closed forests only.

a. All forests **species displaying a global significant response (251)**				**unimodal response curve to elevation and optimum within the sampled range**				no response to elevation or optimum outside the sampled range	total
				shift direction					
				downward		upward			
				all species	(sign. shift)	all species	(sign. shit)		
unimodal response curve to exposure and optimum within the sampled range	shift direction	North	all species	1	(0)	14	(10)	6	21
			(sign. shift)	(0)	(0)	(2)	(2)	(1)	(3)
		South	all species	5	(1)	9	(5)	10	24
			(sign. shift)	(0)	(0)	(3)	(3)	(3)	(6)
no response to exposure or optimum outside the sampled range				56	(17)	90	(41)	60	206
total				62	(18)	113	(56)	76	251

b. Closed forests only **species displaying a global significant response (231)**				**unimodal response curve to elevation and optimum within the sampled range**				no response to elevation or optimum outside the sampled range	total
				shift direction					
				downward		upward			
				all species	(sign. shift)	all species	(sign. shit)		
unimodal response curve to exposure and optimum within the sampled range	shift direction	North	all species	2	(2)	10	(6)	5	17
			(sign. shift)	(0)	(0)	(5)	(3)	(0)	(5)
		South	all species	2	(0)	6	(3)	2	10
			(sign. shift)	(0)	(0)	(2)	(2)	(0)	(2)
no response to exposure or optimum outside the sampled range				59	(21)	85	(30)	60	204
total				63	(23)	101	(39)	67	231

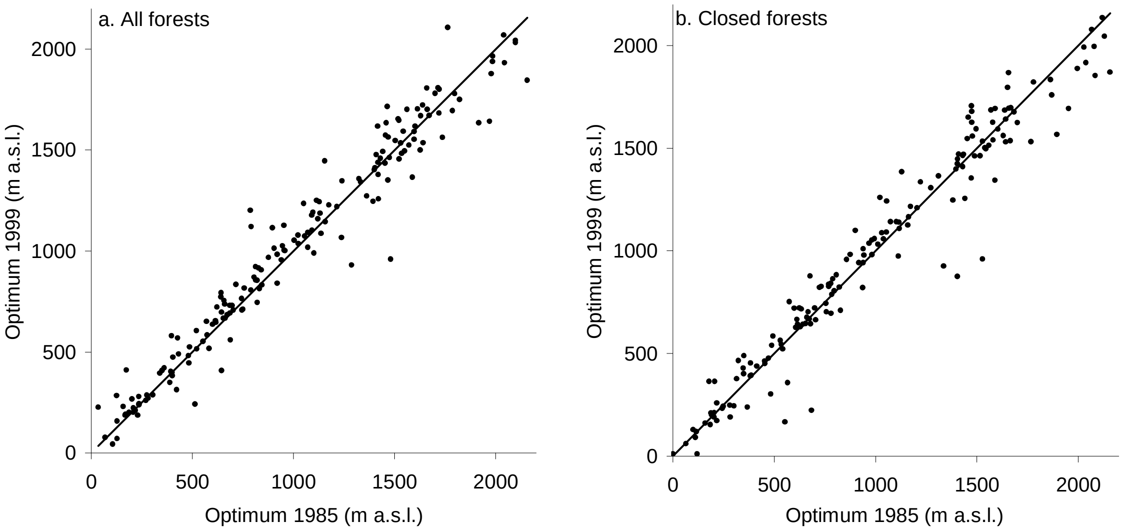

Figure II-4: Species optimum elevation in 1999 as a function of the optimum elevation in 1985 a) in all forests (n=175 species) and b) in closed forests only (n=164 species).

2. Species shifts and plant traits

Because no trend was observed along the exposure gradient, we only analysed differences in species traits according to their shift in elevation. Odds ratio, mean and median elevation shifts by trait category are listed in table 2. Values of the main traits are given in annex 1 for species displaying both a unimodal response curve to elevation and an optimum within the sampled range.

Landolt's indicator values were available for 150 species among the 175 studied. Ascending species had a significantly (n=150, p=0.005 in a Student's t-test) higher mean Landolt's indicator value for temperature (T=3.9) than descending species (T=3.4), meaning that they were more thermophilous. The difference in Landolt's indicator values for light was also significant (n=150, p=0.02), with again a higher mean value for ascending species (L=3.1) than for descending species (L=2.7), meaning that ascending species were more light demanding. The two indicator values for temperature and light were significantly correlated (p<0.0001 according to a Fisher exact test of association between these two categorical variables). There were no other significant differences in Landolt's indicator values. However, when comparing only species displaying a significant shift, the difference in mean indicator values for temperature between ascending (T=3.9) and descending (T=3.5) species became barely significant (n=69, p=0.07 in a Student's t-test), whereas the difference in light indicator values remained significant (L=3.1 and L=2.5, n=69, p=0.002). Other Landolt's indicator values were still not significantly different between ascending and descending species.

According to the light requirements given in Rameau *et al.* (2008), there was a tendency for upward-shifting species to be more heliophilous (table 2, o.r.=1.95, n=170, p=0.045) than descending ones, as with Landolt's indicator value for light. The average shift of heliophilous species was +32.3 m (median=+29.9 m), significantly different from zero (n=113, p=0.001), whereas shade tolerant species were not significantly shifting (table 2).

Raunkiaer's life forms were available for all the 175 studied species. They were significantly not randomly distributed between ascending and descending species (Fisher's exact test of association: p=0.02), either taking into account all species or significantly shifting ones only. Relatively to other categories, there were more ascending species belonging to deciduous phanerophytes (o.r.=3.24), deciduous nanophanerophytes (o.r.=2.35) and evergreen nanophanerophytes (o.r.=1.98), whereas there were relatively more descending species among evergreen phanerophytes (o.r.=0.51), herbaceous chamephytes (o.r.=0.39), hemicryptophytes (o.r.=0.59) and geophytes (o.r.=0.35). Woody chamephytes did not display any departure from the general trend. When applied to the species having a significant shift only, the relationships between Raunkiaer's life forms and shifting behaviour were similar.

In terms of average elevation shifts, only geophytes showed a significant downward shift (-88.0 m, p=0.01, median=-48.3 m) whereas deciduous phanerophytes (+70.4 m, p=0.002, median=+53.8 m) and woody chamephytes (+50.1 m, p=0.01, median=+19.3 m) showed a significant upward shift. The median shift of nanophanerophytes was large (+39.2 m), due to a large shift of deciduous nanophanerophytes (+41.5 m).

When comparing all woody species pooled together (phanerophytes, nanophanerophytes and woody chamephytes) against all herbaceous species (herbaceous chamephytes, hemicryptophytes and geophytes), the odds ratios were largely different from one (2.59 for woody species), indicating a strong tendency for woody species to shift upward and the reverse for herbaceous species. The same tendency was observed among the 74 species shifting significantly only. Woody species displayed an average altitudinal shift of +39.0 m, (median=+34.1 m) significantly different from zero (p<0.0001).

Both low and tall woody species were significantly shifting upward. But only low trees had an odds ratio significantly different from one, *i.e.* a higher relative proportion of ascending species in comparison with all other herbaceous or tall tree species (table 2).

Table II-2: Number of descending and ascending species, odds ratio (o.r.), median and mean species shifts for different plant trait categories, in all forest types (left) and in closed forests only (right). Significance of departure of the odds ratios from one was tested using a chi-square test. Whether the mean shifts were significantly different from zero was tested with a t-test (p≤0.001: *; p≤0.01: **; p≤0.05: *).**

	Species shift in all forests				**Species shift in closed forests only**			
	Number of species (down/up)	o.r.	Median (m)	Mean (m)	Number of species (down/up)	o.r.	Median (m)	Mean (m)
Light requirement								
Missing information	5		+9.0	+5.9	5		-44.9	+2.7
Light demanding	113(34/79)	**1.95***	+29.9	**+32.3****	104(32/72)	**2.33***	+20.5	+14.9
Shade tolerant	57(26/31)	**0.51***	+4.4	-9.7	55(28/27)	**0.43***	-5.4	-37.4
Raunkiaer’s life form								
Phanerophytes	48(14/34)	1.48	+34.7	**+44.5****	47(18/29)	1.01	+11.1	+1.2
• *Evergreen phanerophytes*	*18(9/9)*	*0.51*	*-1.4*	*+1.3*	*18(12/6)*	***0.27*****	*-10.2*	*-9.0*
• *Deciduous phanerophytes*	*30(5/25)*	***3.24****	*+53.8*	***+70.4*****	*29(6/23)*	***2.80****	*+54.0*	*+7.6*
Nanophanerophytes	42(9/33)	**2.43***	+39.2	+25.9	38(12/26)	1.47	+16.4	+2.2
• *Evergreen nanophanerophytes*	*9(2/7)*	*1.98*	*+14.6*	*+20.8*	*8(3/5)*	*1.04*	*+5.4*	*-10.3*
• *Deciduous nanophanerophytes*	*33(7/26)*	*2.35*	*+41.5*	*+27.2*	*30(9/21)*	*1.57*	*+23.2*	*+5.5*
Chamephytes	32(13/19)	0.76	+14.8	+40.0	30(7/23)	2.36	+20.6	+17.1
• *Woody chamephytes*	*25(9/16)*	*0.97*	*+19.3*	***+50.1****	*24(3/21)*	***5.25*****	*+30.9*	***+50.2*****
• *Herbaceous chamephytes*	*7(4/3)*	*0.39*	*-8.0*	*+1.8*	*6(4/2)*	*0.30*	*-83.4*	*-115.1*
Hemicryptophytes	33(15/18)	0.59	+9.1	+7.0	31(17/14)	**0.43***	-8.9	+3.5
Geophytes	19(11/8)	**0.35***	-48.3	**-88.0***	17(9/8)	0.52	-5.4	**-85.1***
Therophytes	1(0/1)	/	+65.7	+65.7	1(0/1)	/	+186.0	+186.0
Woodiness								
Herbaceous species	60(30/30)	**0.39****	-3.6	-22.7	55(30/25)	**0.36****	-8.9	-33.5
Woody species	115(32/83)	**2.59****	+34.1	**+39.0*****	109(33/76)	**2.76****	+19.3	+12.3
• *Tall trees*	*32(10/22)*	*1.26*	*+32.6*	***+54.2*****	*31(12/19)*	*0.98*	*+6.6*	*-9.0*
• *Low trees and shrubs*	*83(22/61)*	***2.13****	*+34.1*	***+33.2*****	*78(21/57)*	***2.59*****	*+23.2*	*+20.8*
Deciduousness								
Missing information	56		+2.4	-23.0	52		-6.8	-19.5
Evergreen	48(19/29)	**0.44***	+11.7	+19.0	45(19/26)	0.47	+3.8	-1.1
Deciduous	71(16/55)	**2.25***	+44.0	**+49.3*****	67(17/50)	2.15	+37.1	+8.4
Dynamics stages								
Found in immature stages	128(42/86)	1.52	+31.7	**+22.2***	119(41/78)	1.82	+19.3	+5.2
Not found in immature stages	47(20/27)	0.66	+6.1	+6.0	45(22/23)	0.55	+1.3	-24.9
Pioneering habit								
Missing information	125		+14.6	+8.3	114		+13.0	-4.3
Not-pioneer species	34(11/23)	0.48	+19.1	**+38.3***	33(11/22)	1.78	+9.2	-1.7
Pioneer species	16(3/13)	2.07	+46.1	**+49.4***	17(8/9)	0.56	+2.2	+2.7
Dispersal mode								
Missing information	26		-2.6	-13.8	26		-7.9	-15.6
Gravity or autodispersed	21(6/15)	1.26	+19.3	+21.9	20(4/16)	2.56	+24.2	+32.3
• *Autodispersed*	*3(0/3)*	*/*	*+32.6*	*+32.2*	*3(2/1)*	*0.28*	*-0.1*	*5.7*
• *Gravity*	*18(6/12)*	*0.98*	*+15.0*	*+20.1*	*17(2/15)*	***4.93****	*+34.2*	***+37.0****
Wind	42(14/28)	0.97	+33.3	**+53.4****	37(15/22)	0.78	+7.2	+11.6
Ants	12(6/6)	0.46	-15.4	-25.4	9(5/4)	0.43	-19.8	-48.2
Birds	29(8/21)	1.36	+41.5	+30.4	26(10/16)	0.89	+25.9	+16.6
Other animals	45(15/30)	0.97	+14.3	+4.6	46(16/30)	1.10	+8.2	-25.3
All species	**175(62/113)**		+19.2	**+17.9***	**164(63/101)**		+9.5	-3.0
Shift per decade			+13.6	**+12.6***			+6.7	-2.1

The information about deciduousness was mostly available for woody species. Deciduous species were significantly more shifting upward (o.r.=2.25) than evergreen species, with a mean shift of +49.3 m (median=+44.0 m) significantly different from zero (n=71, p<0.001). The difference became even more significant when considering phanerophytes only, with an odds ratio of 2.92 for deciduous species (51 ascending and 12 descending among deciduous *versus* 16 ascending and 11 descending among evergreens).

Seed masses were available in the Leda Traitbase for 107 out of the 175 studied species. Seed mass was significantly higher among ascending species (median=14.0 mg) than among those descending (median=3.2 mg) when considering all the 107 species (t-test of difference in means of the logarithms, n=107, p=0.03). This difference became insignificant when considering only species shifting significantly (p=0.85). However, it must be pointed out that a strong and significant relationship exists between seed mass and woodiness (n=107, p<0.0001 in an analysis of variance of woodiness effect on seed mass logarithm). The median seed masses were 2.6 mg and 20.7 mg for herbaceous and woody species, respectively.

The information about the pioneering habit was mostly available for woody species. As a consequence, both pioneer and not-pioneer species were significantly shifting upward. But there were more ascending species among pioneer species (o.r.=2.07) than among not-pioneer species (o.r.=0.48) and the former displayed a larger shift (median=+46.1 m) than the latter (median=+19.1 m). The same trend was observed with the presence of species in early stages of forest development: there were relatively more ascending species among species found in early stages (o.r.=1.52) than among other species (o.r.=0.66) and the former displayed a larger shift (median=+31.7 m) than the latter (median=+6.1 m).

Species dispersed by ants were less ascending than those with other dispersal modes (odds ratio=0.46) and presented a negative average shift. On the opposite, species dispersed by birds were slightly more ascending than others (odds ratio=1.36).

3. Species shifts and successional dynamics

Forest changed in terms of the ratio of closed to open forests between the two sampling periods (figure 5). The percentage area of open forests decreased at all elevations, but the decrease was much more pronounced at lower elevations. Below 1300 m a.s.l., it went from 39% to 20% between the two inventories, whereas it only decreased from 21% to 16% above 1300 m a.s.l.. A parallel trend was observed for forest age which showed a homogeneous and significant ageing of Mediterranean forests at lower elevations, where forests were the youngest (figure 6). Below 1300 m a.s.l., mean age increased significantly from 52.4 to 56.4 years between 1984.7 and 1998.8 (n=20390, p<0.0001). Above 1300 m a.s.l., the age increased insignificantly from 102.0 to 104.8 years.

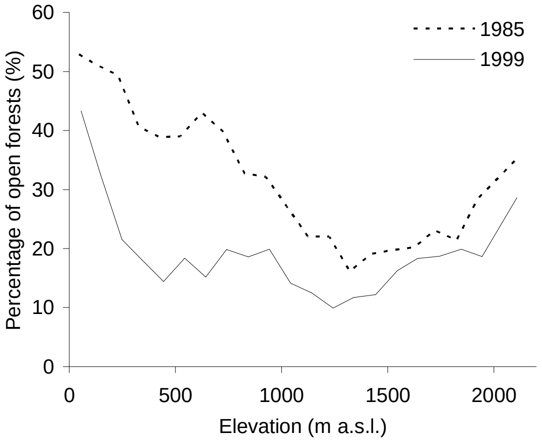

Figure II-5: Percentage area of open forests by 100 m elevation classes at the two inventories (1985: dotted line, 1999: full line).

Because these changes in forest openness and age were not uniformly distributed along the elevation gradient, the response of vegetation in closed or open forests could be different from that observed previously in the entire sample. When considering closed forests only, the sampling area decreased to 1 266 803 ha at the first inventory (11745 plots) and 1 733 310 ha (12623 plots) at the second one. Closed forests still showed a significant ageing trend at most of the lowest elevations classes (figure 7). It was also accompanied by a homogeneous increase of basal area all along the elevation gradient (figure 7).

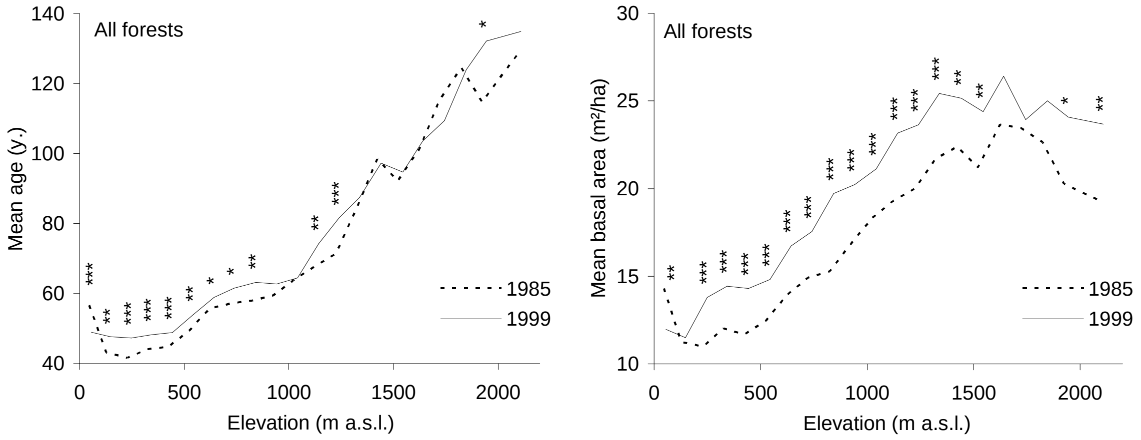

Figure II-6: Average stand age (left) and basal area (right) by 100-m elevation classes at each inventory (1985: dotted line, 1999: full line), in the whole sample. Asterisks designate elevation classes with values significantly different between 1985 and 1999 according to a Student t-test. The meaning of the asterisks is the same as in table 2.

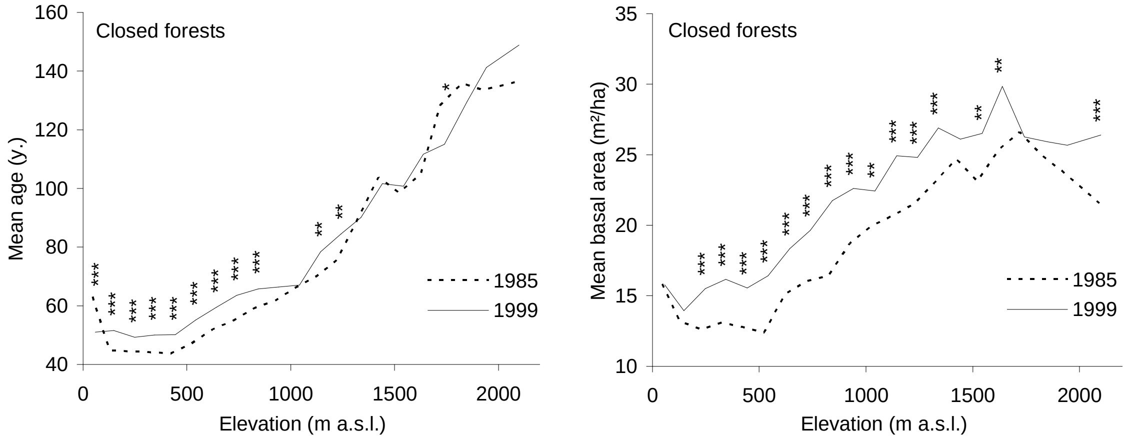

Figure II-7: Average stand age (left) and basal area (right) by 100 m elevation classes at each inventory (1985: dotted line, 1999: full line), in closed forests only. Asterisks designate elevation classes with values significantly different between 1985 and 1999 according to a Student t-test. The meaning of the asterisks is the same as in table 2.

When fitting the logistic model to data from closed forests only, 164 species (table 1b) showed a bell-shaped response to elevation (compared to 175 with all the data), among which 63 were shifting downward and 101 upward (ratio=1.60, *versus* 1.82 in all forests). Although the number of species shifting upward was higher than that of species shifting downward, the mean elevation shift was no longer significantly different from zero and became even negative (-3.0 m). The median shift decreased from +19.2 m to +9.5 m (figure 4b and table 2). Out of these 164 species, 62 species presented a shift statistically significantly different from zero, among which 23 were shifting downward and 39 upward (ratio of 1.70, mean of -8.4 m). The median shift of these 62 species remained high (+56.5 m).

Ascending species still had a significantly higher mean Landolt's indicator value for light (mean L=2.9) than descending species (mean L=2.4, n=137, p=0.01). The difference was no longer significant for temperature (p=0.09). A difference appeared for the moisture indicator value, with more hygrophilous species among descending species (mean indicator value for moisture F=2.5) than ascending species (F=2.2, n=134, p=0.04).

The most prominent difference from previous results was that average shifts were lower, more often negative and no longer significantly different from zero for most of the plant traits categories (light demanding species, phanerophytes, woody species, tall and low trees, deciduous species, species found in immature stages of forest dynamics, pioneer and not-pioneer species, species dispersed by wind) (table 2). Evergreen phanerophytes and hemicryptophytes displayed a significant odds ratio for ascending *versus* descending behavior in closed forests whereas it was not significant in the entire sample, although in the same direction (relatively more descending species). Woody chamephytes comprised much more ascending species (o.r.=5.25) whereas they did not show any pattern in the entire sample. For the pioneering habit, the pattern was reversed in closed forests in comparison to that in all forests: pioneer species comprised relatively less ascending species. Species dispersed by gravity, which displayed no trend in the entire sample, were now composed of more ascending than descending species (o.r.=4.93), and their mean shift was significantly positive (+37.0 m, n=17, $p<0.05$).

E. DISCUSSION

The observed upward shift of species (+13.6 m per decade) in the Mediterranean and southern alpine region, corroborated by the observation that more species were shifting upward than downward, confirms previous findings that forest vegetation is currently responding to some environmental changes in French mountains (Lenoir *et al.* 2008). But the amplitude of the observed shift decreased drastically when considering closed forests only. Moreover, contrary to previous observations that most shifting species were herbaceous and mountainous, we found here that shifting species were woody and shrubby species, light demanding and pioneer.

1. Causes of the observed shift

Several explanations can be proposed for the altitudinal shift of vegetation. First, it could be partly the effect of climate warming. The last episode of continuous and steep warming in the Southern Alps started at the turn of the seventies, between one and two decades before our first inventory, and developed at a rate of 0.5°C/decade until 2000 (Moisselin *et al.* 2002), at the end of the second inventory. This should have pushed species habitats higher in elevation. The fact that the more thermophilous species tended to shift upward more than other species could be an argument in favour of a climatic effect. However, most of our results point to another explanation. A strong link appeared between the shifting of species and successional dynamics, *i.e.* forest closure and ageing.

First, plant life traits more often associated with the shifting behaviour were those related to forest successional dynamics: pioneer habit, potential presence in immature forest stages and potential height of the species. Secondly, the area proportion of open forests shrunk between the two inventories at lower elevations. This forest closure was accompanied by a parallel ageing of forest stands, more pronounced at low altitudes. Lastly, the global upward trend of vegetation became insignificant when calculated for closed forests only, in spite of a still very large sample of plots.

Therefore, the significant upward shift of species in the entire sample can be interpreted as a global change in forest development stage, varying with altitude. The loss of open forests at lower elevation led to the decrease in frequency of species from open forest habitats and the increase of species from closed forests. Thus, the apparent upslope movement was the result of changing dominance or frequency within communities at lower elevations, due to stand maturation, rather than an actual shift of species to higher elevations. A similar role of changing dominance, but due to climate change, on the observed altitudinal shift of species as been already observed by Kelly & Goulden (2008) (see also Breshears *et al.* 2008). Low trees and shrubs are characteristic of immature stages of forest succession in the temperate and Mediterranean zones, giving place to tall trees as forest ages. This explains the large odds ratios observed for these plant traits. The high cover and heavy shade of woody shrubs in open forests is responsible for a low herbaceous species richness (Shachak *et al.* 2008). Thus, forest dynamics at lower elevations could also explain the small odds of the herbaceous plant trait.

The closure of forests at lower elevations also explains both the apparent downward shift of geophytes, shade tolerant and ant-dispersed species, three plant traits associated with late-successional stages (Hermy *et al.* 1999) and the apparent upward shift of light demanding species, which are progressively eliminated from maturing forests due to habitat loss at lower elevation. Because the Landolt's indicator values for temperature and light are highly correlated in our sample of species, even the upward shift of thermophilous species could be explained by the same phenomenon. Moreover, the difference in Landolt's indicator values for temperature between downward and upward shifting species became insignificant in closed forests.

As already noted by Simon & Tamru (1998), forest closure in Mediterranean mountains causes an attenuation of the Mediterranean character and a transition of mesomediterranean vegetation to supramediterranean and mountain ones. Woody species are more frequent in Mediterranean than temperate ecosystems. Quézel and Médail (2003) indicate a decrease in woody species richness from 15 species/100 m^2 on average in mesomediterranean forests, corresponding to our lower elevation plots, to 10 species/100 m^2 at higher elevations. Thus, such a loss of Mediterranean character in the lower elevation belts explains the large odds ratio of upward shift for woody species. This apparent upslope movement of woody species also explains the heavier seed mass of ascending species, because these two plant traits are highly correlated. *Abies alba*, which shifted downward in our study, has been shown to colonise the understorey of Mediterranean mountain forests at lower elevation when they mature (Quézel & Médail 2003; Chauchard *et al.* 2007). Evergreen, broadleaved or not, did not shift upward, contrarily to what was expected in case of climate warming impact (Walther *et al.* 2005c, 2007; Berger *et al.* 2007).

Our interpretation of a major effect of forest successional changes at lower elevations was confirmed by another observation: species with an optimum above 1300 m a.s.l. did not display any significant directional trend. Above 1800 m a.s.l., the tendency was even reversed, towards a slight downward shift. In addition, the discrepancy between the altitudinal homogeneity of the warming trend (fig. 2) and the heterogeneous nature of the species upward shift we have observed is again not in agreement with an effect of climate change.

2. Forest closing, ageing and maturation

The closure and ageing of the forests in the Mediterranean zone during the last decades is the result of several factors. It is the natural legacy of agricultural land abandonment earlier in the 20th century. It is also the result of a continuous decrease in forest pasturing. Finally, it reflects a persistent imbalance between an increasing forest growth and stable or decreasing biomass removals (Dupouey *et al.* 2009). This latter cause could also play a role in the dynamics of closed, mature forests (see also Walther & Grundmann 2001). It has been shown by Tatoni & Roche (1994) that recolonization of old-field and forest revegetation lead to similar dynamic patterns. In our study, closed and open forests were separated by photo-interpretation. But photo-interpretation can not discriminate between the more subtle successional stages linked with the slow wood accumulation in already closed forest stands. Thus, it should be possible that some of the residual changes that we observed between the two inventories in closed forests only, such as the apparent descent of geophytes, be due to varying rates of stand maturation at different elevations.

3. Lag between vegetation shift and climate warming

The amplitude of the vegetation shifts we calculated lagged largely behind the rate of climate warming observed in the same area. If vegetation had exactly tracked the 0.5°C/decade warming rate, the theoretical shift should have been of +89 m/decade, because of an environmental lapse rate of 0.56°C/100 m in the studied area. We observed a shift of only +12.6 m/decade in all forests, 7 times less than expected in the equilibrium model. In closed forests only, the shift even decreased to an insignificant value of +6.7 m/decade. The lagged response to climate warming could be due to a combination of low dispersal capacity (Svenning & Skov 2004) and an ability to acclimate rather than extinct or migrate (Hirzel & Le Lay 2008). In the forest ecosystems we studied, nearly all species are perennials, a life trait which probably favours acclimatisation.

F. CONCLUSION

Land-cover and land-use changes belong to the few major processes, together with climate change, atmospheric pollution and CO_2 fertilisation, potentially able to reshape biodiversity patterns at regional or continental scales within a short time span. Here we have shown that forest belts are subject to the confounding influence of land-use changes, similar to what has been observed above tree-line. The main factor of the apparent upward shift of vegetation was probably the closure and maturation of forest stands, varying in intensity with elevation, and not climate change. The influence of such forest management changes is difficult to detect in forests because stand closure, ageing and maturation in already established stands are more difficult processes to characterise than the woody encroachment of abandoned pastures above the tree-line. Measuring basal area, characterizing openness of forest stands and, even more, counting the age needs specialised observers. Such data are not usually available with classical plant censuses. Our study points out the need for care in interpreting long-term forest vegetation changes when this information is lacking. Since large area in western Europe are undergoing similar trends of forest recolonisation and maturation at lower elevations, previous observations and interpretations of upward shift of vegetation in the mountains should be taken with care.

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G. REFERENCES

Aimé S, Sarrailh JM (1972) Etude comparative du bilan hydrique de quelques bassins des Alpes du Sud. *Annales du Muséum d'Histoire naturelle de Nice*, **2**, 57-75.

Albert CH, Thuiller W, Lavorel S, Davies ID, Garbolino E (2008) Land-use change and subalpine tree dynamics: colonization of *Larix decidua* in French subalpine grasslands. *Journal of Applied Ecology*, **45**, 659-669.

Archaux F, Gosselin F, Bergès L, Chevalier R (2006) Effects of sampling time, species richness and observer on the exhaustiveness of plant censuses. *Journal of Vegetation Science*, **17**, 299-306.

Archaux F, Camaret S, Dupouey J, Ulrich E, Corcket E, Bourjot L, Brêthes A, Chevalier R *et al.* (2008) Can we reliably estimate species richness with large plots? an assessment through calibration training. *Plant Ecology*, **203**, 303-315.

Ashcroft MB, Chisholm LA, French KO (2008) The effect of exposure on landscape scale soil surface temperatures and species distribution models. *Landscape Ecology*, **23**, 211-225.

Bader MY, Ruijten JJA (2008) A topography-based model of forest cover at the alpine tree line in the tropical Andes. *Journal of Biogeography*, **35**, 711-723.

Bartoli C (1966) Etudes écologiques sur les associations forestières de la Haute-Maurienne. *Annales des Sciences Forestières*, **23**, 1-321.

Beckage B, Osborne B, Gavin DG, Pucko C, Siccama T, Perkins T (2008) A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 4197-4202.

Becker M, Picard J, Timbal J (1982) *Larousse des arbres, des arbustes et des arbrisseaux de l'Europe occidentale*. Librairie Larousse, Paris.

Berger S, Sohlke G, Walther GR, Pott R (2007) Bioclimatic limits and range shifts of cold-hardy evergreen broad-leaved species at their northern distributional limit in Europe. *Phytocoenologia*, **37**, 523-539.

Bolli JC, Rigling A, Bugmann H (2007) The influence of changes in climate and land-use on regeneration dynamics of Norway spruce at the treeline in the Swiss Alps. *Silva Fennica*, **41**, 55-70.

Breshears DD, Huxman TE, Adamsa HD, Zou CB, Davison JE (2008) Vegetation synchronously leans upslope as climate warms. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11591–11592.

Carraro G, Klötzli F, Walther G, Gianoni P, Mossi R (1999) *Observed changes in vegetation in relation to climate warming, Final Report NRP 31*. vdf Hochschulverlag, Zurich.

Caussinus H, Mestre O (2004) Detection and correction of artificial shifts in climate series. *Journal of the Royal Statistical Society Series C-Applied Statistics*, **53**, 405-425.

Chauchard S, Carcaillet C, Guibal F (2007) Patterns of land-use abandonment control tree-recruitment and forest dynamics in Mediterranean mountains. *Ecosystems*, **10**, 936-948.

Collett D (1991) *Modelling binary data*. Chapman & Hall, London.

Coudun C, Gégout J (2006) The derivation of species response curves with Gaussian logistic regression is sensitive to sampling intensity and curve characteristics. *Ecological Modelling*, **199**, 164-175.

Council of Europe and Commission of the European Communities (1987) *Map of the Natural Vegetation of the member countries of the European Community and the Council of Europe, scale 1:3 000 000, second edition*. The Office of Official Publications of the European Communities.

Didier L (2001) Invasion patterns of European larch and Swiss stone pine in subalpine pastures in the French Alps. *Forest Ecology and Management*, **145**, 67-77.

Dobbertin M, Hilker N, Rebetez M, Zimmermann NE, Wohlgemuth T, Rigling A (2005) The upward shift in altitude of pine mistletoe (*Viscum album* ssp. *austriacum*) in Switzerland—the result of climate warming? *International Journal Biometeorology*, **50**, 40-47.

Douguédroit A (1981) Reafforestation in the French southern Alps. *Mountain Research and Development*, **1**, 245-252.

Drapier J, Cluzeau C (2001) La base de données écologiques de l'IFN. *Revue Forestière Française*, **53**, 365-371.

Dupouey J, Pignard G, Hamza N, Dhôte J (2009) Estimating carbon stocks and fluxes in french forest biomass, based on national inventory data. In: *Forest and Climate Change* (eds Loustau *et al.*), Quae, Paris. In press.

Fischlin A, Midgley GF, Price JT, Leemans R, Gopal B, Turley C, Rounsevell MDA, Dube OP *et al.* (2007) Ecosystems, their properties, goods, and services. Climate Change 2007: Impacts, Adaptation and Vulnerability. In: *Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE), pp. 211-272. Cambridge University Press, Cambridge.

Gehrig-Fasel J, Guisan A, Zimmermann NE (2007) Tree line shifts in the Swiss Alps: Climate change or land abandonment? *Journal of Vegetation Science*, **18**, 571-582.

Gellrich M, Zimmermann NE (2007) Investigating the regional-scale pattern of agricultural land abandonment in the Swiss mountains: A spatial statistical modelling approach. *Landscape and Urban Planning*, **79**, 65-76.

Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. *Nature*, **369**, 448.

Hermy M, Honnay O, Firbank L, Grashof-Bokdam C, Lawesson J (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation*, **91**, 9-22.

Hirzel AH, Le Lay G (2008) Habitat suitability modelling and niche theory. *Journal of Applied Ecology*, **45**, 1372-1381.

Holtmeier F, Broll G (2007) Treeline advance - driving processes and adverse factors. *Landscape Online*, **1**, 1-32.

Holzinger B, Hulber K, Camenisch M, Grabherr G (2008) Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates. *Plant Ecology*, **195**, 179-196.

Kammer PM, Schöb C, Choler P (2007) Increasing species richness on mountain summits: Upward migration due to anthropogenic climate change or re-colonisation? *Journal of Vegetation Science*, **18**, 301-306.

Keller F, Kienast F, Beniston M (2000) Evidence of response of vegetation to climatic change on high elevation sites in the Swiss Alps. *Regional Environmental Change*, **2**, 70-77.

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11823-11826.

Kleyer M, Bekker R, Knevel I, Bakker J, Thompson K, Sonnenschein M, Poschlod P, van Groenendael J *et al.* (2008) The LEDA Traitbase: A database of life-history traits of the Northwest European flora. *Journal of Ecology*, **96**, 1266-1274.

Körner C (2002) Mountain biodiversity, its causes and function: an overview. In: *Mountain Biodiversity: A Global Assessment* (eds Körner C, Spehn EM), pp. 3-20. Parthenon, New York.

Körner C (2007) The use of ‘altitude’ in ecological research. *Trends in Ecology and Evolution*, **22**, 569-574.

Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, **90**, 68-77.

Landolt E (1977) *Ökologische Zeigerwerte zur Schweizer Flora*. Stiftung Rübel, Zürich.

Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768-1771.

MacDonald D, Crabtree JR, Wiesinger G, Dax T, Stamou N, Fleury P, Gutierrez Lazpita J, Gibon A (2000) Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. *Journal of Environmental Management*, **59**, 47-69.

Moisselin J, Schneider M, Canellas C, Mestre O (2002) Les changements climatiques en France au XXe siècle. Étude des longues séries homogénéisées de données de température et de précipitations. *La Météorologie*, **38**, 45-56.

Motta R, Morales M, Nola P (2006) Human land-use, forest dynamics and tree growth at the treeline in the Western Italian Alps. *Annals of Forest Science*, **63**, 739-747.

Nogués-Bravo D, Araújo MB, Romdal T, Rahbek C (2008) Scale effects and human impact on the elevational species richness gradients. *Nature*, **453**, 216-219.

Ozenda P, Lucas MJ (1987) Esquisse d'une carte de la végétation potentielle de la France à 1/1500000. *Documents de Cartographie Ecologique, Grenoble*, **30**, 49-80.

Parmesan C (2006) Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution and Systematics*, **37**, 637-669.

Pauli H, Gottfried M, Reiter K, Klettner C, Grabherr G (2007) Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994-2004) at the GLORIA*master site Schrankogel, Tyrol, Austria. *Global Change Biology*, **13**, 147-156.

Quézel P, Médail F (2003) *Ecologie et biogéographie des forêts du bassin méditerranéen*. Elsevier, Paris.

Rameau J, Mansion D, Dumé G, Gauberville C, Bardat J, Bruno E, Keller R (2008) *Flore forestière française Tome 3, Région méditerranéenne*. Institut pour le Développement Forestier - CNPPF.

Shachak M, Boeken B, Gruner E, Kadmon R, Lubin Y, Meron E, Ne’eman G, Perevolotsky A *et al.* (2008) Woody species as landscape modulators and biodiversity patterns. *Bioscience*, **58**, 209–221.

Simon L, Tamru B (1998) Cartographie biogéographique et dynamiques de paysage en montagne de Lure. *Mappemonde*, **49**, 26-31.

Stage AR, Salas C (2007) Interactions of elevation, aspect, and slope in models of forest species composition and productivity. *Forest Science*, **53**, 486-492.

Svenning J, Skov F (2004) Limited filling of the potential range in European tree species. *Ecology Letters*, **7**, 565-573.

Tatoni T and Roche P (1994) Comparison of old-field and forest revegetation dynamics in Provence. *Journal of Vegetation Science* **5**: 295-302.

Thimonier A, Dupouey J, Bost F, Becker M (1994) Simultaneous eutrophication and acidification of a forest ecosystem in northeast France. *New Phytologist*, **126**, 533-539.

Thomas C, Cameron A, Green R, Bakkenes M, Beaumont L, Collingham Y, Erasmus B, de Siqueira M *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145-148.

Tutin TG, Heywood VH, Burges NA, Valentine DH, Moore DM (1968-1993) *Flora Europaea, 5 vol.*. Cambridge University Press.

Vittoz P, Guisan A (2007) How reliable is the monitoring of permanent vegetation plots? A test with multiple observers. *Journal of Vegetation Science*, **18**, 413-422.

Vittoz P, Bodin J, Ungricht S, Burga C, Walther GR (2008) One century of vegetation change on Isla Persa, a nunatak in the Bernina massif in the Swiss Alps. *Journal of Vegetation Science*, **19**, 671-680.

Vittoz P, Randin C, Dutoit A, Bonnet F, Hegg O (2009) Low impact of climate change on subalpine grasslands in the Swiss Northern Alps. *Global Change Biology*, **15**, 209-220.

Walther GR, Grundmann A (2001) Trends of vegetation change in colline and submontane climax forests in Switzerland. *Bulletin of the Geobotanical Institute ETH*, **67**, 3-12.

Walther G, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J, Hoegh-Guldberg O *et al.* (2002) Ecological responses to recent climat change. *Nature*, **416**, 389-395.

Walther GR (2004) Plants in a warmer world. *Perspectives in Plant Ecology, Evolution and Systematics*, **6**, 169-185.

Walther G, Beißner S, Pott R (2005a) Climate change and high mountain vegetation shifts. In: *Mountain Ecosystems – Studies in Treeline Ecology* (eds Broll G, Keplin B), pp. 77-96. Springer, Heidelberg.

Walther G, Beißner S, Burga CA (2005b) Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, **16**, 541-548.

Walther G, Berger S, Sykes MT (2005c) An ecological ‘footprint’ of climate change. *Proceedings of the Royal Society B*, **272**, 1427–1432.

Walther GR, Gritti ES, Berger S, Hickler T, Tang ZY, Sykes MT (2007) Palms tracking climate change. *Global Ecology and Biogeography*, **16**, 801-809.

H. ANNEX OF THE CHAPTER TWO

Annex 1: Frequency and elevation optimum of species displaying both a unimodal response curve to elevation and an optimum within the sampled range (0-2200 m a.s.l.). Calculations were separately made for the whole data set (on the left) and for closed forests only (on the right). Corrected frequency = 1000 x number of occurrences of the species / total number of occurrences over all species, weighted by area representativeness of each plot. Optimum (m) calculated as Opt_{elev} in the text of the article. Shift = optimum 1998 minus optimum 1984. In bold: significant shift (*: $p<0.05$; **: $p<0.01$; ***: $p<0.001$). L and T: Landolt indicator values (1 to 5) for light and temperature, respectively. Light requirement: light demanding (l) or shade tolerant (s). Growth form: deciduous phanerophyte (p), evergreen phanerophyte (i), deciduous nanophanerophyte (n), evergreen nanophanerophyte (j), woody chamephyte (z), herbaceous chamephyte (c), epiphyte (e), hemicryptophyte (h), geophyte (g), therophyte (t). Woodiness: woody (w) or herbaceous (h). Deciduousness: evergreen (e) or deciduous (d). Maximum height: tall tree >12m (t) or low tree or shrub <12m (l). Dynamics stage: species found in immature, early, stages (e) or in mature, late, stages (l) of successional dynamics. Pioneer habit: pioneer species (p) or not (n).

	Whole data set					Closed forests only													
Species name	Corrected frequency 1984	Corrected frequency 1998	Optimum 1984	Optimum 1998	Shift between 1984 and 1998	Corrected frequency 1984	Corrected frequency 1998	Optimum 1984	Optimum 1998	Shift between 1984 and 1998	T	L	Light requirement	Growth form	Woodiness	Deciduousness	Maximum height	Dynamics stage	Pioneer habit
Abies alba	5,5	4,5	1474	1463	-11	7,7	5,4	1489	1462	-27	3	1	l	i	w	e	t	l	n
Abies nordmanniana	0,2	0,1	750	712	-38	0,3	0,1	757	703	-54			l	i	w	e	t	l	n
Acer campestre	**2,4**	**3,5**	**905**	**1014**	**109*** **	**2,6**	**3,7**	**876**	**983**	**107*** **	4	3	l	p	w	d	t	l	n
Acer monspessulanus	**2,9**	**2,9**	**614**	**656**	**41***	2,8	3,0	615	642	27	5	3	l	p	w	d	l	e	n
Acer opalus	4,4	5,6	1091	1103	12	**5,7**	**6,2**	**1054**	**1091**	**37****	5	3	l	p	w	d	l	l	n
Acer platanoides						**0,2**	**0,2**	**1403**	**875**	**-528****	4	2	s	p	w	d	t		n
Acer pseudoplatanus	**1,8**	**1,6**	**1410**	**1478**	**68***	**2,4**	**1,8**	**1409**	**1472**	**62***	3	2	s	p	w	d	t	e	n
Alnus glutinosa						**1,0**	**0,6**	**684**	**224**	**-460*** **	4	3	l	p	w	d	t	e	p
Amelanchier ovalis	**15,2**	**12,7**	**945**	**1025**	**80*** **	**15,1**	**13,0**	**938**	**1010**	**71*** **	3	4	l	n	w	d	l	e	p
Anemone nemorosa	0,2	0,4	1627	1500	-126	0,3	0,4	1664	1536	-128	3	2	s	g	h			e	
Aphyllanthes monspeliensis	10,6	9,6	574	584	11	**10,0**	**9,2**	**529**	**564**	**34****	5	4	l	g	h			e	
Arctostaphylos uva-ursi	1,1	0,9	1985	1965	-20	1,4	1,1	2028	1992	-36	2	3	l	z	w	e	l	e	p
Asplenium ceterach	0,4	0,6	422	313	-109	0,3	0,6	367	238	-129	5	5	l	h	h			l	
Asplenium trichomanes	**1,7**	**2,7**	**398**	**580**	**182****	1,6	2,9	322	465	143	3	3	s	h	h			l	
Astragalus sempervirens	**0,3**	**0,2**	**1763**	**2107**	**344*** **						3	3	l	z	w	e	l	e	
Athyrium filix-femina	0,5	0,4	1530	1535	5	0,8	0,5	1527	1534	7	3	2	s	h	h			e	
Berberis vulgaris	0,9	1,3	1821	1751	-71	**1,0**	**1,2**	**1869**	**1760**	**-110***	3	3	l	n	w	d	l	e	
Betula pendula	**0,9**	**0,8**	**1240**	**1348**	**107***	**0,9**	**0,9**	**1221**	**1335**	**114***	3	4	l	p	w	d	t	e	p
Bromus erectus	**5,2**	**5,6**	**813**	**922**	**109*** **	**4,9**	**5,6**	**676**	**877**	**201*** **	4	4	l	h	h			e	
Buxus sempervirens	**16,4**	**11,3**	**757**	**817**	**59*** **	16,1	11,7	783	787	4	5	3	s	j	w	e	l	e	n
Calluna vulgaris	4,9	3,2	482	445	-37	4,3	3,5	541	522	-19	3	3	l	z	w	e	l	e	p
Cardamine heptaphylla	**0,3**	**0,2**	**1468**	**1351**	**-116****	**0,4**	**0,2**	**1472**	**1354**	**-118****	3	2	s	h	h			l	
Castanea sativa	**7,3**	**4,8**	**601**	**636**	**36*** **	**6,4**	**5,7**	**605**	**627**	**22***	5	3	l	p	w	d	t	l	n
Catananche coerulea	**1,9**	**3,1**	**806**	**870**	**65****	**1,6**	**2,9**	**732**	**826**	**94*** **	5	4	l	h	h			e	
Cedrus atlantica	0,8	0,8	663	669	6	0,9	0,9	623	629	7			l	i	w	e	t	l	n
Cistus albidus	5,6	4,2	208	223	15	4,9	3,7	204	211	7			l	j	w	e	l	e	
Clematis alpina	0,2	0,1	2039	2071	31						2	3	s	n	w	d	l	l	
Clematis vitalba	**3,0**	**3,5**	35	227	192**						3	3	l	p	w	d	t	e	
Conopodium majus	0,3	0,3	1453	1436	-17	0,4	0,4	1433	1470	37			s	g	h			e	
Coriaria myrtifolia	0,4	0,3	339	395	56	0,4	0,3	387	393	6			l	n	w	d	l	e	
Cornus mas	**0,6**	**0,4**	**644**	**409**	**-236*** **	**0,6**	**0,4**	**566**	**358**	**-208****	5	3	l	p	w	d	l	e	
Cornus sanguinea	6,4	6,2	487	525	38	6,3	6,5	415	438	24	4	3	l	n	w	d	l	e	
Coronilla emerus	4,2	3,9	672	685	13	4,6	4,5	673	669	-4	4	3	l	n	w	d	l	e	p

Species name	Whole data set					Closed forests only													
	Corrected frequency 1984	Corrected frequency 1998	Optimum 1984	Optimum 1998	Shift between 1984 and 1998	Corrected frequency 1984	Corrected frequency 1998	Optimum 1984	Optimum 1998	Shift between 1984 and 1998	T	L	Light requirement	Growth form	Woodiness	Deciduousness	Maximum height	Dynamics stage	Pioneer habit
Coronilla minima	**2,7**	**3,7**	**877**	**968**	**92*****	**2,5**	**3,6**	**857**	**957**	**100****	5	3	l	z	w	d	l	e	
Coronilla valentina subsp. glauca	0,2	0,3	688	560	-128								l	n	w	d	l	e	
Corylus avellana	**4,2**	**3,8**	**1091**	**1178**	**87*****	**4,5**	**4,3**	**1074**	**1141**	**68****	3	3	s	n	w	d	l	e	
Cotinus coggygria	**1,2**	**1,5**	**645**	**697**	**52***	**1,4**	**1,6**	**612**	**666**	**54***	5	4	l	n	w	d	l	e	
Cotoneaster nebrodensis	**0,4**	**0,8**	**1917**	**1635**	**-282*****	**0,5**	**0,9**	**1952**	**1693**	**-259*****	4	4	l	n	w	d	l	e	
Crataegus monogyna	**13,3**	**13,6**	**814**	**856**	**42*****	**13,7**	**14,0**	**770**	**826**	**57*****	4	4	l	p	w	d	l	e	p
Cytisus purgans	**1,9**	**1,0**	**920**	**983**	**63****	1,3	1,2	982	982	0			l	n	w	d	l	e	p
Cytisus scoparius	**4,5**	**3,6**	**697**	**730**	**33****	3,6	4,2	699	722	23	4	3	l	n	w	d	l	e	
Cytisus sessilifolius	6,6	6,8	1071	1092	21	**7,6**	**7,4**	**1031**	**1087**	**56*****	5	3	l	n	w	d	l	e	p
Daphne laureola	**2,5**	**2,8**	**840**	**907**	**67****	**3,1**	**3,2**	**806**	**883**	**77****	4	2	s	j	w	e	l	e	
Digitalis purpurea	**0,6**	**0,6**	**1096**	**1192**	**96***	0,7	0,6	1117	1109	-8	4	3	l	h	h			e	
Dorycnium pentaphyllum	9,2	7,0	399	399	0	8,3	6,9	381	390	10	5	4	l	z	w	e	l	e	
Dryopteris carthusiana	**0,3**	**0,2**	**1394**	**1246**	**-147***	**0,4**	**0,3**	**1381**	**1247**	**-134***	3	2		h	h			e	
Dryopteris filix-mas	0,7	1,0	1454	1574	120	0,8	1,2	1559	1514	-44	3	2	s	h	h			e	
Echinops ritro	0,8	1,0	1003	1054	50	0,8	0,9	968	1037	69			l	h	h			e	
Epilobium angustifolium	**1,8**	**1,2**	**1639**	**1724**	**85****	2,3	1,4	1637	1685	49	3	4	l	h	h			l	
Epilobium montanum	**0,9**	**0,9**	**1522**	**1647**	**125****	1,1	1,1	1578	1626	48	3	2	s	h	h			l	
Erica cinerea	1,7	1,2	553	553	0	1,4	1,4	535	544	9			l	z	w	e	l	e	n
Eryngium campestre	3,1	2,8	745	708	-37	2,7	2,4	679	645	-34	5	4	l	h	h			e	
Euphorbia amygdaloides	1,3	2,0	350	408	58	1,3	2,3	483	302	-181	4	2	s	c	h	e		l	
Euphorbia characias	**4,2**	**3,7**	**106**	**43**	**-63***								l	z	w	e	l	e	
Euphorbia dulcis	**1,0**	**1,5**	**2155**	**1846**	**-310*****	**1,4**	**1,7**	**2157**	**1871**	**-286*****	3	2	s	g	h			e	
Euphorbia serrata	0,2	0,2	394	403	9						5	4	l	h	h			e	
Euphorbia spinosa	**0,6**	**0,8**	**641**	**773**	**132*****	**0,5**	**0,5**	**599**	**720**	**121***			l	z	w	d	l	e	
Fagus sylvatica	9,4	6,7	1215	1220	4	12,2	7,9	1205	1210	5	3	2	s	p	w	d	t	l	n
Fragaria vesca	4,4	4,8	1602	1619	17	5,6	5,5	1641	1642	0	3	3	l	h	h			e	
Fraxinus excelsior	**3,3**	**3,6**	**896**	**1115**	**219*****	2,7	4,0	980	1053	72	4	3	l	p	w	d	t	e	n
Fraxinus ornus	**1,1**	**1,3**	**521**	**606**	**85***	1,3	1,3	487	540	53	5	3	l	p	w	d	l	e	
Fumana ericoides	2,5	2,3	480	481	1	2,1	1,9	452	463	11	5	4	l	z	w	e	l	e	
Fumana procumbens	**0,4**	**0,7**	**656**	**755**	**99***	0,3	0,6	633	717	84	4	4	l	z	w	e	l	e	
Fumana thymifolia	0,6	0,3	401	383	-18	0,4	0,2	314	377	63			l	z	w	e	l	e	
Galium odoratum	0,8	0,7	1403	1412	9	1,3	0,8	1403	1424	21	3	1	s	g	h			l	
Galium rotundifolium	1,3	1,4	1136	1088	-48	1,7	1,4	1114	1140	25	3	1	s	g	h			l	
Galium sylvaticum	0,2	0,4	1641	1537	-104	0,2	0,5	1642	1531	-111	4	2	s	g	h			e	
Genista cinerea	7,6	6,0	1023	1036	13	7,2	5,5	1011	1033	22	4	4	l	n	w	d	l	e	
Genista hispanica	6,5	5,3	703	709	6	**7,3**	**5,5**	**666**	**703**	**37****			l	z	w	d	l	e	
Genista pilosa	9,9	8,5	843	833	-11	10,3	8,9	821	822	2	4	4	l	z	w	d	l	e	
Genista scorpius						2,0	2,1	0,04	11	11	5	3	l	n	w	d	l	e	
Gentiana lutea	0,9	0,9	1984	1939	-45	1,2	1,0	2078	1995	-83	2	4	l	h	h			e	
Geranium nodosum	0,4	0,4	1535	1483	-52	0,6	0,5	1545	1498	-47	4	2	s	h	h			l	
Globularia vulgaris	**0,6**	**0,5**	**1287**	**931**	**-356*****	**0,5**	**0,4**	**1336**	**926**	**-410*****			l	c	h	e		e	
Hedera helix	**9,5**	**9,7**	**158**	**229**	**71*****	9,8	10,7	110	91	-20	4	2	s	i	w	e	t	e	
Helichrysum stoechas	2,1	2,6	235	279	44	1,9	2,2	217	258	41	5	4	l	z	w	e	l	e	
Helleborus foetidus	**4,5**	**5,8**	**1128**	**1244**	**116*****	4,6	6,2	1172	1216	44	3	2	l	c	h	e		e	
Hepatica nobilis	**5,2**	**5,1**	**1419**	**1379**	**-40***	6,9	5,7	1430	1410	-20	4	2	s	h	h			l	
Heracleum sphondylium	0,1	0,1	1786	1695	-91						3	3	l	h	h			e	
Hippophae rhamnoides	0,3	0,2	1175	1228	53						3	4	l	n	w	d	l	e	p
Hordelymus europaeus	0,2	0,4	1523	1455	-68	0,3	0,5	1516	1463	-53	3	2	s	h	h			l	
Hypericum montanum	**0,3**	**0,2**	**1969**	**1642**	**-327*****	**0,4**	**0,3**	**1894**	**1568**	**-327****	3	3	s	h	h			e	
Ilex aquifolium	1,7	2,1	744	764	20	2,0	2,4	755	744	-11	4	2	s	i	w	e	l	l	n
Juglans regia	0,3	0,4	686	731	44	0,3	0,4	780	695	-85	5	3	l	p	w	d	t	l	n
Juniperus communis	**19,3**	**15,7**	**1468**	**1565**	**97*****	**20,6**	**16,5**	**1474**	**1626**	**152*****	4	4	l	i	w	e	l	e	p
Juniperus oxycedrus	12,3	9,2	236	238	2	11,7	8,8	202	190	-12			l	i	w	e	l	e	p
Juniperus phoenicea	2,0	2,0	389	350	-40	1,7	1,6	454	451	-3			l	i	w	e	l	e	p
Juniperus sabina	0,2	0,2	1721	1802	81						4	4	l	j	w	e	l	e	
Laburnum alpinum	0,2	0,2	1543	1593	50	**0,3**	**0,2**	**1496**	**1594**	**98***	3	3	s	p	w	d	l	e	p
Laburnum anagyroides	1,5	1,2	1324	1358	34	2,1	1,5	1311	1365	54	4	3	l	p	w	d	l	e	

Species name	Whole data set Corrected frequency 1984	Corrected frequency 1998	Optimum 1984	Optimum 1998	Shift between 1984 and 1998	Closed forests only Corrected frequency 1984	Corrected frequency 1998	Optimum 1984	Optimum 1998	Shift between 1984 and 1998	T	L	Light requirement	Growth form	Woodiness	Deciduousness	Maximum height	Dynamics stage	Pioneer habit
Lactuca perennis	0,2	0,4	1441	1493	52						4	5	l	h	h			e	
Laserpitium gallicum	**0,5**	**0,9**	**1518**	**1655**	**137***	**0,5**	**0,8**	**1474**	**1679**	**205****	3	5	l	h	h			l	
Laserpitium siler	0,3	0,3	1700	1781	81	**0,2**	**0,4**	**1656**	**1868**	**212***	3	5	l	h	h			e	
Lathyrus vernus	**0,3**	**0,3**	**1736**	**1563**	**-173***	**0,4**	**0,3**	**1766**	**1531**	**-235****	3	2	s	g	h			l	
Lavandula angustifolia	9,3	7,5	1055	1074	19	8,9	7,2	1038	1058	19	5	3	l	z	w	e	l	e	
Lavandula latifolia	4,3	2,7	304	288	-16	**4,4**	**2,7**	**283**	**190**	**-93***			l	j	w	e	l	e	
Ligustrum vulgare	**3,6**	**4,3**	**125**	**284**	**159*****						4	3	l	n	w	d	l	e	
Lilium martagon	0,4	0,3	2097	2033	-64	0,4	0,3	2129	2045	-84	3	3	s	g	h			e	
Lonicera alpigena	0,5	0,5	1596	1554	-42	0,7	0,7	1629	1562	-68	2	2	s	n	w	d	l	e	
Lonicera etrusca	**3,2**	**2,3**	**174**	**411**	**237*****	**3,2**	**2,3**	**206**	**363**	**158*****	5	3	l	n	w	d	l	e	
Lonicera nigra	**1,8**	**0,6**	**1463**	**1716**	**253*****	**2,3**	**0,7**	**1473**	**1706**	**233*****	2	2	s	n	w	d	l	e	
Lonicera periclymenum	**2,1**	**1,8**	**514**	**242**	**-272*****	**2,0**	**2,1**	**552**	**167**	**-385*****	4	3	l	n	w	d	l	e	
Lonicera xylosteum	3,9	8,6	958	1002	44	4,3	9,4	942	979	38	3	3	l	n	w	d	l	e	
Luzula nivea	**1,7**	**1,7**	**1659**	**1808**	**149*****	**2,4**	**2,0**	**1651**	**1796**	**145*****	3	2	s	h	h			l	
Majanthemum bifolium	0,3	0,3	1399	1403	4	0,4	0,3	1397	1398	1	3	2	s	g	h			l	
Malus sylvestris	0,3	1,0	716	834	118	0,4	1,0	723	822	100	4	3	l	p	w	d	l	e	
Melica uniflora	0,2	0,6	1362	1272	-89						3	2	s	g	h			l	
Mercurialis perennis	**0,5**	**0,8**	**1420**	**1259**	**-161*****	**0,7**	**0,9**	**1441**	**1255**	**-186*****	3	1	s	g	h			e	
Meum athamanticum	0,2	0,2	2044	1933	-111	0,3	0,2	1995	1888	-107	2	4	l	h	h			e	
Odontites luteus	2,3	3,0	201	267	66	**2,2**	**2,4**	**178**	**364**	**186*****	4	4	l	t				e	
Ononis fruticosa	0,5	0,9	1132	1187	55	0,5	0,9	1162	1165	3	4	3	l	n	w	d	l	e	p
Ononis rotundifolia	0,2	0,2	1719	1684	-36	0,3	0,2	1700	1625	-74	4	3	l	z	w	d	l	e	
Ononis spinosa	**1,0**	**0,9**	**1050**	**1236**	**186*****	**1,0**	**0,9**	**1021**	**1260**	**239*****	4	4		z	w		l	e	
Orthilia secunda	1,1	1,8	1571	1524	-47	1,5	2,2	1579	1540	-38	3	2	s	h	h			l	
Ostrya carpinifolia	0,9	0,8	820	855	35	1,2	0,8	779	841	62	5	2	l	p	w	d	t	e	n
Osyris alba	3,1	3,2	237	243	6	2,8	3,0	248	242	-6	5	3	l	j	w	e	l	e	
Oxalis acetosella	1,2	1,0	1671	1672	1	1,8	1,2	1683	1677	-5	3	1	s	g	h			l	
Paris quadrifolia	0,3	0,2	1430	1459	29	0,3	0,3	1430	1464	34	3	2	s	g	h			l	
Phillyrea media	7,2	6,3	270	260	-10	6,4	5,8	243	233	-11	5	3	l	i	w	e	l	e	
Phyteuma spicatum	0,3	0,5	1978	1878	-100	0,5	0,5	2038	1916	-122	3	2	s	h	h			e	
Picea abies	3,2	2,3	1596	1592	-5	4,4	2,7	1603	1593	-10	2	1	l	i	w	e	t	l	n
Pinus halepensis	10,4	6,9	208	201	-7	10,7	6,6	159	161	2			l	i	w	e	t	l	n
Pinus nigra subsp. laricio	1,3	1,0	821	746	-75	**1,5**	**1,2**	**827**	**709**	**-118****	5	4		i	w	e	t	l	n
Pinus nigra subsp. nigra	4,6	4,3	941	956	15	5,0	4,2	939	942	3			l	i	w	e	t	l	n
Pinus pinaster	6,3	3,7	69	78	9	6,1	3,8	217	172	-45				i	w	e	t	l	n
Pinus sylvestris	19,8	13,5	1157	1145	-12	**20,8**	**14,4**	**1158**	**1126**	**-33*****	3	4	l	i	w	e	t	l	n
Pinus uncinata	1,4	0,9	2097	2050	-47	1,7	1,0	2067	2078	11	2	4	l	i	w	e	t	l	n
Pistacia terebinthus	3,7	3,2	281	270	-11	**3,1**	**2,9**	**301**	**245**	**-56*****	5	4	l	p	w	d	l	e	
Polygala calcarea	**0,2**	**0,2**	**791**	**1121**	**330*****						5	4	l	c	h	d		e	
Polygonatum multiflorum	**0,2**	**0,2**	**1480**	**960**	**-520*****	**0,3**	**0,2**	**1527**	**960**	**-567*****	3	2	s	g	h			l	
Polygonatum odoratum	0,2	0,5	1238	1067	-171						3	3	l	g	h			e	
Polygonatum verticillatum	0,5	0,4	1417	1439	22	0,7	0,5	1404	1448	44	2	2	s	g	h			l	
Polypodium vulgare	2,8	5,0	583	517	-66	3,1	5,1	655	646	-9	3	2	s	h	h			l	
Populus tremula	**1,4**	**0,8**	**1155**	**1446**	**291****	**1,3**	**0,9**	**1129**	**1385**	**256****	3	4	l	p	w	d	t	e	p
Prenanthes purpurea	**1,7**	**1,2**	**1549**	**1496**	**-53****	2,4	1,5	1539	1502	-37	3	2	s	h	h			l	
Prunus avium	**3,0**	**3,6**	**827**	**917**	**90***	2,8	4,1	788	864	76	4	3	s	p	w	d	t	l	n
Prunus mahaleb	**1,9**	**2,7**	**621**	**722**	**101***	1,5	2,7	661	676	15	5	4	l	p	w	d	l	e	
Prunus spinosa	5,6	5,4	654	667	14	5,5	5,4	629	631	2	4	4	l	n	w	d	l	e	p
Pseudotsuga menziesii	0,7	0,7	789	807	18	0,9	0,8	796	805	9	3	2	l	i	w	e	t	l	n
Psoralea bituminosa	3,0	3,8	219	211	-8	3,0	3,6	188	210	22			l	c	h	e		e	
Pteridium aquilinum	5,9	4,5	686	692	6	**5,7**	**4,9**	**704**	**664**	**-40***	3	3	l	g	h			e	
Pyrus communis	0,5	0,7	832	815	-17	0,5	0,7	770	838	68	4	3	l	p	w	d	t	e	n
Quercus coccifera	**6,6**	**3,8**	**128**	**71**	**-58*****	**6,2**	**3,3**	**120**	**11**	**-109*****			l	j	w	e	l	e	
Quercus ilex	**24,3**	**18,0**	**128**	**158**	**30***	22,3	17,3	63	60	-3	5	3	l	i	w	e	t	e	n
Quercus petraea	**3,2**	**1,9**	**920**	**840**	**-80*****	**3,2**	**2,2**	**937**	**821**	**-116*****	4	3	s	p	w	d	t	l	n
Quercus pubescens	**30,6**	**22,4**	**570**	**651**	**82*****	**30,9**	**23,4**	**493**	**585**	**92*****	5	3	l	p	w	d	t	e	n
Rhamnus alaternus	4,5	5,0	167	186	19	4,2	4,8	100	128	28	5	4	l	j	w	e	l	e	
Rhamnus alpinus	0,4	0,7	1628	1670	41	0,4	0,7	1590	1693	103	3	3	l	n	w	d	l	e	

	Whole data set					Closed forests only													
Species name	Corrected frequency 1984	Corrected frequency 1998	Optimum 1984	Optimum 1998	Shift between 1984 and 1998	Corrected frequency 1984	Corrected frequency 1998	Optimum 1984	Optimum 1998	Shift between 1984 and 1998	T	L	Light requirement	Growth form	Woodiness	Deciduousness	Maximum height	Dynamics stage	Pioneer habit
Rhamnus saxatilis	__0,9__	__2,6__	__660__	__737__	__77**__	__0,9__	__2,5__	__623__	__721__	__99***__	5	3	l	n	w	d	l	e	
Ribes alpinum	__0,7__	__1,1__	__1588__	__1366__	__-222***__	__0,9__	__1,2__	__1589__	__1343__	__-245***__	2	3	s	n	w	d	l	e	
Ribes petraeum	0,4	0,1	1614	1704	90	0,5	0,2	1667	1697	31	2	3	s	n	w	d	l	e	
Ribes uva-crispa	0,5	1,1	1661	1702	40	0,6	1,1	1657	1694	37	3	2	s	n	w	d	l	e	
Rosmarinus officinalis	__4,9__	__3,7__	__231__	__187__	__-44**__	4,6	3,2	184	153	-31	5	3	l	n	w	d	l	e	
Rubia peregrina	25,7	20,3	171	191	21	24,8	19,8	116	119	4	5	3	l	z	w	e	l	e	
Rubus idaeus	__3,1__	__2,7__	__1561__	__1701__	__141***__	__4,1__	__3,1__	__1570__	__1686__	__116***__	3	3	l	n	w	d	l	l	
Rumex acetosella s.l.						0,3	0,3	2084	1854	-230	3	5	l	h	h			e	p
Sambucus racemosa	__0,5__	__0,6__	__1417__	__1619__	__202***__	0,7	0,7	1478	1559	81	3	3	l	n	w	d	l	e	
Sanguisorba minor	__6,3__	__5,6__	__1115__	__1252__	__137***__	__6,4__	__5,5__	__1054__	__1243__	__188***__	3	4	l	h	h			e	
Satureja montana	1,8	1,7	954	1005	51	1,9	1,5	917	942	26	5	4	l	z	w	e	l	e	
Solidago virgaurea	__0,8__	__1,7__	__1458__	__1636__	__177**__	__1,0__	__1,9__	__1458__	__1650__	__193**__	4	2	s	h	h			e	
Sorbus aria	__13,4__	__13,0__	__1121__	__1159__	__38***__	__15,4__	__14,5__	__1102__	__1142__	__39***__	4	3	l	p	w	d	t	e	n
Sorbus aucuparia	__4,0__	__3,9__	__1715__	__1808__	__94***__	4,9	4,3	1778	1823	44	3	3	l	p	w	d	l	e	n
Sorbus domestica	__1,1__	__2,1__	__427__	__569__	__142***__	__1,3__	__2,2__	__350__	__489__	__139**__	5	3	l	p	w	d	t	l	n
Sorbus torminalis	0,8	1,4	432	490	58	1,0	1,7	382	454	71	5	3		p	w	d	t	e	n
Spartium junceum	2,7	2,2	275	286	11	2,5	2,1	281	248	-33	5	3	l	n	w	d	l	e	
Staehelina dubia	__6,0__	__4,8__	__361__	__421__	__61***__	__5,4__	__4,5__	__349__	__402__	__52**__	5	4	l	z	w	e	l	e	
Stellaria holostea	0,3	0,5	1101	990	-111	__0,3__	__0,6__	__1113__	__975__	__-138*__	5	2	s	c	h			e	
Stellaria nemorum	0,2	0,2	1503	1547	44	0,3	0,3	1452	1547	94	3	2	s	h	h			l	
Teucrium chamaedrys	__17,1__	__15,2__	__643__	__794__	__151***__	__16,2__	__15,1__	__574__	__752__	__178***__	4	3	l	z	w	e	l	e	
Teucrium lucidum	0,2	0,3	1332	1342	10	0,3	0,3	1272	1308	36			l	z	w		l	e	
Teucrium montanum	__0,8__	__2,6__	__953__	__1127__	__174***__	__0,7__	__2,4__	__901__	__1099__	__198***__	3	4	l	z	w	e	l	e	
Teucrium polium	4,1	3,8	522	516	-7	3,6	3,5	472	476	4			l	z	w	d	l	e	
Teucrium scorodonia	__5,7__	__4,3__	__616__	__647__	__31**__	4,7	5,0	641	642	1	4	2	l	g	h			e	
Thymus vulgaris	__16,8__	__12,5__	__404__	__474__	__70***__	__15,4__	__11,6__	__347__	__428__	__81***__	5	3	l	z	w	e	l	e	
Tilia cordata	0,2	0,6	1071	1019	-52						4	2	s	p	w	d	t	e	n
Tilia platyphyllos	__0,2__	__0,3__	__787__	__1202__	__415**__						4	2	s	p	w	d	t	l	n
Ulex parviflorus	0,9	0,6	187	202	14	0,9	0,5	191	200	9			l	j	w	e	l	e	
Vaccinium myrtillus						3,8	2,4	2119	2136	17	3	2	s	z	w	d	l	e	
Veronica officinalis	0,9	1,1	1797	1780	-16	1,1	1,3	1863	1834	-28	3	3	l	c	h	d		e	
Viburnum lantana	__7,5__	__7,5__	__1023__	__1079__	__56***__	__8,3__	__8,2__	__994__	__1060__	__65***__	4	3	l	n	w	d	l	e	

III. LONG TERM CHANGES IN PLANT COMMUNITIES OF THE MAURIENNE VALLEY, FRENCH ALPS

A. INTRODUCTION

Different movements will affect the vegetation of the Alps in response to climate warming. Along the altitudinal gradient, species will be pushed toward higher elevations. Because the adiabatic lapse rate is much larger (0.6°C/100m of ascent) than the average distance between temperature isolines in the lowlands (roughly 0.7°C/100 km in France), species should follow their climatic niche more easily in the mountains.

Besides the elevational gradient, vegetation of the Alps is also strongly distributed as a function of the degree of continentality of the climate, with a clear distinction between the pre-, intermediate- and inner-alpine phytogeographical zones (Ozenda 1985). Climate change could also promote shifts of vegetation along this complex gradient.

It has been suggested, from paleoecological evidence, that species communities are not moving as an entity (Jackson & Overpeck 2000), but are evolving through independent species migration. Due to the differential response of species to climate change, species assemblages could be modified in the future, giving rise to new communities. Hence, the successive vegetation belts found along the elevational gradient (collinean, mountain, subalpine, alpine and nival) or the continentality zones should move (Ozenda & Borel 1995) but also evolve in response to climate change.

Numerous alpine valleys have experienced a rapid and intense increase in human activities during the last century. Levels of industrialization, urbanization and, especially through the Alps, transportations have all globally increased. These activities already had a visible effect on air quality. Vegetation, both cryptogamic and phanerogamic, is known to be a sensitive indicator of temporal variations in acid and nitrogen atmospheric deposition (van Herk *et al.* 2002, Becker *et al.* 1992, Thimonier *et al.* 1992, Thimonier *et al.* 1994, Diekmann & Dupré 1997, Brunet *et al.* 1998, Dupouey *et al.* 1998, Dupouey *et al.* 1999, Lameire *et al.* 2000, Økland *et al.* 2004, Gilliam 2006, Bernhardt-Romermann *et al.* 2007, Schwabe *et al.* 2007, Hülber *et al.* 2008, Römermann *et al.* 2008). Thus, other effects than the sole climate change must be looked for in long-term vegetation resampling studies in the Alps, especially in the lower forest belts which are in contact with the most artificialized areas.

Networks specifically designed for the long-term monitoring of vegetation dynamics under the impact of global change has been settled only very recently, such as the GLORIA network in alpine environments (Grabherr *et al.* 2000). In forests of Europe, the BioSoil project has monitored vegetation only once, yet. National forest inventories provide a slightly broader perspective. In France, we could compare results of the national forest inventory of vegetation in the southern Alps between the 1980s and the 1990s (see previous chapter). But for longer time span, one needs to be opportunistic and use ancient vegetation data wherever they are available. Most often, these data were not initially planned to be reinventoried.

Here, we studied changes in forest plant communities between the 1950s and the 2000s in the upper Maurienne valley using data from a previous phytosociological survey (Bartoli 1966).

Ancient phytosociological surveys are numerous all over the world. They have been seldom used in long-term resampling studies, because the plots were most often not accurately localized in the initial survey. Here we show that such ancient studies can still be used, even without knowledge of the location of the plot, provided the initial sampling scheme can be reproduced today. In the case of the Maurienne valley, the objective of Bartoli was to efficiently describe the main forest vegetation types in the area. Thus he designed a stratified sample based on well defined ecological criteria (elevation, exposure, position along the continentality gradient, type of geological substratum, dominant tree species). Fifty years later, we rebuilt the same sampling design in the same area. This procedure has, among others, the advantage of avoiding the bias of stand maturation in permanent plots. In permanent plots, the impact of global changes on vegetation dynamics is often difficult to disentangle from that of stand ageing and maturation (canopy closure, litter accumulation, soil acidification…).

Another difficulty arises when working with ancient data: there are often not enough plots to correctly model individual species distribution or test changes in individual species occurrences. This is an intrinsic characteristic of life, where rarity is the rule. Thus, even with rather large datasets of several hundreds of vegetation plots, the statistical power is too low to correctly model the distribution of more than a few tens of species because most of the species are rare. One way to solve this problem is to study the changes in plant community characteristics instead of the changes in individual species occurrence. Here we used two kinds of such global properties of the plant community. Mean Ellenberg and Landolt indicator values on the one hand, calibrated in neighbouring regions of Germany and Switzerland, respectively. On the second hand, we built local indices of community indicator values by mean of multivariate analyses. Instead of studying changes in species frequency and occurrences, which needs a too large number of plots to reach a satisfying statistical power, we analyzed changes in global community indicators of ecological conditions. For example, we tested if the temperature indicator value had increased. This procedure requires fewer plots to sample.

Of course, in non-permanent plot networks, it is no longer possible to directly analyse the appearance or disappearance of species, or even the changes in their raw frequency of occurrence in the total sample, or the average changes in mean indicator values of communities because the plots are not covering the exact same ecological conditions at the two sampling dates. Instead, the analysis must rely on the shifts in the relationships between species occurrence or community characteristics and environmental conditions, especially those linked to climate (elevation, exposure) if impact of climate change is the focus: did the modelled altitudinal optimum of species changed between the two inventories? Did the relationship between temperature indicator value of plant communities and altitude or exposure changed? We no longer tested if vegetation in a plot or a set of plots had changed, but if the location of a given type of vegetation had changed in the valley. Specific statistical models have to be built in order to answer such questions.

In the present resampling study of the Maurienne valley, we expected an upward shift of plant communities along the elevational gradient as a response to climate warming. However, road traffic has dramatically increased in the valley since the aperture of the tunnel connecting France to Italy, in 1980. Microparticles, nitrogen and other atmospheric deposition has increased since the first survey with probable effects on vegetation (Paul 2000, Deletraz 2002, Laffray 2008). Thus, we also tested for changes in the nutrient status of plant communities, *i.e.* indicator values for pH and nitrogen.

B. MATERIAL AND METHODS

1. Study area

Maurienne valley is an inner-alpine valley of the French Alps (figure 1). The general east-west orientation (figure 2) induces the presence of two main opposite slopes, north- and south-facing, which largely control vegetation distribution in the valley. A second important factor of control is the type of geological bedrock. Siliceous substrates dominate at the western, lower part, of the valley and calcareous substrate at the eastern, upper part, of the valley.

The valley is marked by a dry continental alpine climate, *i.e.* harsh winters, prevailing dry summers, large seasonal amplitude in temperatures and decreasing precipitations along the continentality gradient, from west to east. The study area extends from 700 m a.s.l. to 2200 m a.s.l. Forests cover 18% of the valley, with a high proportion of extensively managed protection forests (44%), which prevent intense erosion affecting this region because of steep slopes.

Due to the strong bioclimatic and geological gradients, the area presents a high vegetation diversity, reinforced by its location at the intersection between various phytogeographic regions: medioeuropean, submediterranean, subatlantic and sarmatic species are found (Bartoli 1966), additionally to the alpine one.

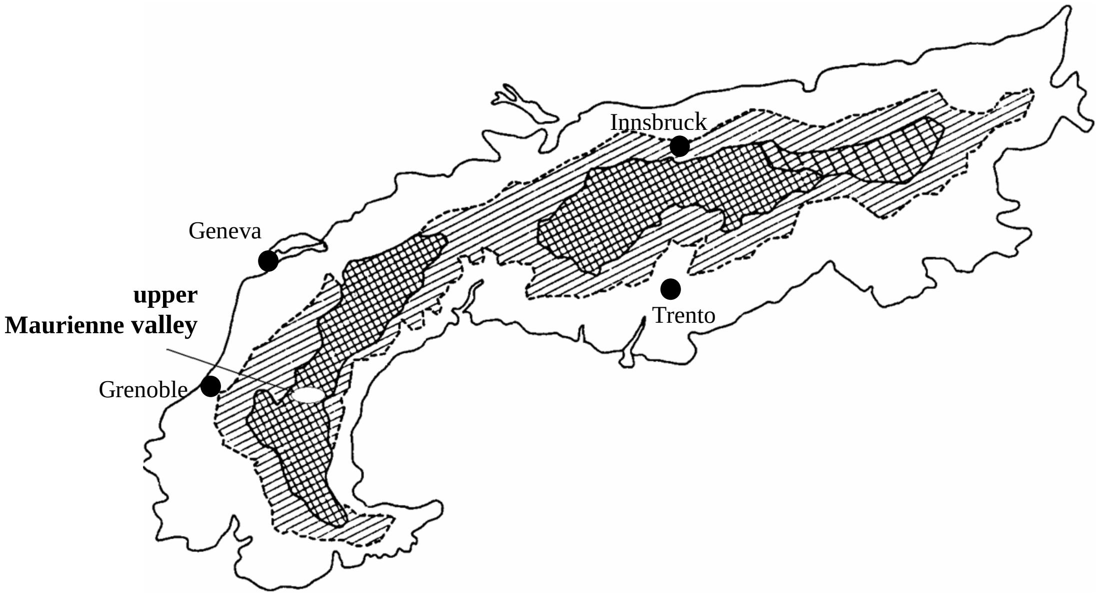


Figure III-1: Location of the study area in the Alps. Biogeographic zones according to Ozenda (1985): pre-Alps (white), inner-alpine axis (grey), zone of high continentality (dark grey)..

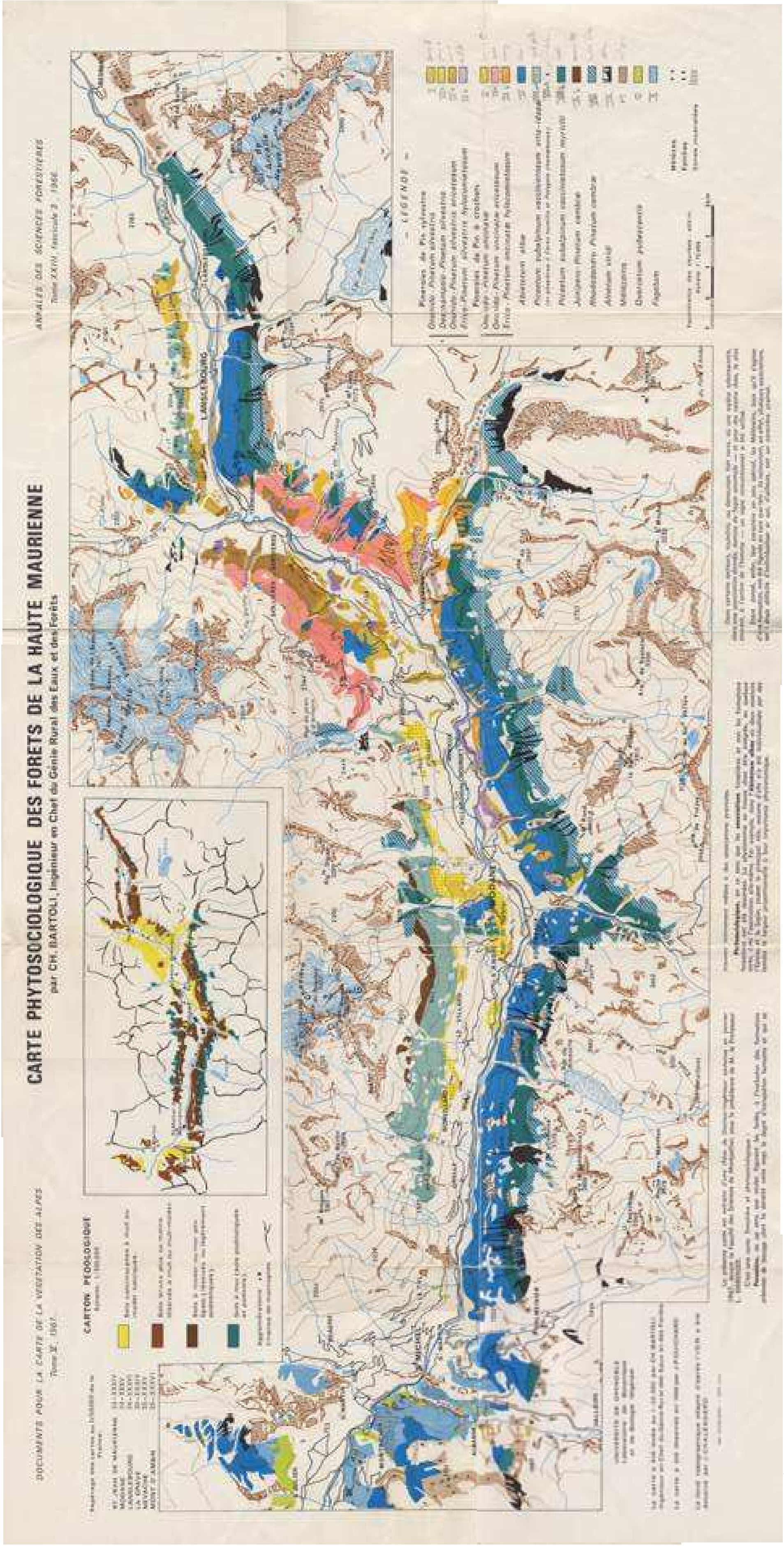


Figure III-2: Phytosociological map of upper Maurienne valley forests established by Bartoli (1966).

2. Sampling protocol

a. Historical data

We used one of the first extensive phytosociological forest survey conducted in France, published by Bartoli in 1966. Two other studies were also available for the same valley, in the lower septentrional part (Bassuel 1976) and in the middle Maurienne (Fournier 1985), but we preferred the Bartoli's one because his relevés were older and he drew a precise map of phytosociological units, which revealed crucial for preparing the resampling design. The objective of his study was to define and map forest site types based on the identification of species ecological groups, thanks to floristic and ecological analyses. Data were mainly collected between 1952 and 1956, and a few additional plots surveyed in 1964, the average date being 1954.5 (later noted as '1955'). Ten main phytosociological units and twenty-three sub-units were defined based on their floristic and ecological homogeneity (table 1). In a final step, Bartoli established a phytosociological map of upper Maurienne forests at the 1:75000 scale (figure 2). Drafts of this map at the 1:20000 scale, with field work annotations, were kindly put at our disposal by the author's family. The exact position of Bartoli's plots was not noted on the maps, and unfortunately lost during a fire of the Bartoli archives. The publication of Bartoli contains tables of relevés for each sampled phytosociological unit (table 1), with information, for each sampled plot, on elevation, exposure, slope and cover percentage of lower strata. We constructed a binary variable classifying the plots into two groups of geological substrate (calcareous or not) according to the phytosociological unit they belonged to (table 1). A species list was available for each plot, including all encountered vascular plants, terricolous mosses and lichens, and split into three strata: tall trees, tree species in the regeneration layer and herbaceous species. Species cover was noted according to the cover-abundance scale of Braun-Blanquet (1951). At the total, 396 different species were observed, including vascular plants, mosses and lichens, with a mean of 26.1 species per plot.

This first sample comprised a total of 247 plots representing the range of variations observed in elevation (700 to 2200 m a.s.l.), exposure (distributed into 8 classes: N, NE, E, SE, S, SW, W, NW) and geological substrate. They were also homogeneously distributed along the continentality east-west gradient.

b. Re-sampling

We designed a re-sampling scheme as close as possible to the first one. Based on GIS data, we built a new stratified sample with the same number of plots per sampling stratum as in Bartoli's initial scheme. The sampling strata were elevation (divided into fifteen 100-m classes between 700 and 2200 m a.s.l.), exposure (8 same classes as used by Bartoli, see above), phytosociological unit (10 main units of the Bartoli's map) and type of geological substrate (calcareous or non-calcareous).

Table III-1: Phytosociological units of the Maurienne valley according to Bartoli (1966). Percentage of plots 1955: percentage of plots sampled by Bartoli in each phytosociological unit, Percentage of plots 2002: percentage of plots sampled in 2002 in each of the phytosociological units of Bartoli map.

Phytosociological unit	Name of phytosociological units	Latin name of the phytosociological units	% of plots 1955	% of plots 2002	Substrate type
I	Xerophilous pine forest (*Pinus sylvestris*) on calcimorphic soil	*Ononido-Pinetum silvestris*	8.1	9.4	Calcareous
II	Xerophilous pine forest (*Pinus uncinata*) on calcimorphic soil	*Ononido-Pinetum montanae-uncinatae*	6.1	5.4	Calcareous
III a b	Meso-xerophilous and mesophilous pine forest (*Pinus sylvestris*) on calcimorphic soil	*Ononido-Pinetum silvestris ericetosum*	7.7	7.2	Calcareous
III c		*Erico-Pinetum silvestris hylocomietosum*			Calcareous
IV a	Meso-xerophilous and mesophilous pine forest (*Pinus uncinata*) on calcimorphic soil	*Ononido-Pinetum montanae- uncinatae ericetosum*	13.0	11.2	Calcareous
IV b		*Erico-Pinetum montanae-uncinatae hylocomietosum*			Calcareous
IV c		*Pinetum montanae- uncinatate caricetosum ferruginaeae*			Calcareous
V a	Fir forest with spruce	*Abietetum albae melampyretosum* - type	15	17.0	Non-calc.
V b		- with *Adenostyles alliariae*			Non calc.
V c		- with *Saxifraga cuneifolia*			Non-calc.
V d		- with *Carex alba*			Calcareous
VI a	Xerophilous-acidophilous pine forest (*Pinus sylvestris*)	*Deschampsio-Pinetum silvestris*	8.1	7.6	Non-calc.
VI b	Meso-xerophilous pine forest (*Pinus cembra*)	*Junipero-Pinetum cembrae*			Non-calc.
VII a1	Spruce forest	*Piceetum subalpinum vaccinietosum vitis idaeae*	14.2	13.0	Non-calc.
VII a2		*Piceetum subalpinum polygaletosum*			Calcareous
VII b		*Piceetum subalpinum vaccinietosum myrtilli*			Non-calc.
VII c		*Piceetum subalpinum adenostyletosum*			Non-calc.
VIII abc	Mesophilous pine forest (*Pinus cembra*)	*Rhododendro-Pinetum cembrae*	11.7	13.9	Non-calc.
VIII d		*Calamagrostio-villosae Pinetum cembrae*			Non-calc.
VIII e		*Rhododendro-Pinetum cembrae pinetosum uncinatae*			Calcareous
IX	Green alder forest	*Alnetum viridis*	4.4	5.4	Non-calc.
X a	Beech forest - on calcimorphic soil		11.7	9.9	Calcareous
X b	- on brown calcimorphic soil				Calcareous

i. GIS plot selection

In a first step, we digitized the boundaries of phytosociological units displayed on the 1:20000 map. Then, we intersected this map with a digital elevation model at 50-m resolution (IGN, France), in order to delineate the sampling strata according to elevation, exposure and phytosociological units. In each stratum, we randomly drew the plots to be surveyed in our second sampling campaign. We drew double the number of plots than were surveyed during the first campaign in order to keep enough freedom of choice in the following steps of plot selection. Then, we visually discarded plots located too close to the border between two strata, or plots in inaccessible areas. Finally, within each stratum, we ordered plots to be visited giving priority to those most distant from each other in order to minimize spatial autocorrelation. For example, we exceptionally sampled more than one plot in contiguous cartographic units.

ii. Plot selection during fieldwork

Plots were resampled during the summers of 2002 and 2003. In the field, we went to the previously defined location of each candidate plot following a GPS route. Then we looked for a site belonging, as much as possible, to the supposed phytosociological unit, precisely controlling for elevation and exposure classes to be resampled with altimeter and compass. We did not try to find a location bearing the same list of species as defined by Bartoli for the phytosiological unit selected, which would have introduced a bias in our analysis. However, we stuck to the dominant tree species initially associated by Bartoli with the sampled phytosociological unit, because it was part of the definition of the units. Additionally, the final location was chosen in a homogeneous and preferably closed stand. Finally, the different teams involved resampled 231 plots, during three weeks in June and July 2002 (135 plots) and five weeks in July 2003 (96 plots). This survey is later referred as the ‘2002’ inventory. This procedure lead to a final sample highly similar to the initial one, but at the cost of considerable travel expenses. Seven classes among the fifteen elevation classes were under- or over-represented by more than 25% in the second inventory (classes 900-1000, 1100-1200, 1600-1700, 1700-180 and the three classes from 1900 to 2200) and four among the eight exposure classes (N, NE, SE, NW). Indeed, an exact match between the two inventories was not required because the modelling strategy used in the following data analysis could accommodate small discrepancies.

iii. Data collection

At each plot, we measured elevation in m a.s.l. with both a GPS and an altimeter, slope in degrees from the horizontal with a clinometer, slope aspect in degrees from North with a compass (0 for a north-facing slope) and mask effect (vertical angular position of the top of the opposite slope) with a clinometer. Topographic position along the slope was recorded into 5 classes (upper, middle and bottom slope, hillside bench, valley bottom). The nature of the bedrock (calcareous or not) was detected by effervescence of fine earth and stones in the upper soil layer with 3M hydrochloric acid. Geographic coordinates of the plot were recorded with a GPS or, when GPS data were suspected to be not enough accurate, on a map. Geographic coordinates, mask effect and topographic position along the slope were not recorded at the first inventory.

A floristic inventory was performed in a homogeneous zone corresponding to the minimal area, as it was done in the first case. Practically, the survey of the plot was done from the centre to the periphery and stopped when no new species were encountered after a given time. At least two observers participated in the search. On average, one hour was spent looking for species in each plot. All vascular plants and terricolous mosses were separately noted and given a cover-abundance note in the same three vertical strata previously defined. When identification of a plant was difficult, we kept it for later determination. Some individuals belonging to the genera *Hieracium*, *Carduus* and *Festuca* were difficult to identify when found only in vegetative stage, and were often not determined at the species level. Each stratum was given a global cover note, whereas such a note was only available for the whole understory vegetation at the first inventory.

In the second inventory, 630 taxa were observed in 231 plots, leading to a mean species number per plot of 36.9. There were 727 taxa observed at either of the two inventories, among them 299 were present at both. Out of the 727 taxa found, 660 were vascular taxa, 63 mosses and 4 lichens. 98 vascular taxa and 9 mosses were identified at the genus level only. There were 97 taxa observed by Bartoli only, whereas 331 taxa were observed at the second inventory only.

Nomenclature was homogenised following *Flora Europaea* (Tutin *et al.* 1968-1993).

3. Data analyses

Because we worked with non-permanent plots, *i.e.* plots which were not sampled twice, we could not analyse changes in species occurrence at a given locality or changes in the mean elevation of species. Instead, we focused on temporal changes in the relation linking vegetation to its abiotic environment. We tested if, for given abiotic conditions (elevation, exposure, bedrock type), vegetation changed between the 1950s and the 2000s. Moreover, the number of plots available was too low to accurately model the ecological niche of each individual species and its changes over time. Thus, we used multi-species characteristics of the plant communities, *i.e.* mean indicator values of Ellenberg (Ellenberg 1974) and Landolt (Landolt 1977), as well as position of plots along ordination axes. We tested if the relationships between these multi-species characteristics and the environment (elevation, exposure, bedrock type) changed between the two inventories.

This procedure should be separated into three steps:

- First, we calculated two types of indicators synthesising the variations in species composition between plots. The first type was obtained by averaging, at each plot, the species indicator values determined by experts (Ellenberg and Landolt indicator values); the second type was the position of plots along axes of a correspondence analysis.
- Then, variations of these different biotic indicators among plots were explained by abiotic environmental factors, thanks to the construction of an explanatory model taking into account topographical position and substrate type measured at each plot.
- Finally, in order to test vegetation changes between the two inventory periods, we introduced and tested the effect of the sampling cycle (first or second one) in the aforementioned models. A significant effect of sampling period in the model would imply that the relation between vegetation composition and environmental abiotic variables has changed. A shift toward more thermophilous vegetation was expected in response to global warming, but thanks to Ellenberg and Landolt indicator values, we were able to test changes in other factors indicated by vegetation such as nitrogen availability in soils.

All calculations were made using SAS software, version 9.1.

a. Species selection

We considered understory forest species belonging to the herbaceous and shrub layers only (terricolous mosses, vascular cryptogams and phanerogams, ligneous or herbaceous), discarding all data recorded in the tree layer, because this stratum is much more under the control of forest management decisions than the lower layers.

b. Vegetation indicators

i. Indicator values

Several experts have established list of indicator values of species for main ecological factors of the environment. They were based on the previous authors' knowledge (including field observations, experiments and literature review) of species preferences. Species have been classified on an arbitrary scale, with low values for species having preference for lower levels of the factor, and high values for species having preference for higher levels of the factor. Here we used two different sets of indicator values. The first one was that of Ellenberg (Ellenberg 1974). He established it for central European flora, for six ecological factors: light (L), mean temperature (T), continentality of the climate (K), soil moisture (F), soil pH (R), and soil nitrogen availability (N). Values range from 1 to 9, even for moisture values (F) of the species found in our study, although the F values reach 12 for some species in the overall Ellenberg dataset. The second set of indicator values was that of Landolt, established for the Swiss flora, with the same indicator values as Ellenberg plus three additional ones: humus content (H), soil dispersion and deficiency of aeration (D), and salinity (S). His scale ranges from 1 to 5. Salinity value was not used in our analyses.

Thanks to these coefficients, we were able to estimate an ecological value of the environment as indicated by vegetation, by calculating the mean indicator value for each plot over all present species. Not all species had a known indicator value for all the ecological factors. Most often, species with missing values belonged to the lists, but were regarded as indifferent to one or more of the ecological factors. Some were absent from the Ellenberg or Landolt lists because they occurred in the Maurienne valley but not in Germany or Switzerland. Lichens and mosses did not have any indicator values. Taxa identified at the genus level only could not be used as well. Finally, plots with less than eight species with a known value for a given ecological factor were excluded from the subsequent analyses concerning this factor.

Weighted mean indicator values per plot were also calculated taking into account the cover-abundance note of each species. The inclusion of species recorded in the tree layer was also tested. Results were robust to these alternative specifications and are not reported.

ii. Missing indicator values

Out of the 567 taxa determined at the species level, 517 were reported in the Ellenberg list, 325 found in the first inventory and 465 in the second. The number of missing values (taxa) for each ecological factor, the number of plots discarded due to a too low number of available species and the percentage of taxa with indicator value available per plot are given in table 2. For most of the ecological factors under study, the number of plots with less than 8 available species, which had to be discarded from the analyses, was low (<5), except for the Ellenberg temperature value, where 30 plots had to be excluded. The mean percentage of species per plot which had an Ellenberg value available was higher than 73.0% for all Ellenberg values but temperature (58.5%), and was higher than 78% for all Landolt values.

Slightly more species (534) belonged to Landolt's list than to Ellenberg's one, 321 in the first inventory and 481 in the second. Less than 3 plots having less than 8 available species were discarded from the calculation of the mean indicator values in the first inventory, and none in the second inventory.

Table III-2: Missing indicator values.

		Number of taxa for which the indicator value is		Number of plots excluded (indicator value available for less than 8 species) over a total of 479 plots	Percentage of taxa with indicator value available per plot Mean (min-max)
		available	missing		
Ellenberg	N	471	188	2	83.6 (57.9-100)
	R	427	232	5	73.0 (48.0-96.0)
	F	478	181	5	81.1 (52.6-100)
	K	482	177	1	86.6 (64.3-100)
	T	368	291	30	58.5 (36.0-86.7)
	L	507	152	1	91.8 (66.7-100)
Landolt	F	512	147	2	82.7 (52.0-100)
	R	507	152	3	80.7 (47.8-100)
	N	515	144	2	84.4 (52.0-100)
	H	510	149	2	81.9 (52.0-100)
	D	500	159	3	77.9(47.8-100)
	L	516	143	2	84.4 (52.0-100)
	T	515	144	2	84.4 (52.0-100)
	K	516	143	2	84.4 (52.0-100)

iii. Correlation between indicator values

Some of the indicator values are known to be quite redundant. For example, indicator values for pH and nitrogen, or for temperature and moisture, are sometimes highly correlated depending on the region under study. It is important to be aware of these correlations in order to avoid over-interpretation of changes in the mean indicator values along time. If the indicator values for two different ecological factors are highly correlated, their changes should not be interpreted separately. Hence, we examined Spearman rank correlations among indicator values for all the calculated ecological factors. High correlations were expected for indicator values given by the two authors for a same ecological factor (*e.g.* nitrogen between Ellenberg and Landolt indicator values). Low indicator values were expected for indicator values for different ecological factors (*e.g.* between Ellenberg light and acidity indicator values).

These correlations were calculated either based on the species individual values, or on the mean indicator values per plot.

c. Plot ordination

Ordination of vegetation data synthesises the information contained in the species assemblages, providing all together: (i) an identification and ranking of the main factors structuring plant communities, (ii) a local calibration of species indicator values for the same previous factors and (iii) a ranking of the plots according to these factors. In a sense, it provides the same kind of information as Ellenberg or Landolt indicator values, but tailored to the region under study.

We used correspondence analysis (also named reciprocal averaging), one of the most common non-constrained ordination technique for vegetation analysis. Only species common to both inventories (tree stratum excluded) were entered in the calculations. X^2 distances between plots were calculated by comparison of their species composition and, using these distances, the plots and species were positioned along successive orthogonal factorial axes, each carrying the maximum possible variance. We ran the analyses including all plots together but also after separating calcareous and non-calcareous plots.

A first visual interpretation of the ecological meaning of the axes was done by representing the position of the phytosociological units of Bartoli along each factorial axis. Then, we calculated Spearman rank correlations between the position of the plots on these axes and Ellenberg and Landolt mean indicator values.

We mainly analyzed the first three axes, which explained most of the variance, but also examined results on the first ten axes.

Then we ran the analysis only using species with a total number of occurrences higher than two at each of the inventories, then only using those with a total number of occurrences higher than five at each of the inventories. When testing the shift in the position of plots along the axes of correspondence analysis between the two inventories (see below “testing for changes in vegetation between the two inventories”) based on these alternatives, the results were only slightly less significant, but still under the probability threshold value of 0.05, compared to those that we present below. Therefore, we choose to present only the results obtained from the correspondence analysis ran with all species common to the first and second inventories.

d. Testing for changes in vegetation between the two inventories

To study vegetation changes between the two inventories, we tested in a linear covariance model if the link between previously defined vegetation indicators on the one hand, and the abiotic environmental variables that were available for both Bartoli’s and our plots, on the other hand, had changed over time. For that, we constructed explanatory models with vegetation indicator values of the plots (mean indicator values of Landolt or Ellenberg, or position of the plots along axes of correspondence analysis) as dependent variables, and fixed environmental variables (elevation, exposure, substrate) as independent, explanatory, variables. We entered and tested the inventory cycle number in the model. Substrate and inventory cycle were entered as class variables, all other variables were continuous. Models were written as:

$$\mathbf{I_{ijk} = cst + a \times elevation_{ijk}^2 + b \times elevation_{ijk} + c \times ns_{ijk} + d \times ns_{ijk}^2 + substrate_i + inventory_j + \varepsilon_{ijk}} \quad \mathbf{(1)}$$

with:

I_{ijk} : value of the synthetic biotic indicator (mean Ellenberg or Landolt value, or position on a factorial axis) for plot k, surveyed during inventory j and developed on bedrock type i,

cst : constant,

$elevation_{ijk}$: elevation of the plot (700 to 2210 m a.s.l.)

ns_{ijk} : cosine of the exposure of the plot counted from the North (-1 at South$\leq ns \leq 1$ at North),

$substrate_i$: effect of the type of bedrock, binary variable (effervescent, considered as calcareous, or not effervescent, considered as not calcareous),

$inventory_j$: effect of the inventory cycle number, binary variable (first or second inventory)

ε_{ijk} : error term.

Geological substrate variable was missing for 33 plots at the second inventory because the hydrochloric acid test was negative for some soils, even if they were sometimes obviously calcareous according to the vegetation. Thus, we redistributed these 33 points to each of the two soil categories according to their vegetation composition. It was possible to do so without ambiguity using the mean Ellenberg indicator values for pH and nitrogen, which were highly related to the type of bedrock.

Significance of each independent variable was tested against the complete model (type III test). When a variable was found not significant ($p>0.10$), it was excluded from the final model, except for the inventory cycle variable which was always kept. Thus, we selected a parsimonious model. The test F-value helped rank the explanatory variables: the higher it was for a given number of degrees of freedom, the more significant was the variable for explaining the vegetation indicator studied. Generally, when entering squared elevation in addition to elevation alone, the model was slightly improved. This means that the relation of the mean indicator value with elevation was not strictly linear.

In order to test the temporal shift of the relation linking vegetation indicators to abiotic environmental factors, we looked at the significance of the inventory cycle variable, entered in two classes, according to a type III test. Then, we examined the direction of the shift by looking at the least-square means of the vegetation indicator at each inventory cycle. Least-square means are predicted population margins. They give the mean value of the vegetation indicator at each date, the effect of all other variables being held constant. As an illustration, we plotted, for each vegetation indicator, least-square means at each inventory date against elevation classes.

e. Development of forest structure from 1985 to 2000

To help interpret the results, we looked for changes in dendrometric characteristics of forest stands in the Maurienne valley. No information was available in the Bartoli study. The earliest data came from the French National Forest Inventory. Two inventories were available for the Maurienne natural forest region, first in 1985 (206 plots, no understory vegetation data available) and second in 2000 (173 plots). We looked at the evolution of tree cover, number of stems per hectare, basal area and age of the plots. We calculated the mean of each of the aforementioned variables by elevation classes at each date, and plotted it to get a visual indication of forest development. For part of the sample, only elevation classes were available, so all elevations were grouped into these classes and each class was represented by the median of its values.

C. RESULTS

1. Abiotic models of vegetation indicators

a. Ellenberg indicator values

i. Correlation between Ellenberg indicator values

There were significant correlations between Ellenberg indicator values calculated for the set of species found in our study: most were significant at the $p<0.001$ level. Highest correlations occurred between nitrogen and moisture, nitrogen and light, pH and moisture, pH and light, and temperature and moisture (lower left part of table 3). However, these correlations only reached -0.48 at the maximum. Thus, the indicator values of Ellenberg for various ecological factors carry largely independent information. It must be remembered that these correlations were calculated for the set of species recorded in our study. They give the phytogeographical constraints on the indicator values of species for our study area.

Mean indicator values calculated for the plots (lower left part of table 4 and figure 3) were also mostly highly correlated ($p<0.001$). These correlations, at the plot level, depend from both the previous correlations at the species level and how species are associated in each plot. Strongest correlations occurred between nitrogen (N) and moisture (F) (corr=0.72***), nitrogen (N) and light (L) (corr=-0.75***), moisture (F) and temperature (T) (corr=-0.73***) and moisture (F) and light (L) (corr=-0.66***).

The correlation between light and temperature was negative when calculated on values for species, but positive with mean values for plots (tables 3 and 4), indicating that the way how species were associated in plots reversed the relation existing within the regional pool of species. It means that species preferring cooler conditions *i.e.* from high elevations had a tendency to be also heliophilous species in our study region, but that plots from high elevations were probably more closed and contained more shade tolerant species than those from lower elevations.

The relationship between mean values for pH and nitrogen (figure 3a) was not linear: nitrogen indicator values were low at both ends of the pH range, but could reach high values at intermediate pH, *i.e.* nitrogen was apparently more available at intermediate pH values. Hence, the relation was positive for low values of pH, and negative for high values of pH.

Table III-3: Spearman rank correlations between indicator values for the species found in the two inventories, weighted by their frequency of occurrence. Test probabilities were calculated with indicator values of species not weighted by their frequency of occurrence. Because most of the correlations were significant at p<0.001, probabilities were coded as follows: p<0.001: no star; p<0.01: **; p<0.05: *; p>0.05: ns. Lower left part of the table: correlations between Ellenberg indicator values. Upper right part of the table: correlations between Landolt indicator values.

	N	R	F	L	T	K	H	D	Landolt
N	/	0.02^{ns}	**0.52**	**-0.31**	-0.11**	**-0.43**	0.14	**0.33**	N
R	0.09*	/	**-0.41**	0.23	0.23	0.18	**-0.45**	**-0.36**	R
F	**0.39**	**-0.37**	/	**-0.35**	**-0.41**	**-0.51**	**0.42**	**0.59**	F
L	**-0.35**	**0.34**	-0.24	/	0.04^{ns}	**0.39**	**-0.59**	-0.29	L
T	-0.04^{ns}	0.28	**-0.48**	-0.14**	/	0.17	-0.19	-0.16	T
K	-0.17	-0.10*	-0.09*	0.08*	-0.15**	/	-0.24	**-0.37**	K
							/	**0.40**	H
								/	D
Ellenberg	N	R	F	L	T	K			

Table III-4: Spearman rank correlations between mean indicator values calculated for the plots. Because most of the correlations were significant at p<0.001, probability was coded as following: p<0.001: no star; p<0.01: **; p<0.05: *; p>0.05: ns. Lower left part of the table: correlations between mean Ellenberg indicator values. Upper right part of the table: correlations between mean Landolt indicator values. Diagonal cells, in italics: correlations between mean Ellenberg and mean Landolt indicator values.

	N	R	F	L	T	K	H	D	Landolt
N	*0.95*	-0.45	**0.81**	-0.69	-0.33	**-0.84**	0.55	0.68	N
R	-0.32	*0.97*	-0.72	0.52	0.60	0.63	**-0.81**	-0.73	R
F	**0.72**	**-0.59**	*0.95*	-0.72	-0.68	**-0.90**	**0.84**	**0.85**	F
L	**-0.75**	0.46	**-0.66**	*0.97*	0.24	**0.77**	**-0.78**	-0.66	L
T	-0.29	**0.62**	**-0.73**	0.18	*0.93*	0.50	-0.64	-0.54	T
K	-0.50	-0.005^{ns}	-0.22	0.26	0.02^{ns}	*0.47*	**-0.74**	**-0.78**	K
/	0.57	-0.80	0.81	-0.78	-0.59	-0.04^{ns}	/	**0.80**	H
/	0.69	-0.67	0.77	-0.66	-0.55	-0.28	/	/	D
Ellenberg	N	R	F	L	T	K	/	/	Ell*Land

ii. Modelling mean Ellenberg indicator values with abiotic environmental factors

Each of the Ellenberg indicator values was largely explained by selected topographic and substrate variables (table 5a). Interestingly, the best models were for temperature (T, r^2=74.3%), moisture (F, r^2=69.2%) and pH (R, r^2=65.1%) indicator values. Variations in light (L) and nitrogen (N) values were also significantly explained by environmental variables (r^2=54.1% and 44.3%, respectively). The worst model was for continentality (K), with r^2=13.8% (table 5a). Tests results showed which abiotic variables were the more significant predictors of a given indicator value. Variations in temperature indicator values were mostly explained by squared elevation (F_{III}=782, p<0.001), secondly by exposure (F_{III}=176, p<0.001) and thirdly by substrate (F_{III}=23.7, p<0.001) (table 5a). The relation was negative with squared altitude (see also figure 4a) and with cosine of exposure, which was in accordance with the biological requirements of species and communities, *i.e.* thermophilous species and communities preferentially found at lower elevations and south exposed. Nitrogen (N), moisture (F) and light (L) were first explained by the exposure variable ($F_{III(N)}$=120, $F_{III(F)}$=494 and F_{III}=264, respectively), in accordance with received light and, as a consequence, soil water balance of the plot, then by substrate type, also responsible for soil moisture status and soil biogeochemistry, and then by elevation or squared elevation, also influencing light and soil moisture of the plot (table 5a and figure 4b). pH (R) was first explained by substrate type (F_{III}=379), as expected, then by elevation (figure 4c) and thirdly by exposure. No indicator value was explained by squared cosine of the exposure.

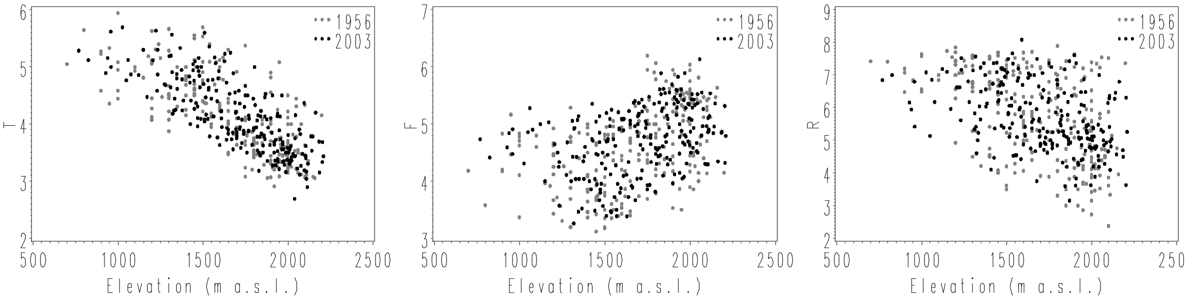


Figure III-4: Relationship between mean Ellenberg indicator values and elevation. First (grey) and second (black) inventories were distinguished.

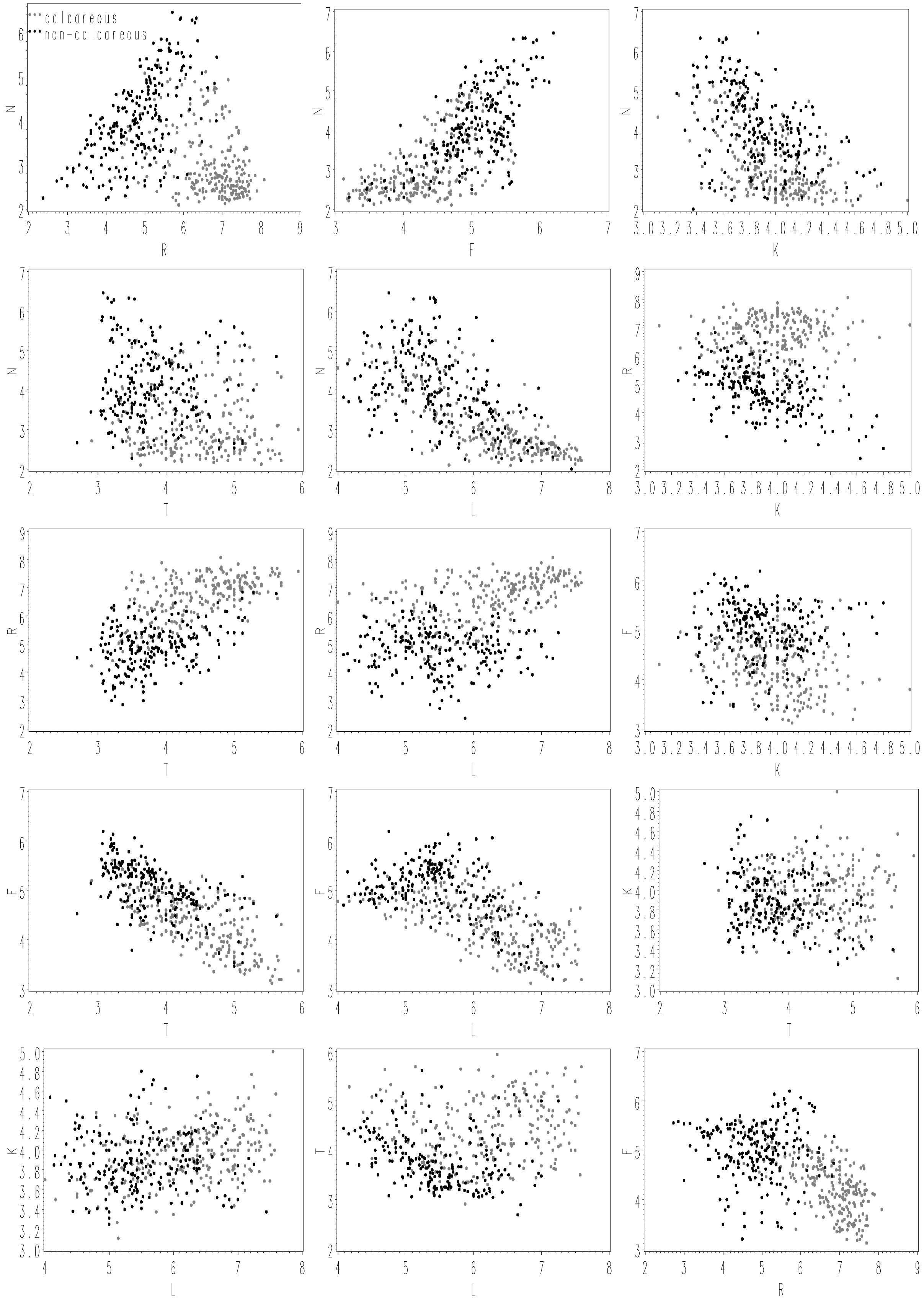


Figure III-3: Relationships between mean Ellenberg indicator values. Calcareous (grey) and non-calcareous (black) plots were distinguished. Correlation values are reported in table 4.

b. Landolt indicator values

i. Correlation between Landolt indicator values

Most of the indicator values for species were highly correlated to each other (Spearman rank correlation test, $p<0.001$) (upper right part of table 3). Best correlations occurred between soil dispersion and moisture, light and humus content, continentality and moisture, and nitrogen availability and moisture. Correlations between continentality and pH, and continentality and temperature, which were negative when calculated with Ellenberg indicator values, became positive when calculated with Landolt values.

Mean indicator values calculated for the plots were also all correlated to each other ($p<0.001$) (upper right part of table 4), and the relations were tighter than with Ellenberg values. The most linear relations occurred between R and H (corr=-0.81***), F and N (0.81***), F and H (0.84***), N and K (corr=-0.84***), F and K (-0.90***), H and K (-0.74***), H and L (-0.78***), K and L (0.77***), K and D (-0.78***), F and D (0.85***), and H and D (0.80***).

The directions of the correlations between indicator values were the same when calculated at the species or the plot levels, when significant.

As observed for Ellenberg values, the relationship between mean values for pH and nitrogen (figure 5) was not linear, with an optimum of nitrogen availability at median pH values.

ii. Modelling mean Landolt indicator values with abiotic environmental factors

As with mean Ellenberg values, mean Landolt indicator values were largely explained by topographic and geological substrate variables. r^2 varied between 51.8 and 77.8% for most of the indicators, and equalled 40.9% for nitrogen value. Continentality value itself, which had a low r^2 with Ellenberg values, displayed now a remarkably high r^2 of 57.4%. The order of environmental variables explaining each mean indicator value (table 5b and figure 6) was similar to the corresponding Ellenberg values, except for continentality value. Mean Landolt indicator value for continentality was first explained by exposure ($F_{III(K)}=193$, $p<0.001$) which was not an explanatory variable for mean Ellenberg value for continentality, and then by substrate type and elevation (table 5b). Indicator values for soil dispersion and humus content were not available in the Ellenberg dataset. Dispersion was first explained by substrate type ($F_{III}=190$, $p<0.001$), as it is an indicator of soil structure, and then by exposure and elevation (table 5b); humus content (H) was first explained by exposure ($F_{III}=319$, $p<0.001$), followed by substrate type and elevation.

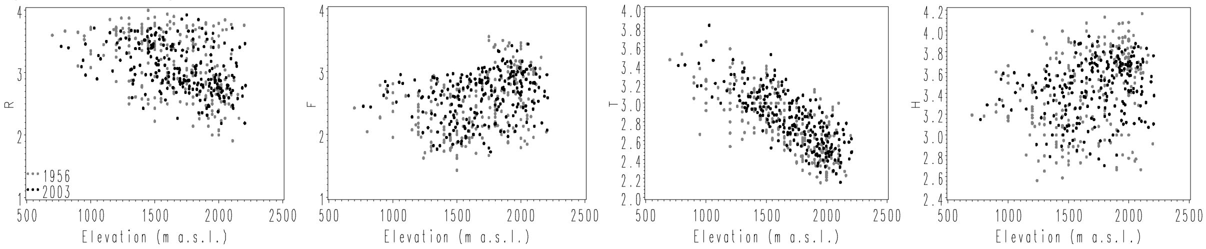


Figure III-6: Relationships between mean Landolt indicator values and elevation. First (grey) and second (black) inventories were distinguished.

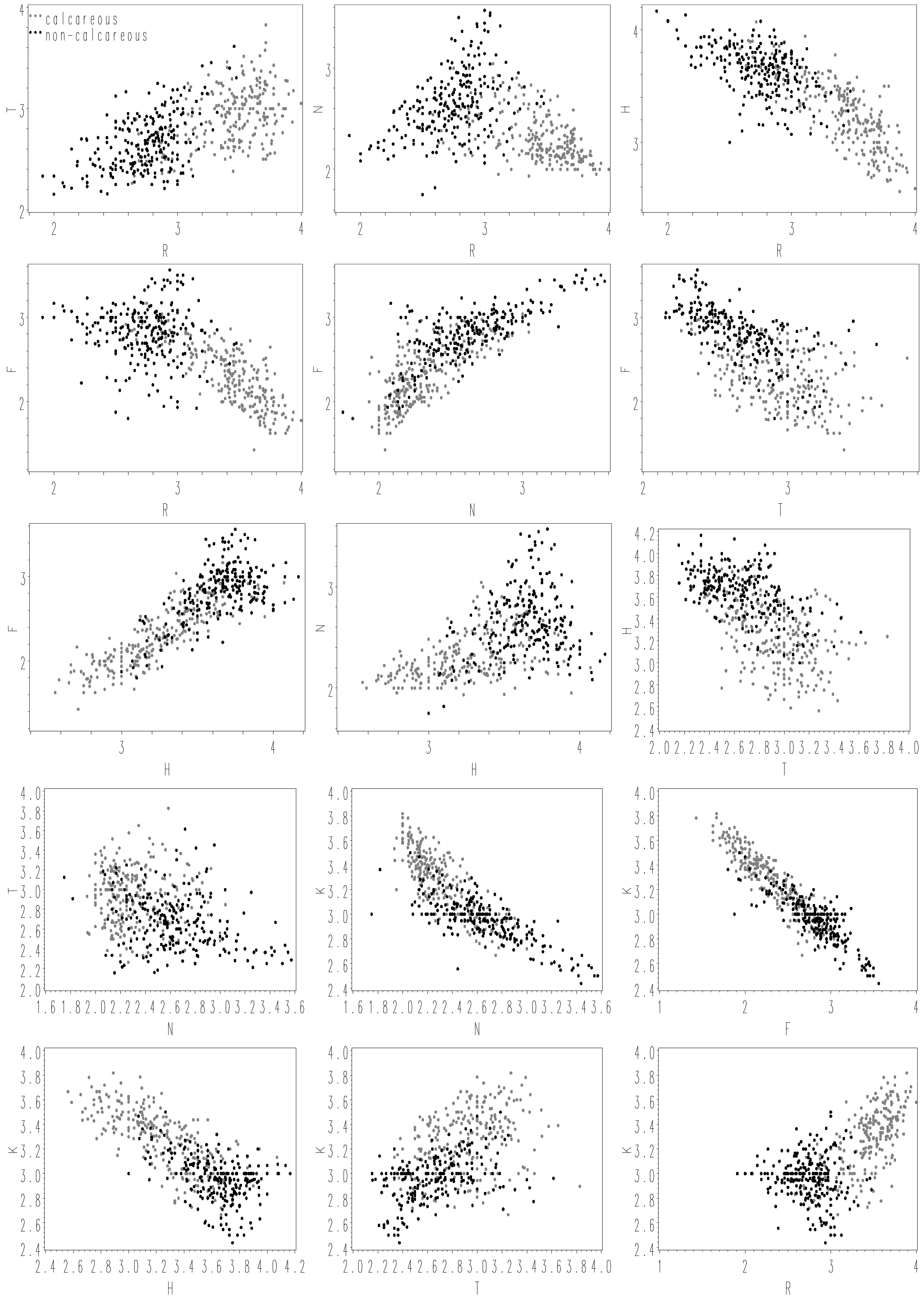


Figure III-5: Relationships between mean Landolt indicator values. Calcareous (grey) and non-calcareous (black) plots were distinguished. Correlation values are reported in table 4.

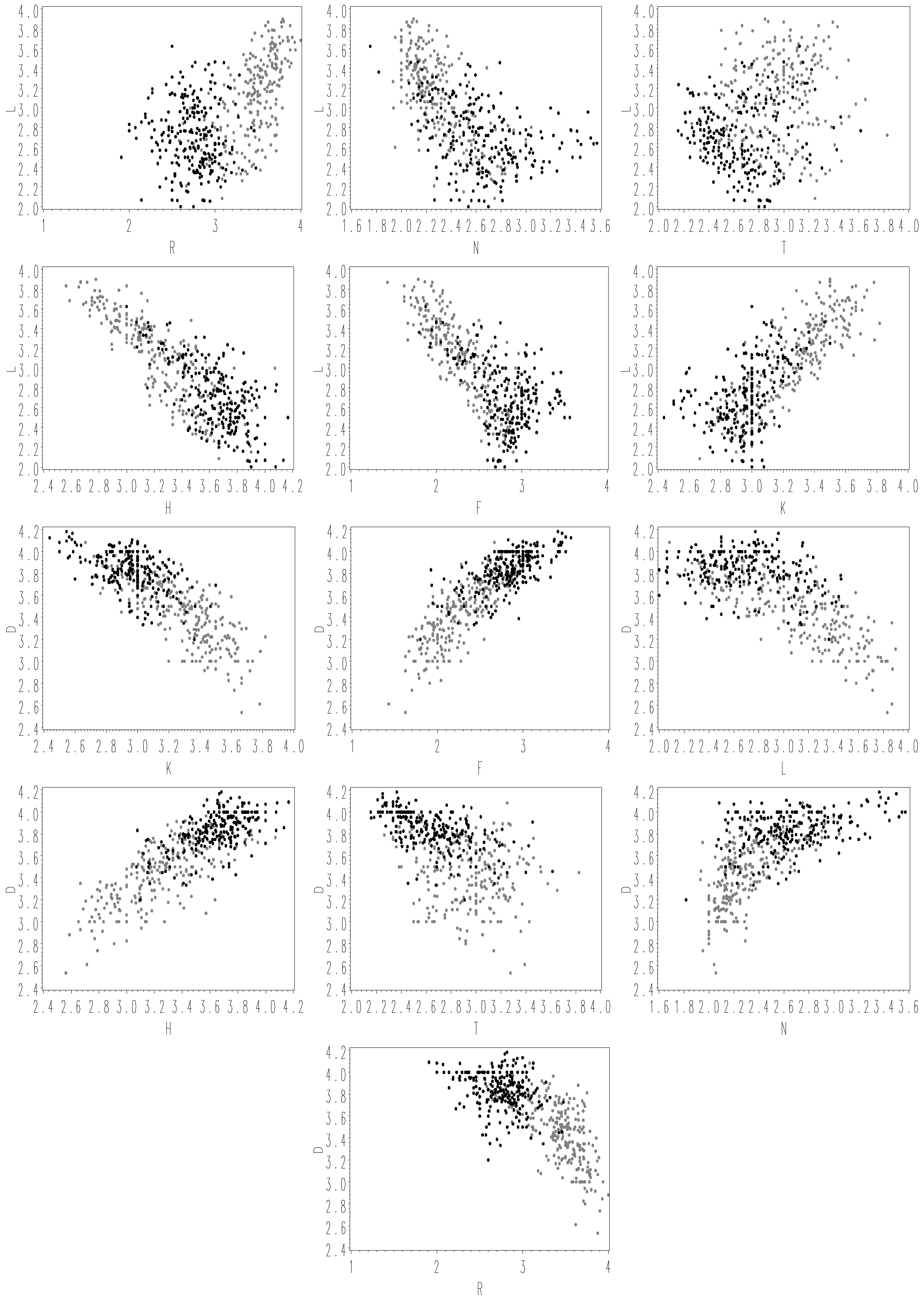


Figure III-5 (continued): Relationships between mean Landolt indicator values. Calcareous (grey) and non-calcareous (black) plots were distinguished. Correlation values are reported in table 4.

Table III-5: Explanatory models of indicator values as a function of abiotic environmental variables, for mean Ellenberg indicator values (a, upper table) and mean Landolt indicator values (b, lower table). For each indicator value, r^2 of the whole model, F-value of type III test and associated probability for the effect of each abiotic environmental variable entered in the model, F-value of type III test and associated probability for the effect of the inventory cycle number, and least-square mean (LSM) of the dependent variable (mean indicator value) at each date, are given. Probabilities as follows: $p<0.001$: *; $p<0.01$: **; $p<0.05$: *; $p>0.05$: ns; when p was slightly higher than 0.05, the probability was given. The direction (positive or negative) of the relation between the given indicator value and the explanatory variable was given in parentheses: (+) or (-); (+) for exposure means that higher values of the indicator were observed on north-facing slopes and vice-versa; (+) for elevation means that higher values of the indicator were observed at higher elevations and vice-versa; (+) for the substrate type means that higher values of the indicator were observed on calcareous soils, and vice-versa.**

a. Ellenberg indicator values		r^2 (%)	Elevation (F, p, direction)	Elevation^2 (F, p, direction)	Exposure (F, p, direction)	Expo^2 (F, p, direction)	Substrate (F, p, direction)	**Cycle** (F, p)	LSM 1955	LSM 2002	
All substrates	T	74.3	/	782***(-)	176***(-)	/	23.7***(+)	1.5^{ns}	4.12	4.16	=
	N	44.3	7.6**(-)	5.4*(+)	120***(+)	/	106***(-)	**32.4*****	3.37	3.76	>
	R	65.1	90.7***(-)	/	53.2*(-)	/	379***(+)	0.0^{ns}	5.75	5.76	=
	F	69.2	19.5***(-)	34.6***(+)	494***(+)	/	65.3***(-)	$\mathbf{2.8^{0.09}}$	4.62	4.68	>
	L	54.1	/	70.3***(+)	264***(-)	/	111***(+)	$\mathbf{3.4^{0.06}}$	5.92	5.82	<
	K	13.8	11.1***(+)	7.8**(-)	/	/	18.7***(+)	**37.7*****	4.01	3.85	<
Calcareous	T	66.8	/	331***(-)	152***(-)	/	/	5.1*	4.40	4.51	>
	N	30.1	20.5***(-)	15.5***(+)	31.9***(+)	/	/	**30.3*****	2.85	3.33	>
	R	55.4	/	77.4***(-)	187***(-)	/	/	**18.4*****	6.80	6.49	<
	F	53.6	22.7***(-)	32.5***(+)	202***(+)	/	/	0.6^{ns}	4.28	4.32	=
	L	45.1	11.2***(+)	6.6*(-)	123***(-)	/	/	**9.2****	6.35	6.11	<
	K	14.8	16.1***(+)	13.4***(-)	/	/	/	**26.4*****	4.06	3.88	<
Non-calcareous	T	74.4	573***(-)	/	48.4***(-)	4.4*(-)	/	0.6^{ns}	3.83	3.80	=
	N	30.3	/	/	90.9***(+)	/	/	**16.3*****	3.83	4.26	>
	R	19.0	31.1***(-)	/	/	/	/	**16.5*****	4.64	5.05	>
	F	62.5	/	101***(+)	310***(+)	/	/	**5.8***	4.95	5.06	>
	L	49.2	13.0***	18.7***(+)	153***(-)	/	/	0.01^{ns}	5.53	5.53	=
	K	11.2	13.5***(+)	/	/	/	/	**12.4*****	3.95	3.83	<

b. Landolt indicator values		r^2 (%)	Elevation (F, p, direction)	Elevation^2 (F, p, direction)	Exposure (F, p, direction)	Expo^2 (F, p, direction)	Substrate (F, p, direction)	**Cycle (F, p)**	LSM 1955	LSM 2002	
All substrates	T	77.8	968***(-)	/	344***(-)	/	11.6***(+)	**53.9*****	2.75	2.85	>
	N	40.9	9.3**(-)	9.0**(+)	86.9***(+)	$3.7^{0.06}$(+)	86.6***(-)	**19.9*****	2.42	2.53	>
	R	69.6	/	85.3***(-)	67.0***(-)	/	496***(+)	0.8^{ns}	3.10	3.08	=
	F	70.2	18.9***(-)	27.7***(+)	416***(+)	/	189***(-)	**18.5*****	2.51	2.60	>
	H	63.5	/	23.9***(+)	319***(+)	/	177***(-)	0.5^{ns}	3.45	3.43	=
	D	51.8	5.4*(-)	6.7*(+)	107***(+)		190***(-)	**4.8***	3.61	3.66	>
	L	53.8	/	63.1***(+)	237***(-)	/	133***(+)	$\mathbf{3.8^{0.052}}$	2.95	2.89	<
	K	57.4	28.5***(+)	30.5***(-)	191***(-)	/	175***(+)	**12.8*****	3.15	3.09	<
Calcareous	T	68.9	/	408***(-)	168***(-)	/	/	**30.1*****	2.88	2.99	>
	N	24.2	26.0***(-)	22.4***(+)	19.4***(+)	/	/	**25.5*****	2.24	2.38	>
	R	49.7	/	32.9***(-)	145***(-)	$2.6^{0.10}$(-)	/	**32.5*****	3.52	3.36	<
	F	49.1	24.6***(-)	27.9***(+)	168***(+)	/	/	**19.6*****	2.22	2.36	>
	H	52.8	6.3*(-)	8.0**(+)	239***(+)	/	/	**5.5***	3.21	3.27	>
	D	32.3	14.1***(-)	12.4***(+)	69.3***(+)	/	/	**20.8*****	3.37	3.52	>
	L	44.3	9.3**(+)	5.6*(-)	129***(-)	/	/	**7.3****	3.17	3.05	<
	K	36.6	37.7***(+)	37.4***(-)	79.3***(-)	/	/	**15.7*****	3.33	3.23	<
Non-calcareous	T	78.5	625***(-)	/	197***(-)	/	/	**18.7*****	2.63	2.70	>
	N	25.3	$2.9^{0.09}$(+)	/	62.5***(+)	4.2*(+)	/	**10.4****	2.58	2.71	>
	R	23.9	48.0***(-)	/	/	/	/	**17.3*****	2.68	2.81	>
	F	58.7	/	74.8***(+)	273***(+)	/	/	**7.1****	2.78	2.86	>
	H	43.4	10.7**(+)	7.7**(-)	119***(+)	/	/	**16.1*****	3.69	3.60	<
	D	30.9	9.7**(-)	5.7*(+)	49.6***(+)	/	/	1.7^{ns}	3.84	3.82	=
	L	49.0	30.0***(-)	38.8***(+)	128***(-)	/	/	0.2^{ns}	2.71	2.70	=
	K	35.8	/	5.5*(-)	127***(-)	/	/	$2.3^{0.13}$	2.97	2.94	<

c. Consistency of vegetation indicators: correlation between Ellenberg and Landolt values

Ellenberg and Landolt indicator values were initially built by the authors for the same ecological factors, but in different geographical areas (central Europe for the former, Switzerland for the later), so that they were not available for the same lists of species in our study. It appeared that most of the values showed a positive linear relationship (diagonal cells in table 4 and figure 7). Landolt values for dispersion (D) and humus content (H), which did not exist in the Ellenberg system, also showed strong relationships with some of the Ellenberg values. Humus content (H) was correlated with Ellenberg values for pH (R, corr=-0.80***), moisture (F, corr=0.81***) and light (L, corr=-0.78***). Dispersion had high correlations with nitrogen (N, corr=0.69***), pH (R, corr=-0.67***) and moisture (F, corr=0.77***). Only continentality values, which were available from both authors, showed a weak correlation. This indicator value also showed the biggest difference between Ellenberg and Landolt regarding the final explanatory model explaining its variations (tables 5a and 5b).

d. Ordination results

i. Ecological meaning of the ordination axes: distribution of phytosociological units along the axes

When correspondence analysis was run with all species common to both inventories, first axis explained 5.40% of the inertia, second axis 3.50% and third axis 2.73%.

In the plane of the first two axes, a clear structuration of plots appeared according to their phytosociological unit (figure 8). On the first axis, phytosociological units were distributed following their water requirements: green alder woods (IX), a hygrophilous and north-facing unit, were located at the negative end, whereas xerophilous pine forests, found on calcimorphic soils, dominated by *Pinus sylvestris* (I) or *Pinus uncinata* (II), which are the most xerophilous units in the area, were located at the opposite, at the positive extremity of the first axis. In between, from the negative to the positive values, *i.e.* from hygrophilous to dry vegetation, we found mesophilous pine forests of *Pinus cembra* (VIII), spruce (VII) and fir forests (V), then xero-acidophilous pine forests of *Pinus sylvestris* and mesoxerophilous pine forests of *Pinus cembra* (VI), beech forests (X), and finally meso-xerophilous and mesophilous pine forests of *Pinus uncinata* (IV) and meso-xerophilous and mesophilous pine forests of *Pinus sylvestris* (III), before the two aforementioned most xerophilous units.

A clear distinction also appeared along the first axis according to the bedrock type (figure 9), with plots on non-calcareous soils at negative values and plots on calcareous soil at positive values along the axis. In addition, the order of phytosociological units also corresponded to a gradient of nitrogen availability (not shown), with moist green alder forests characterized by a high frequency of nitrophilous species,, at negative values, and xerophilous pine forests on calcimorphic soils containing less nitrophilous species, at positive values along the axis. Therefore, first axis mainly expressed the role of soil type, through three characteristics: water balance, bedrock type and nitrogen availability.

The clearest cut appeared on the second axis: beech forests (unit X), which are located in the western part of the valley, at lower elevation, were detached from other groups at positive values of axis 2. Other groups were positioned toward negative values of the second axis, but more aggregated, first with fir forests (group V) and xerophilous pine forests of *Pinus sylvestris* (I), followed by meso-xerophilous and mesophilous pine forests of *Pinus sylvestris* (III) and spruce forests (VII), then by meso-xerophilous and mesophilous pine forests of *Pinus uncinata* (IV), and finally by xerophilous pine forests of *Pinus uncinata* (II), xero-acidophilous pine forests of *Pinus sylvestris* and mesoxerophilous pine forests of *Pinus cembra* (VI), mesophilous pine forests of *Pinus cembra* (VIII) and green alder forests (IX), at the negative extremity of the second axis. This order followed the upward altitudinal forest belt order, so that this second axis expressed an elevational gradient. Indeed, when representing position of plots along axis 2 as a function of their elevation, we observed a negative relationship (figure 10).

Based on the phytosociological units only, we could not observe a clear pattern on the third axis.

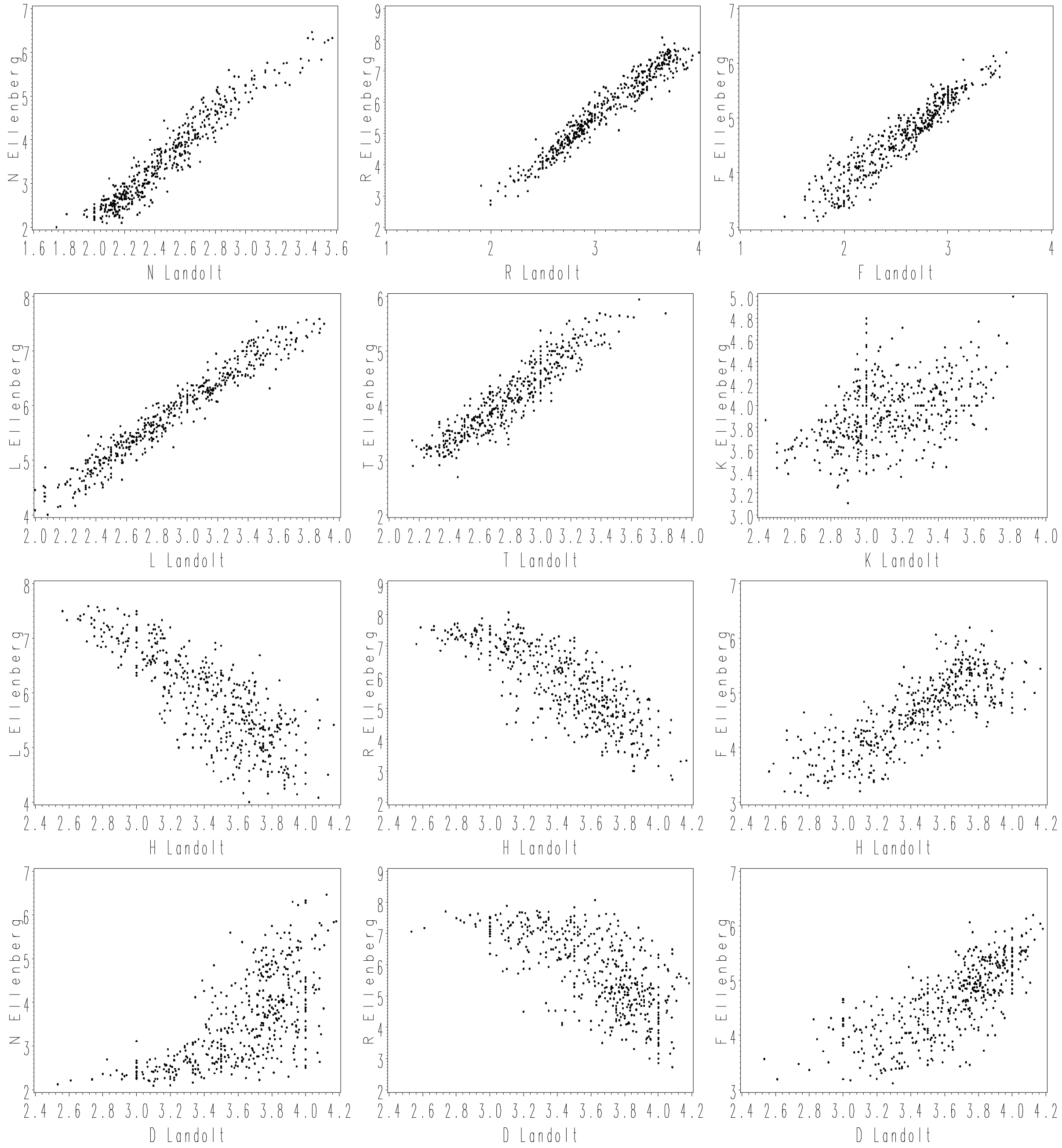


Figure III-7: Mean Ellenberg indicator values against their correspondent mean Landolt values. Correlations values are reported in table 4.

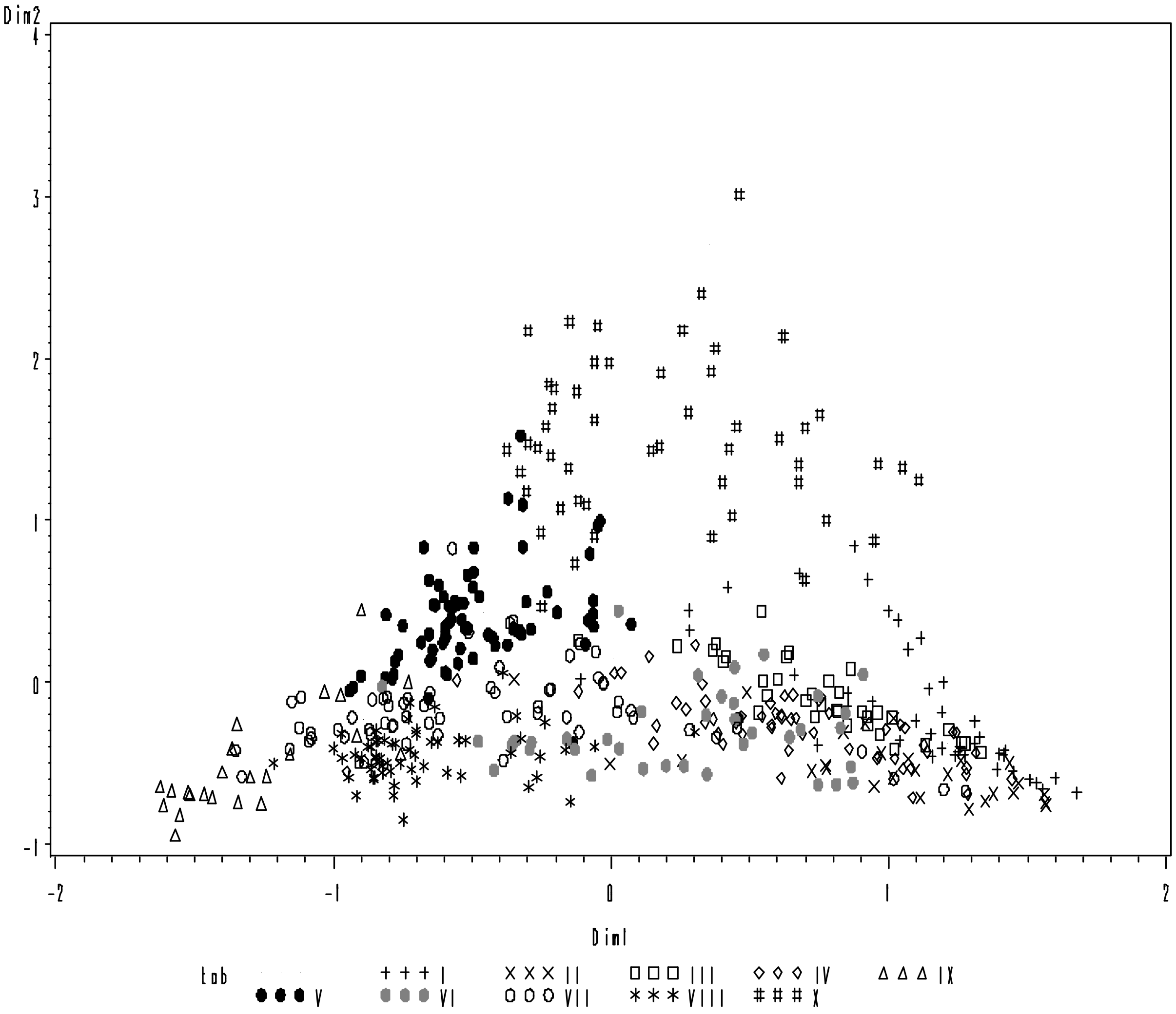
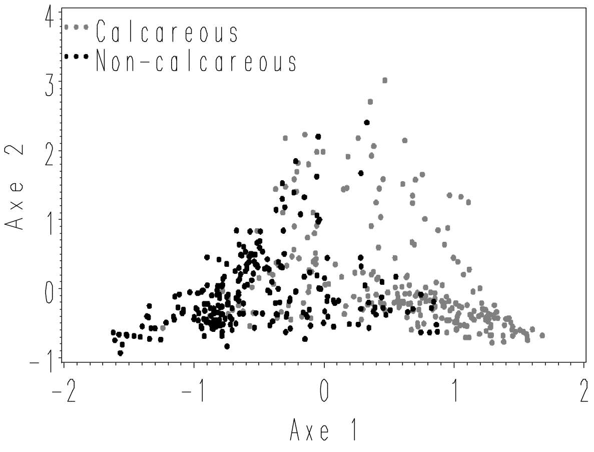


Figure III-8: Position of plots on the first and second axes of the correspondence analysis. Phytosociological units were distinguished. See table 1 for the meaning of the phytosociological unit numbers.



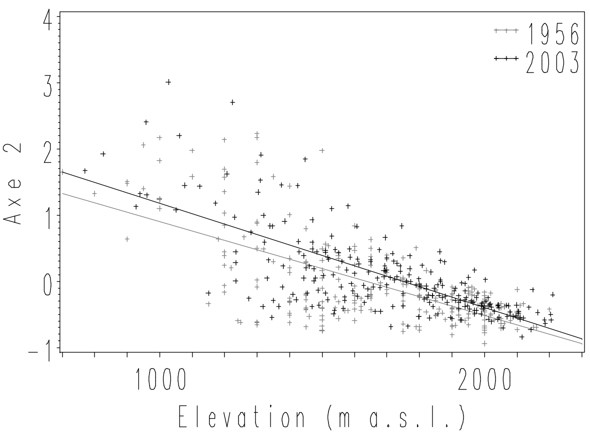


Figure III-9: Position of plots on the two first axes of correspondence analysis. Calcareous (grey) and non-calcareous (black) plots were distinguished.

Figure III-10: Second axis of the correspondence analysis against elevation. First (grey) and second (black) inventory were distinguished.

ii. Ecological meaning of the ordination axes: correlation with mean Ellenberg indicator values

The study of correlations between position of plots along the factorial axes and mean Ellenberg indicator values confirmed the previous interpretations. First axis, which was interpreted as a water balance, substrate type and nitrogen availability axis, showed a tight relation with the three corresponding Ellenberg indicator values: pH (R, corr=0.74***), nitrogen (N, corr=-0.77***) and especially soil moisture (F, corr=-0.93***) (table 6 and figure 11). First axis also showed a positive relationship with temperature (T, corr=0.70***) and light (L, corr=0.73***). Relation was weak with continentality indicator value (corr=0.23***).

Second axis, which was previously defined as an elevation and temperature axis showed a positive but not very strong relation with temperature (corr=0.43***) and nitrogen indicator value (corr=0.38***), but the stronger correlation was observed with light (corr=-0.60***). Correlations with other indicator values were lower or not significant (table 6 and figure 12).

Third axis exhibited a strong correlation with pH (R, corr=0.68***) and also, but to a lesser extent with temperature (T, corr=0.36***) values.

iii. Ecological meaning of the ordination axes: correlation with mean Landolt indicator values

The position of plots on the axes of correspondence analysis plotted against Landolt indicator values showed the same pattern as with Ellenberg values, and absolute value of correlation coefficients between first axis and Landolt indicator values were all higher than 0.73 (table 6 and figure 13): first axis showed tight relations with soil indicator values, positive with pH (R, corr=0.79***), and negative with nitrogen (N, corr=-0.78***), water content (F, corr=-0.97***), humus content (H, p=-0.88***) and soil dispersion (D, corr=-0.85***). Patterns were tighter with other indicator values than for Ellenberg values, particularly with continentality values (corr=0.88***).

As previously with Ellenberg indicator values, the second axis showed a positive relationship with Landolt temperature indicator value (corr=0.40***) and negative with light (corr=-0.60***), but patterns were generally not so clear than for the first axis (table 6 and figure 14). Strongest correlations of third axis occurred with pH (R, corr=0.61***), humus content (H, corr=-0.43***), and temperature (T, corr=0.33***) Landolt indicator values.

iv. Ecological meaning of the ordination axes: modelling with abiotic environmental factors

Previous interpretations of the ordination axes of vegetation were based on the analysis of univariate correlations with vegetation characteristics (phytosociological units defined by Bartoli and Ellenberg or Landolt indicator values). Thus, there was some potential circularity in the interpretation. So, we analysed the ordination axes with multivariate explanatory models using abiotic environmental factors measured at each plot. Results of multivariate explanatory models were in accordance with previous interpretations. Positions of plots along the axes were largely explained by the selected environmental variables for the first and second axes (r^2=76.6% and 55.0%, respectively, table 7). Axis 1 was firstly and largely explained by exposure (F_{III}=502, p<0.001), then by substrate type (F_{III}=330, p<0.001), and finally by elevation (table 7). Axis 2 was firstly explained by squared elevation (F_{III}=64.7, p<0.001) and elevation (table 7). Then, it was explained by substrate type and squared exposure. Third axis was only slightly explained by environmental variables (r^2=6.4%), first by substrate type and then by exposure and elevation.

Finally, it can be concluded from the previous analyses that the first axis of the ordination expressed mostly a gradient of exposure, soil moisture, nitrogen availability and bedrock type, whereas the second axis expressed a gradient of temperature, elevation and received light.

Table III-6: Spearman rank correlation between axes of the correspondence analysis and mean Ellenberg and Landolt indicator values, dissociated between calcareous and non-calcareous soils. Because most of the correlations were significant at $p<0.001$, probabilities were coded as follows: $p<0.001$: no star; $p<0.01$: **; $p<0.05$: *; $p>0.05$: ns.

		Axe 1		Axe 2		Axe 3		Axe 4	
		Ellenberg	Landolt	Ellenberg	Landolt	Ellenberg	Landolt	Ellenberg	Landolt
All substrates	T	**0.70**	**0.73**	**0.43**	**0.40**	**0.36**	**0.33**	0.16	**0.27**
	N	**-0.77**	**-0.78**	**0.38**	**0.28**	0.15	0.12**	**0.31**	**0.34**
	R	**0.74**	**0.79**	0.08$^{0.09}$	0.07$^{0.14}$	**0.68**	**0.61**	-0.16	**-0.24**
	F	**-0.93**	**-0.97**	0.01^{ns}	0.10*	-0.15	-0.15**	-0.09$^{0.06}$	0.07$^{0.13}$
	L	**0.73**	**0.73**	**-0.60**	**-0.60**	0.15	0.19	-0.03^{ns}	-0.07$^{0.13}$
	K	0.23	**0.88**	**-0.23**	**-0.22**	**-0.23**	0.07$^{0.10}$	**-0.38**	**-0.22**
	H	/	**-0.88**	/	**0.15**	/	**-0.43**	/	-0.04^{ns}
	D	/	**-0.85**	/	0.09*	/	**-0.25**	/	0.19
Calcareous	T	**0.43**	**0.40**	**0.68**	**0.67**	**-0.55**	**-0.62**	0.05^{ns}	0.05^{ns}
	N	**-0.77**	**-0.72**	**0.36**	**0.27**	**-0.24**	**-0.25**	-0.02^{ns}	-0.11$^{0.07}$
	R	**0.65**	**0.74**	**0.34**	0.15*	**-0.31**	-0.15*	-0.04^{ns}	-0.01^{ns}
	F	**-0.86**	**-0.94**	-0.19	0.00^{ns}	**0.36**	0.22**	-0.02^{ns}	0.09$^{0.16}$
	L	**0.89**	**0.90**	**-0.39**	**-0.36**	-0.17**	-0.18**	**-0.30**	**-0.27**
	K	**0.38**	**0.91**	-0.22	-0.11$^{0.09}$	0.18**	-0.09$^{0.18}$	0.03^{ns}	-0.03^{ns}
	H	/	**-0.89**	/	0.00^{ns}	/	**0.39**	/	**0.23**
	D	/	**-0.80**	/	0.18**	/	-0.02^{ns}	/	0.10$^{0.12}$
Non-calcareous	T	**0.59**	**0.78**	**0.63**	**0.44**	0.13$^{0.07}$	**0.26**	0.13$^{0.06}$	-0.01^{ns}
	N	**-0.62**	**-0.63**	**0.48**	**0.36**	**0.40**	**0.41**	**-0.19****	**-0.24**
	R	-0.03^{ns}	0.11$^{0.11}$	**0.33**	**0.38**	**0.71**	**0.64**	**-0.32**	**-0.28**
	F	**-0.93**	**-0.92**	-0.05^{ns}	0.04^{ns}	-0.03^{ns}	0.02^{ns}	0.03^{ns}	-0.03^{ns}
	L	**0.43**	**0.38**	**-0.73**	**-0.75**	**0.24**	**0.24**	**-0.30**	**-0.29**
	K	0.04^{ns}	**0.74**	**-0.15***	**-0.27**	**-0.65**	-0.21**	0.11$^{0.11}$	0.04^{ns}
	H	/	**-0.61**	/	0.13*	/	**-0.57**	/	**0.43**
	D	/	**-0.61**	/	-0.08^{ns}	/	-0.17*	/	0.15*

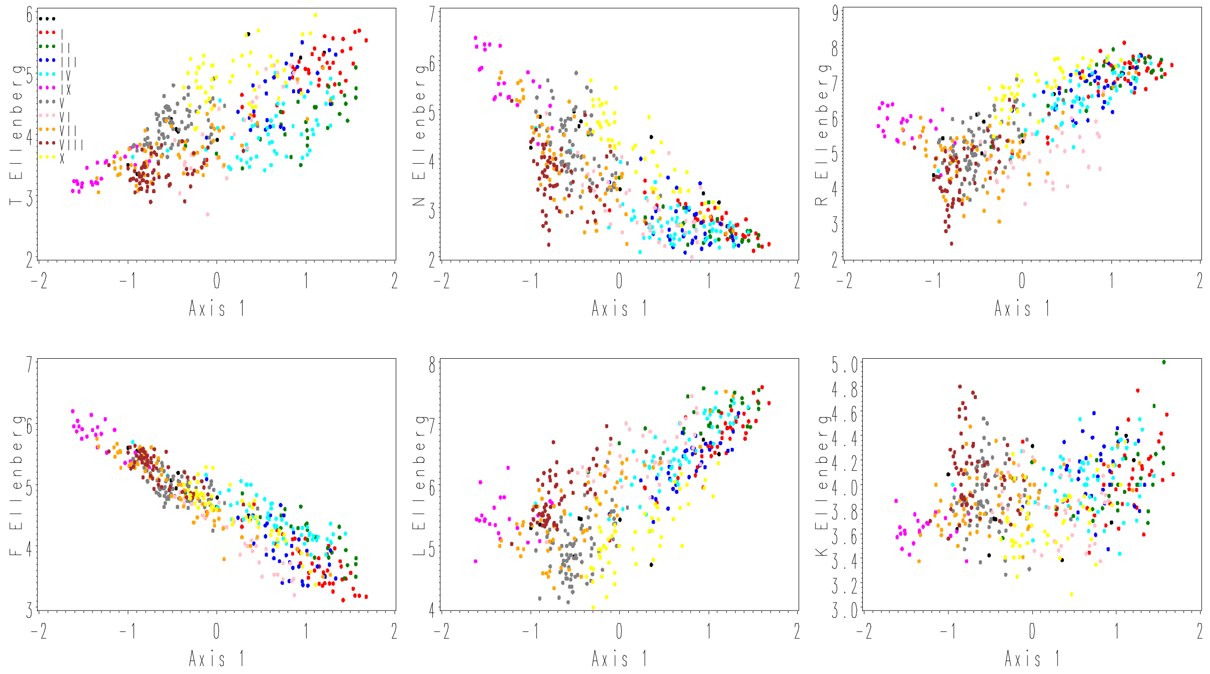


Figure III-11: Position of plots along the first axis of correspondence analysis against mean Ellenberg indicator values. Correlation values are reported in table 6.

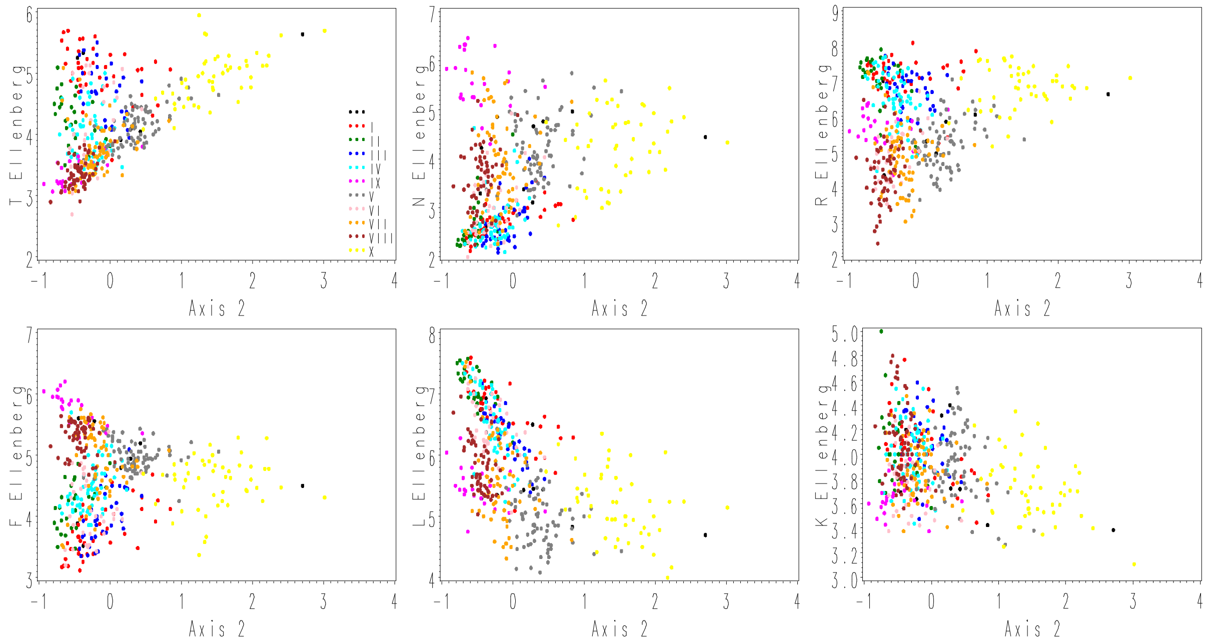


Figure III-12: Position of plots along the second axis of the correspondence analysis against mean Ellenberg indicator values. Correlation values are reported in table 6.

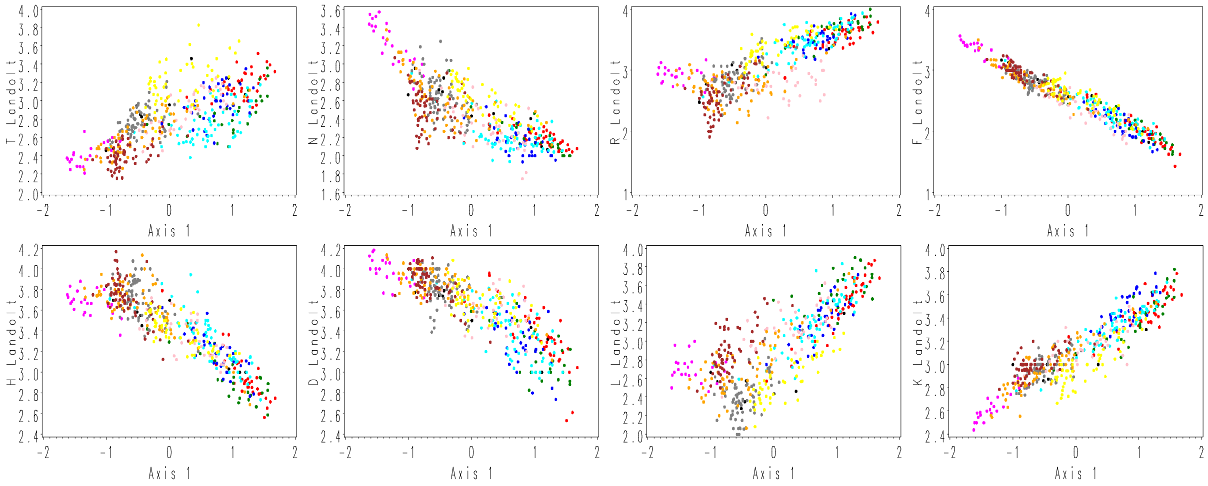


Figure III-13: Position of plots along the first axis of the correspondence analysis against mean Landolt indicator values. Correlation values are reported in table 6.

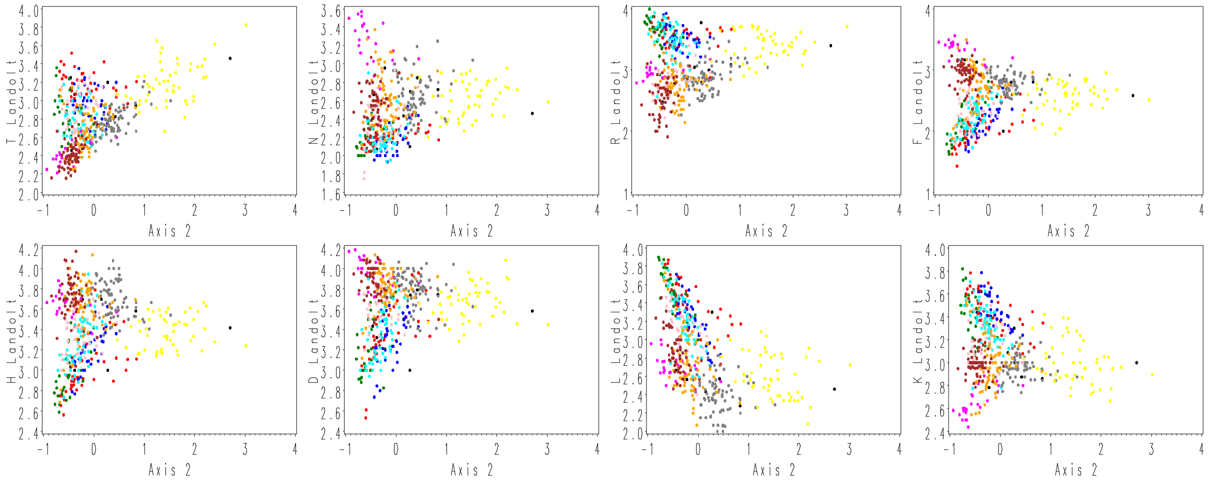


Figure III-14: Position of plots along the second axis of the correspondence analysis against mean Landolt indicator values. Correlation values are reported in table 6.

Table III-7: Explanatory models of factorial axes as a function of abiotic environmental variables. Results are given for correspondence analysis run on all plots, on plots on calcareous soils only, and on plots on non-calcareous soils only. For legend, see table 5. The direction (positive or negative) of the relation between the given axis and the explanatory variable is given by the sign in parentheses: (+) or (-); (+) for exposure means that higher values of the axis were found on north-facing slopes and vice-versa; (+) for elevation means that higher values of the axis were found at higher elevations and vice-versa; (+) for the substrate type means that higher values of the axis were found on calcareous soils, and vice-versa.

	Axis	r²(%)	Elevation (F, p, direction)	Elevation² (F, p, direction)	Exposure (F, p, direction)	Expo² (F, p, direction)	Substrate (F, p, direction)	**Cycle** (F, p)	LSM 1955	LSM 2002	
All substr.	1	76.6	8.1**(+)	16.2***(-)	502***(-)	/	330***(+)	$3.7^{0.053}$	0.068	-0.000	<
	2	55.0	64.7***(-)	30.0***(+)	9.4**(+)	9.8**(-)	6.6*(-)	**13.7*****	-0.052	0.102	>
	3	6.4	7.2**(-)	/	6.3*(+)	9.4**(+)	13.6***(+)	0.0^{ns}	0.001	0.011	=
	4	43.4	55.3***(-)	/	187***(-)	/	265***(-)	**7.0****	-0.046	0.061	>
Calc.	1	47.4	24.9***(+)	25.7***(-)	158***(-)	/	/	**10.0****	0.143	-0.090	<
	2	59.3	18.9***(-)	5.2*(+)	10.3**(-)	$3.1^{0.08}$(-)	/	1.1^{ns}	0.076	0.015	=
	3	28.3	10.2**(+)	6.7*(-)	36.3***(+)	$3.6^{0.06}$(-)	/	**40.0*****	0.198	-0.218	<
	4	10.6	/	5.7*(-)	/	15.7***(-)	/	0.0^{ns}	0.014	0.006	=
Non-calc.	1	65.4	93.3***(-)	/	331***(-)	/	/	$2.7^{0.10}$	0.080	-0.025	<
	2	64.3	38.2***(-)	19.2***(+)	16.0***(+)	/	/	**32.0*****	-0.135	0.191	>
	3	2.3	/	5.0*(-)	/	/	/	0.0^{ns}	0.019	0.016	=
	4	42.0	21.9***(+)	28.9***(-)	/	/	/	**85.5*****	0.313	-0.175	<

2. Vegetation changes between the two inventories

Significance of the inventory cycle number variable (*i.e.* significance of the observed changes in a given vegetation indicator between the two inventory periods, all other abiotic variables being held constant) was tested by a type III test. Direction and intensity of the shift was given by the difference between least-square means (LSM) at the two inventories.

a. Shift in mean Ellenberg and Landolt indicator values

The increase in the **temperature** indicator value between inventories, which was expected as a response of vegetation to climate warming, was highly significant when using Landolt indicator values (F_{III}=53.9, p<0.001; LSM_{1955}=2.75, LSM_{2002}=2.85, table 5b), whereas it was not at all significant (F_{III}=1.5, p=ns; table 5a) when using Ellenberg indicator values. The plot of LSM for temperature indicator values averaged by 100m elevation classes showed that the increase between 1955 and 2002 was almost homogeneously distributed along the elevational gradient with Landolt indicator values, but occurred only under 1300 m a.s.l. and in classes 1700 and 1800 m a.s.l. with Ellenberg indicator values. In order to quantify in meters the mean shift of plant communities between inventories, we transposed the increase of Landolt indicator value for temperature (given by LS-means) in elevation equivalent, from results of the same explanatory model as before, but without the squared variables (Landolt indicator value for temperature as dependent variable; elevation, cosine of the exposure, substrate type and inventory date as independent variables). The observed increase in Landolt indicator value for temperature was equivalent to a shift of 139 m of plant communities, or 29.0m/decade *i.e.* an equivalent increase in temperature of 0.16°C/decade considering the adiabatic lapse rate of 0.56°C/100 m of ascent observed in our study area (see previous chapter).

Light values showed a slight significant decrease with Ellenberg (F=3.4, p=0.06) and with Landolt (F=3.8, p=0.05) indicator values (table 5a and 5b), indicating a tendency toward a more shade tolerant flora, which was consistent with the negative correlation between Ellenberg temperature and light values for species, but not with the positive correlation existing between temperature and light indicator values for plots. The decrease in light values was most expressed at middle elevations, between 1100 and 1800 m a.s.l. for both Ellenberg and Landolt values. Furthermore, **continentality** values showed a decrease between the two inventories, highly significant for both, Ellenberg (F_{III}=37.7, p<0.001; LSM_{1955}=4.01, LSM_{2002}=3.85) and Landolt (F_{III}=12.8, p<0.001; LSM_{1955}=3.15, LSM_{2002}=3.09) indicator values. It suggests a retreat of the continental part of the Maurienne valley climate. This decrease was more homogeneously distributed along the entire elevation gradient with Ellenberg values than with Landolt values.

Effect of inventory cycle variable was highly significant for Ellenberg and Landolt indicator values for **nitrogen** (F_{III}=32.4, p<0.001, and F_{III}=19.9, p<0.001, respectively), showing a significant increase in this value, *i.e.* eutrophication of the vegetation, by 0.4 for Ellenberg and 0.1 for Landolt (Ellenberg: LSM_{1955}=3.37, LSM_{2002}=3.76; Landolt: LSM_{1955}=2.42, LSM_{2002}=2.53; table 5a and 5b). This was not consistent with the increase in Landolt temperature value as the correlation was negative between these two factors, implying that each of these indicator values was evolving independently. When looking at the illustration of calculated LSM by elevation classes and by date (figure 15 and 16), it appeared that increase in nitrogen happened at almost all elevations, but was more pronounced at lower elevation.

Interestingly, soil indicator values for **pH** (R) which are usually strongly correlated with nitrogen values did not show any significant trend neither with Ellenberg, nor with Landolt values (table 5a and 5b). On the other hand, **moisture** (F) increased between each inventory, *i.e.* plants indicated more humid sites, slightly when using Ellenberg indicator value (F_{III}=2.8, p=0.09; LSM_{1955}=4.62, LSM_{2003}=4.68) and more significantly when using

Landolt indicator value (F_{III}=18.5, $p<0.001$; LSM_{1955}=2.51, LSM_{2003}=2.60), which was consistent with the increase in nitrogen value as these two indicator values were positively correlated, but not consistent with the increase in temperature value as temperature and moisture were negatively correlated. Again, this increase appeared to happen at lowest elevations, as for nitrogen. To disentangle the response of the moisture indicator value from that of nitrogen increase, we added the mean indicator value for nitrogen to the previous model. As expected, the explanatory model was greatly improved (r^2=82.4% for Ellenberg moisture value, r^2=85.5% for Landolt moisture value) and the shift in the moisture indicator became insignificant for Landolt values (p=0.08). It even decreased slightly ($p<0.05$) for Ellenberg values, contrary to the previous increase when the correlation with nitrogen was not taken into account. Landolt indicator value for **dispersion** (D), a factor only available in the Landolt system, showed a significant increase toward soils with more fine particles and/or poorer oxygen supply, consistent with nitrogen and moisture increase as values were positively correlated (table 4). The last soil indicator value available, for Landolt only, **humus content** (H), did not show a significant trend.

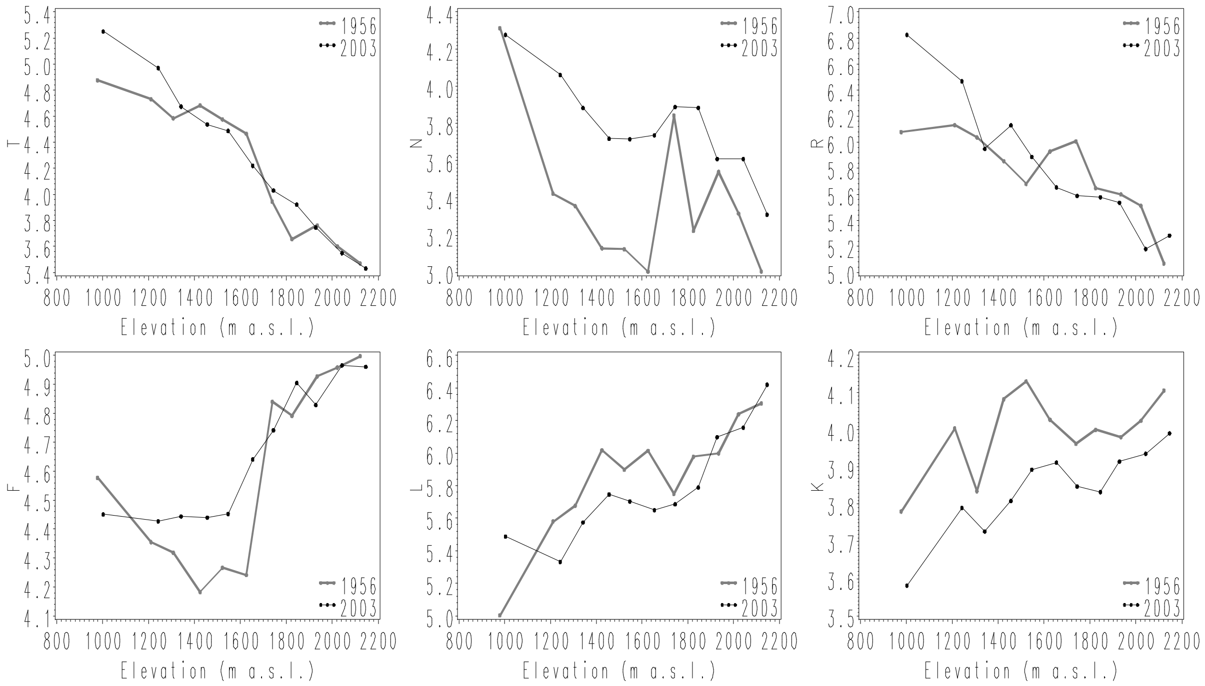


Figure III-15: Changes of least-square means (LSM) for Ellenberg indicator values along the elevational gradient between each inventory. For illustration purpose, variables were entered differently than in explanatory models constructed for testing the inventory cycle effect: models were run independently for each inventory cycle, and elevation was entered as classes and plotted with mean elevation of the class. Moreover, squares of elevation or exposure were not entered. Finally, models were constructed at each date with the variables: elevation in classes, cosine of exposure, and substrate type in classes, except for the continentality value, for which exposure was not entered in the model for illustration, like in the explanatory model.

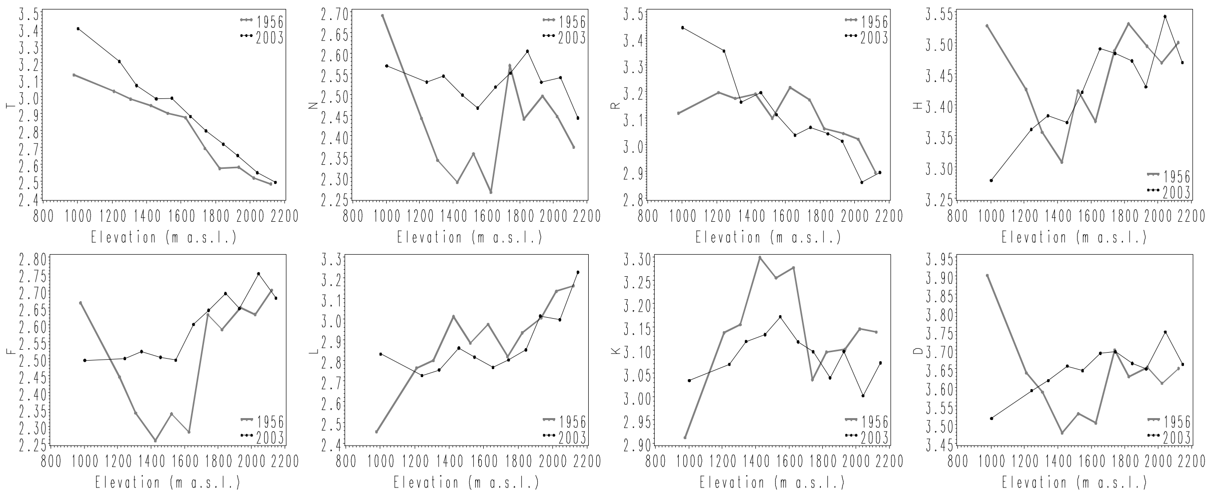


Figure III-16: Changes of least-square means (LSM) for Landolt indicator values along the elevational gradient between each inventory. See figure 15 for further details. Here, model for continentality was built with exposure variable.

i. Calcareous versus non-calcareous soils

When we built the models explaining Ellenberg and Landolt values with abiotic environmental variable for each substrate type separately and looked at the effect of the inventory cycle number, some of the trends previously observed on all plots were preserved, but some other indicator values showed opposite trends between each substrate type.

Ellenberg indicator values for **nitrogen** and **continentality** and Landolt indicator values for **temperature**, **nitrogen** and **moisture** displayed the same significant trends on each substrate type than on all plots (table 5a and 5b). The **equivalent in elevation shift** calculated from Landolt temperature indicator value was lower on **non-calcareous soils (+97.0 m a.s.l.)** than on **calcareous soils (+176.7 m a.s.l.)**.

However, other indicator values showed different behaviour on calcareous and non-calcareous soils. Ellenberg indicator value for **temperature**, which did not shift significantly on all plots, increased slightly significantly (F_{III}=5.1, $p<0.05$) on calcareous soils only. Ellenberg and Landolt **light** values and Landolt **continentality** values which were decreasing on all plots, showed a significant decrease on calcareous soils only (Light: $F_{III(Ell.)}$=9.2, $p<0.01$ $F_{III(Land.)}$=7.3, $p<0.01$, continentality: $F_{III(Land.)}$=15.7, $p<0.001$), and showed no trend on non-calcareous soils. **Humus content** and **reaction** values (pH), which showed no trend when considering all plots, displayed significant opposite trends on each soil type. pH indicator value, which did not shift significantly, now showed a highly significant decrease on calcareous soils ($F_{III(Ell.)}$=18.4, $p<0.001$ and $F_{III(Land.)}$=32.5, $p<0.001$), and a highly significant increase on non-calcareous soils ($F_{III(Ell.)}$=16.5, $p<0.001$ and $F_{III(Land.)}$=17.3, $p<0.001$). Thus, on each soil type, pH evolved toward neutral values. These shifts were in agreement with the observed increase in nitrogen indicator value: N and R indicator values were positively correlated for low pH values (Spearman correlation test: corr(Ell.)=0.60, $p<0.001$ and corr(Land.)=0.44, $p<0.001$), *i.e.* on non-calcareous soils, so that an increase in the nitrogen indicator value was consistent with an increase in the pH indicator value, and N and R indicator values were negatively correlated for high values of pH (Spearman correlation test: corr(Ell.)=-0.35, $p<0.001$ and corr(Land.)=-0.53, $p<0.001$), *i.e.* on calcareous soils, so that a nitrogen increase was consistent with a decrease in pH on calcareous soils. Hence, because of the triangular relation existing between nitrogen (N) and pH (R) indicator values, where high values of nitrogen were observed only for middle values of pH, the shift toward neutral values of pH could be an artefact caused by nitrogen increase. We tested the effect of nitrogen increase on pH shift by adding mean value for nitrogen in the previous models. Explanatory models of variations in the pH indicator value were improved (on calcareous soils r^2(Ell.)=58.9% and r^2(Land.)=61.6%, on non-calcareous soils r^2(Ell.)=58.0% and

r^2(Land.)=42.8%). The shift in pH value was still significant with the same trend as before, but much weaker (a decrease on calcareous soils $F_{III,\ Ell.}$=8.5, p(Ell.)<0.01 and $F_{III,\ Land}$=15.7, p(Land.)<0.001, an increase on non-calcareous soils $F_{III,\ Ell.}$=4.2, p(Ell.)<0.05 and $F_{III,\ Land.}$=14.4, p(Land.)<0.001). This means that the opposite shift of pH values on each soil type was strongly but not entirely linked to the the nitrogen increase.

In agreement with the previous trends in pH values, Landolt value for humus content increased on calcareous soils ($F_{III(H)}$=5.5, p<0.05) and decreased on non-calcareous soils ($F_{III(H)}$=16.1, p<0.001). The previous increase in the other Landolt indicator of soil structure, dispersion, appeared to be significant on calcareous soils only ($F_{III(D)}$=20.8, p<0.001).

Landolt moisture value, which showed a nearly significant increase when tested on all plots, showed a slight significant increase on non-calcareous soils only (F_{III}=5.8, p<0.05). Once again, because the correlation of moisture with nitrogen value could be able to explain the observed shift in moisture values, we tested the effect of nitrogen increase on moisture shift of both Ellenberg and Landolt values. As for the behaviour on all substrates, the shift in moisture became not significant on calcareous soils for Landolt values (r^2(Land.)=77.3% p(cyc.)=ns) and on non-calcareous soils for Ellenberg and Landolt values (r^2(Ell.)=78.7% p(cyc.)=ns and r^2(Land.)=81.3% p(cyc.)=ns), and decreased (r^2=74.7% p(cyc.)<0.001) for Ellenberg values on calcareous soils.

ii. Nitrogen map

Because nitrogen indicator values displayed a very significant increase, we mapped the variations in mean nitrogen Ellenberg value in our study area (figure 17). Since coordinates of the plots were available for the second inventory only, this map could not be used to study the changes in the mean nitrogen value in the valley, but only to visualize the present distribution of nitrogen availability in soils. Most of the plots displaying high nitrogen levels were located in the western, lower part of the area, where highway traffic has dramatically increased since the opening of the Fréjus tunnel in 1980, some others being located in the eastern, upper part of the study area. The majority of high nitrogen values were also observed on north-facing slopes. Thus, this map suggests two possible interpretations: a role of the increasing road traffic or a role of natural variations in exposure and soil moisture.

iii. Continentality map

In the same way, we built the map of current mean Landolt indicator values for continentality in the Maurienne valley. As expected, high continentality plots were located at the eastern, upper part of the valley where the inner-alpine climate is the more pronounced. A shift of vegetation from the lower part of the valley *i.e.* the less continental bioclimatic area, to the upper part *i.e.* the more continental bioclimatic area, could be interpreted as a displacement of vegetation from intermediate Alps to inner-Alps, following climate advance.

Present distribution of other vegetation indicator values were also mapped and are given in annex 1.

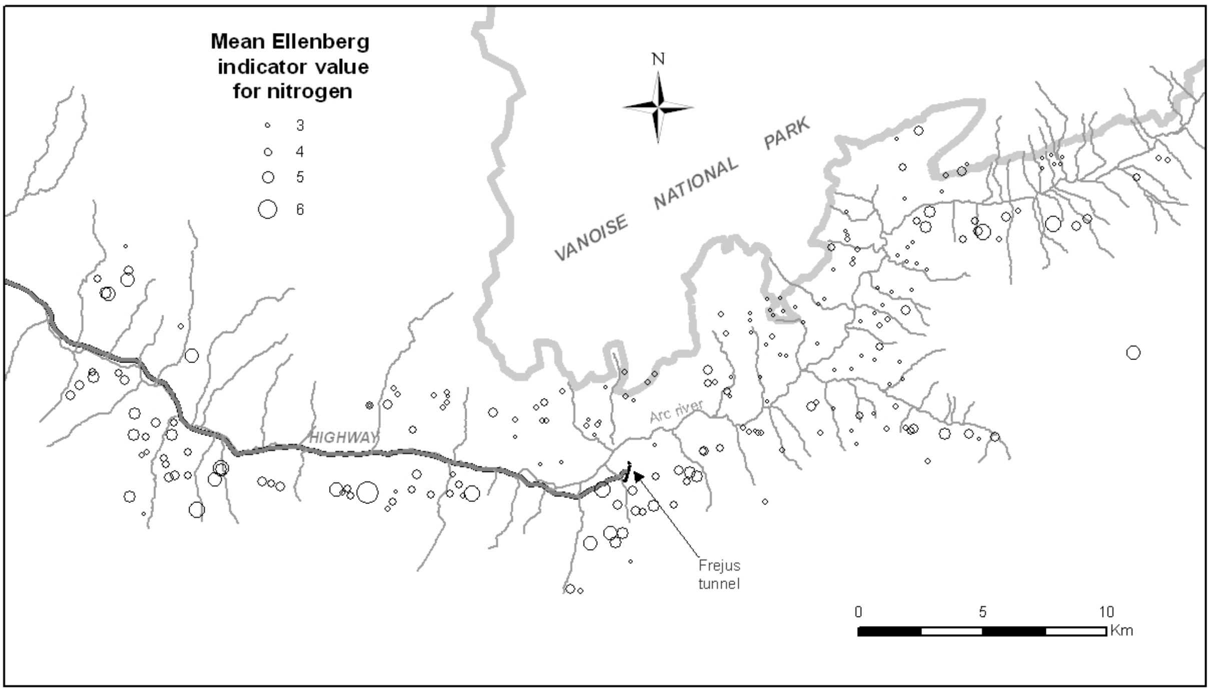


Figure III-17: Map of mean Ellenberg indicator value per plot for nitrogen in the upper Maurienne valley. The size of the bubble is proportional to the mean value for the plot. Rivers indicate the location of valley bottoms. The highway is drawn and extends into the Fréjus tunnel. Limit of the Vanoise national park is shown.

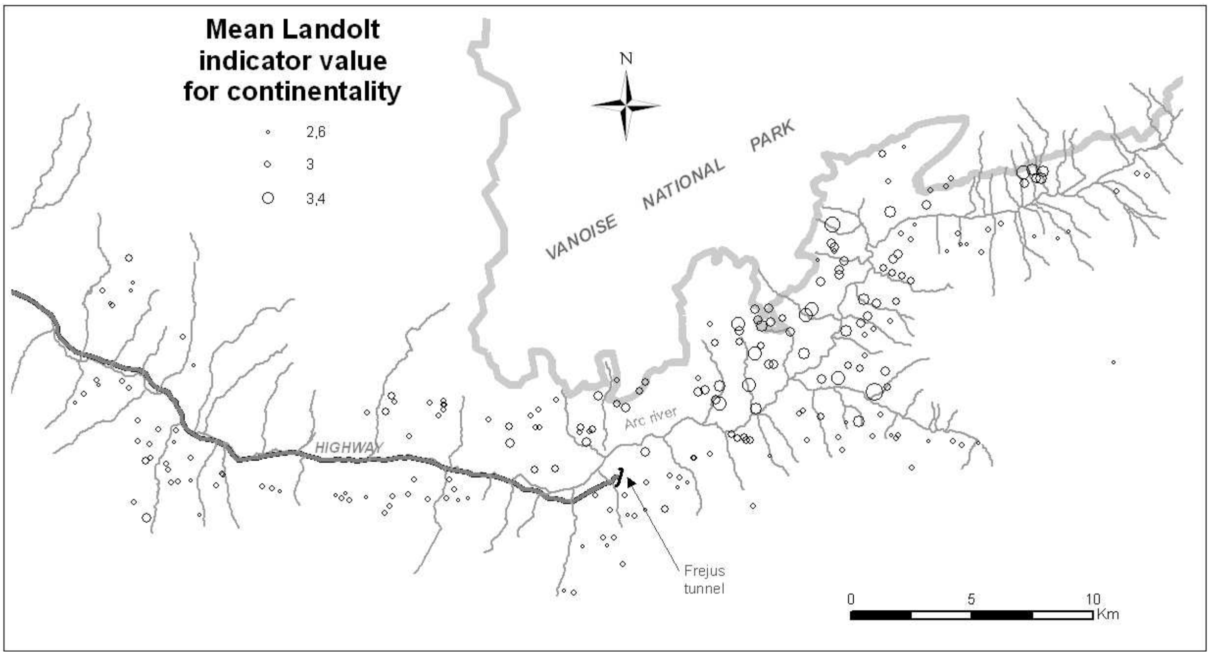


Figure III-18: Map of mean Landolt indicator value per plot for continentality. Other information as in previous figure.

b. Shift in the position along the correspondence analysis axes

The role of the inventory cycle number was near to be significant (F_{III} =3.7, p=0.053) in the position of vegetation plots along the first ordination axis, linked to soil type. This shift was toward negative values of the axis, *e.g.* more acid soils, toward north slopes and more nitrophilous vegetation. This shift was consistent with results obtained with Ellenberg and Landolt values, although not so marked. Decrease was not homogeneous along the elevational gradient (figure 19), and occurred mostly above 1250 m a.s.l.

Positions along the second axis, corresponding to an elevation gradient, showed a highly significant increase ($F_{III}=13.7$, $p<0.001$), also consistent with results obtained from Ellenberg and Landolt values. Because the correlation was negative between first axis and elevation, a positive shift in the position of plots along the axis expressed a shift of vegetation towards higher elevations. This increase occurred along the entire elevational gradient (figure 19) and was weaker above 1900 m a.s.l. The third axis, also corresponding to substrate, did not show any significant shift between the two inventories.

i. Calcareous versus non-calcareous soils

When correspondence analysis was run on calcareous and non-calcareous soils separately, the ecological meaning of the ordination axes changed slightly on each soil type. The explanatory model of first axis variations by abiotic environmental variables showed that exposure was the first explanatory factor (table 7), followed by elevation on each soil type, but significance of exposure was higher on non-calcareous than on calcareous soils. Moreover, the first axis obtained on each soil type showed the strongest correlation with moisture indicator values for Ellenberg and Landolt: (corr(ell)=-0.86***, corr(Land)=-0.94*** on calcareous soils; corr(ell)=-0.93***, corr(Land)=-0.92*** on non-calcareous soils). Then, correlations with other values were slightly different depending on which soil type correspondence analysis was run.

On calcareous soils, first axis showed high correlations with light values for both indicators (corr(ell)=0.89***, corr(Land)=0.90***), which confirms that first axis expressed light received in relation with the exposure gradient. Then, it was strongly correlated with Landolt values for continentality, humus content and soil dispersion, and highly correlated with both Landolt and Ellenberg values for nitrogen and pH (table 6), expressing a gradient in soil structure.

On non-calcareous soils, first axis also expressed a gradient in soil structure according to Landolt values, but not a pH gradient as on calcareous soils (table 6). The correlation between first axis and temperature indicator values was high, suggesting a more marked temperature gradient than on calcareous soils, and at the contrary, the light gradient was less obvious.

In conclusion, first axis expressed a combined soil moisture, exposure, nitrogen and pH gradient on calcareous soils, whereas it expressed only a moisture, exposure and nitrogen gradient on non-calcareous soils, without any role of pH.

Regarding significance of the inventory cycle effect, *i.e.* the shift between the two inventories, first axis was the only one to display a similar behaviour on both soil types, with a significant shift on calcareous soils ($F_{III}=10.0$, $p<0.01$) and a nearly significant shift on non-calcareous soils ($F_{III}=2.7$, $p<0.10$). The shift toward more hygrophilous and nitrophilous vegetation was more pronounced on calcareous than on non-calcareous soils.

The second axis corresponded to a temperature gradient for both soil types as it was firstly explained by elevation in explanatory models (table 7), and had the strongest correlation with temperature indicator value on calcareous soils, and the strongest after light values on non-calcareous soils (table 6). We observed opposite behaviour on each soil type regarding the shift between the two inventories. Indeed, positions of plots along the second axis showed a highly significant and positive shift indicating a more thermophilous vegetation on non-calcareous soils only, whereas Landolt indicator values for temperature increased on both soil types.

The third axis, which corresponded to a gradient of geological substrate when the ordination was run on all plots, probably corresponded to a temperature difference between northern and southern slopes on calcareous soils as it was firstly explained by exposure in explanatory models and not by elevation, but had the strongest correlation with temperature values. On non-calcareous soils, it was only explained by elevation in explanatory models, but strongest correlations with indicator values occurred with pH and nitrogen values, and also humus content given by Landolt values and continentality given by Ellenberg values. It showed a highly significant decrease on calcareous soils only, corresponding to a shift of vegetation toward more hygrophilous conditions. This shift, also observed on first axis, was consistent with an increase in Ellenberg and Landolt indicator values for moisture.

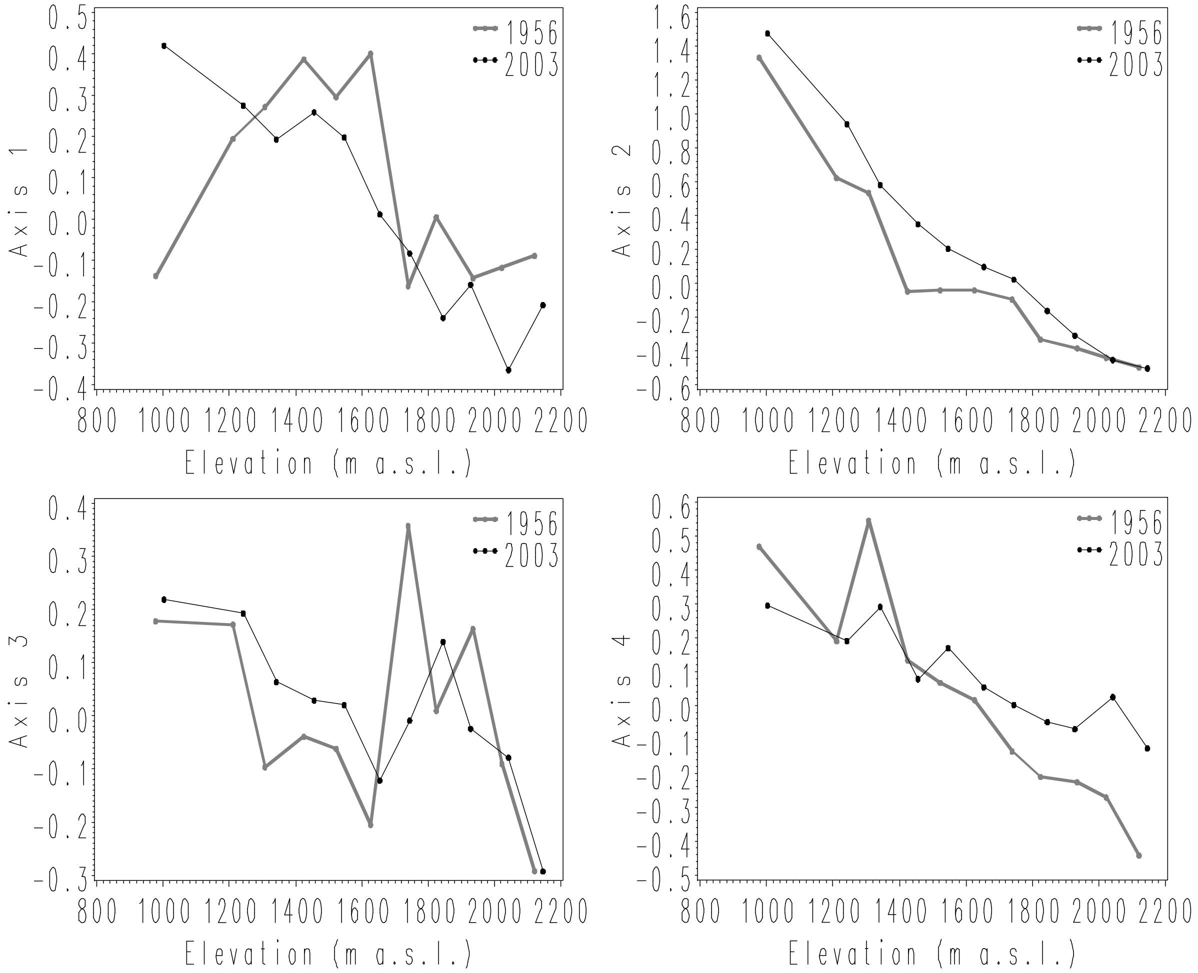


Figure III-19: Changes in least-square means (LSM) of position of the plots on the first four ordination axes, as a function of elevation and inventory cycle. The model used for illustration purposes was built separately for each inventory and included only the following explanatory variables: elevation in classes, squared cosine of exposure, and substrate type in two classes.

c. Changes in stand dendrometric characteristics

Data of French National Forest Inventory provided information on forest structure and stand development that were not available in our own dataset. However, the observed time interval between successive cycles of the National Forest Inventory did not cover the same 48 years (from 1955 to 2002) of our study, but the last 15 years only (from 1985 to 2000). Thus, it gave the direction of forest evolution during the last part only of the time span of our study .

Tree cover increased largely in below 800 m a.s.l., and slightly above 1000 m a.s.l. (figure 20a), where our study took place, indicating a closure of forests. Number of stem per hectare increased largely at all elevations (figure 20b), expressing considerable stem recruitment. Mean basal area (figure 20c) increased mostly under 800 m a.s.l. and slightly above 1000 m a.s.l.. However, age recorded for even-aged forests showed a decrease above 600 m a.s.l. (figure 20d) suggesting that forests became younger, which was consistent with the increase in number of stem per ha, but looked contradictory to the increase in tree cover and basal area.

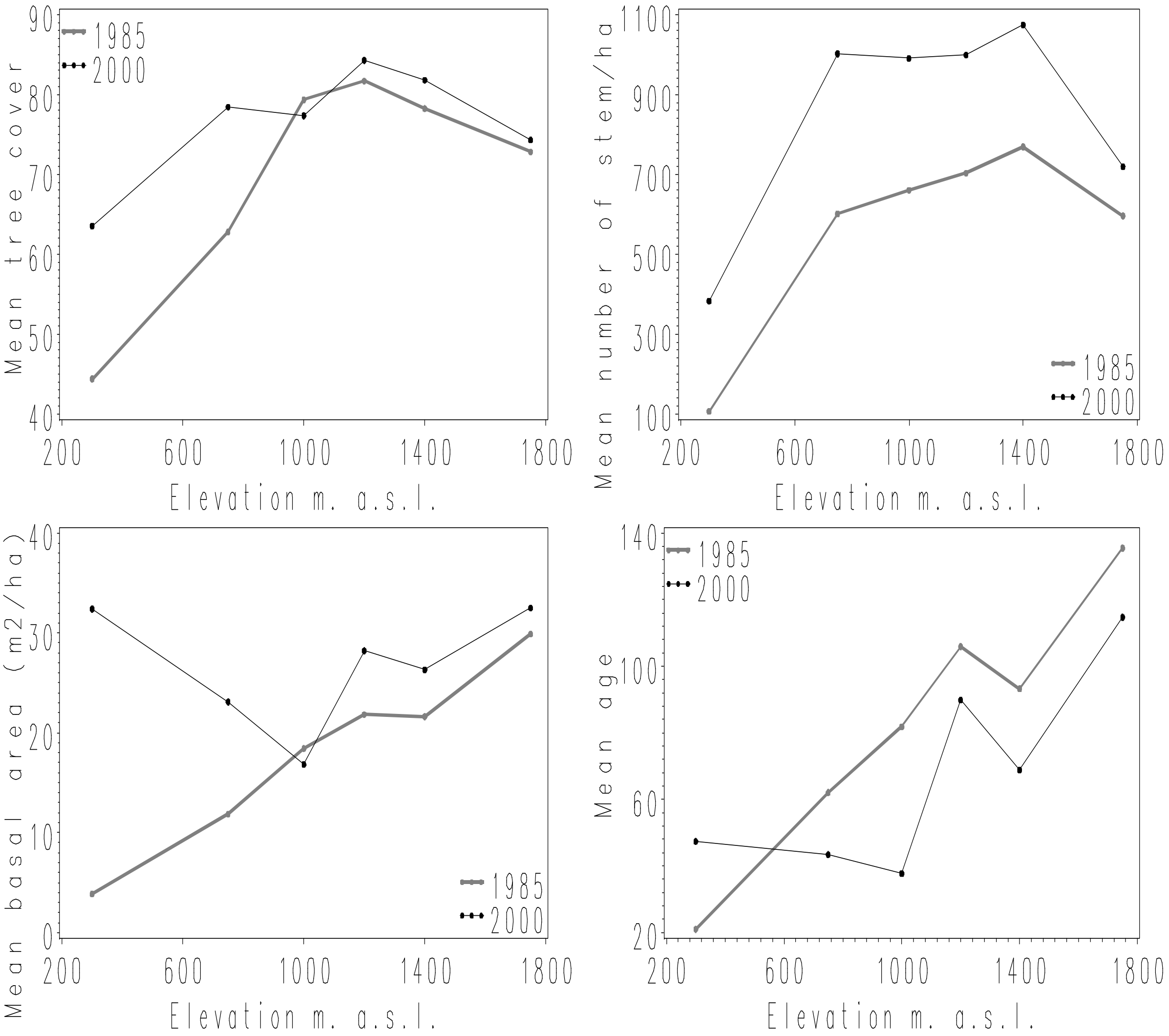


Figure III-20: Changes in stand dendrometric characteristics between 1985 and 2000: a. tree cover (in percentage), b. number of stem per ha, c. basal area per ha, and d. stand age, averaged by elevation classes and inventory cycle.

D. DISCUSSION

1. Response to climate change

The expected change toward **more thermophilous** plant communities was only expressed by Landolt indicator values and was highly significant. Among all the 8 indicator values of the Landolt system, it was temperature which showed the most significant change. Moreover, Landolt indicator values for temperature displayed significant changes on both soil types even when analyzed separately. Ellenberg temperature value showed a significant increase on calcareous soils only. We think that Landolt indicator values for temperature are more adapted to our study region than Ellenberg ones, for different reasons. First, they were calibrated for Switzerland, a phytogeographic region which is more similar to the Maurienne valley than Germany. This calibration region covers a larger range of elevations. Secondly, and as a side effect of the previous cause, the percentage of missing values in the calculation of mean temperature values per plot was much higher using Ellenberg data (42%) than Landolt ones (16%). Thus, mean Landolt averages are probably more reliable. Finally, the explanatory model explaining variations in temperature indicator values fitted slightly better with Landolt (r^2=78%) than Ellenberg values (r^2=74%). More importantly, elevation and exposure had a more influential role in the model, and bedrock type a lesser impact. Hence, we conclude that the lack of response of Ellenberg temperature value is probably due to a poor adequation to the study area.

When looking at other climatic parameters indicated by vegetation, continentality showed a highly significant decrease with both Ellenberg and Landolt indicator values, also significant on each soil type taken independently. This continentality indicator increased more with Ellenberg than Landolt values. The change in climate as indicated by vegetation was fully accounted for by changes in the continentality indicator value of Ellenberg, and by changes in both the temperature and then the continentality indicator values of Landolt. The positive and significant linear relationship of today mean Ellenberg and Landolt values for continentality with longitude (r^2=16.2% and r^2=10.4%, respectively) suggests that the decrease in continentality value could be a consequence of the advance of pre-alpine climate into the inner-alpine zone of the Maurienne valley.

These responses of vegetation to climate were confirmed by ordination analyses: changes in indicator values for temperature and continentality were confirmed by the significant changes observed in position of plots along the second ordination axis, which corresponded to a gradient of temperature and elevation whatever the geological substrate. Moreover, the position of present plots (second inventory) on the second ordination axis showed quadratic relation with longitude (r^2=46.3%), confirming the existence of a climatic gradient between the lower, eastern part of the valley and the upper, western part of the valley, which can be related to the continentality gradient, as illustrated by indicator values for continentality. Thus, the observed shift of plot positions along the second axis could also be interpreted as the retreat of continental flora in the valley, as suggested by Ellenberg and Landolt indicator values. On calcareous soils, temperature increase was confirmed by a shift along the third axis, corresponding to received warmth on each slope (as it was correlated to indicator value for temperature and was firstly explained by exposure in explanatory models). On non-calcareous soils, changes toward more thermophilous vegetation were confirmed by the significant negative shift of positions along axis 2, corresponding to elevation, light and temperature.

It is very difficult to verify if such tendencies also exist in the local climate. Few meteorological stations are under disposal in mountain regions. But, above all, the climatic series from these stations are often not homogeneous along time, due to frequent changes in the exact location of the station or changes in the method of measurement. Meteo-France has started to standardize the French climatic series, *i.e.* to correct them for the previous bias. The meteorological station closest to the Maurienne valley, among those already standardized, is the Grenoble station. Thus, we studied some of the trends at this station using these standardized data (figure 21). Unfortunately, the data were standardized up to the year 2000 only.

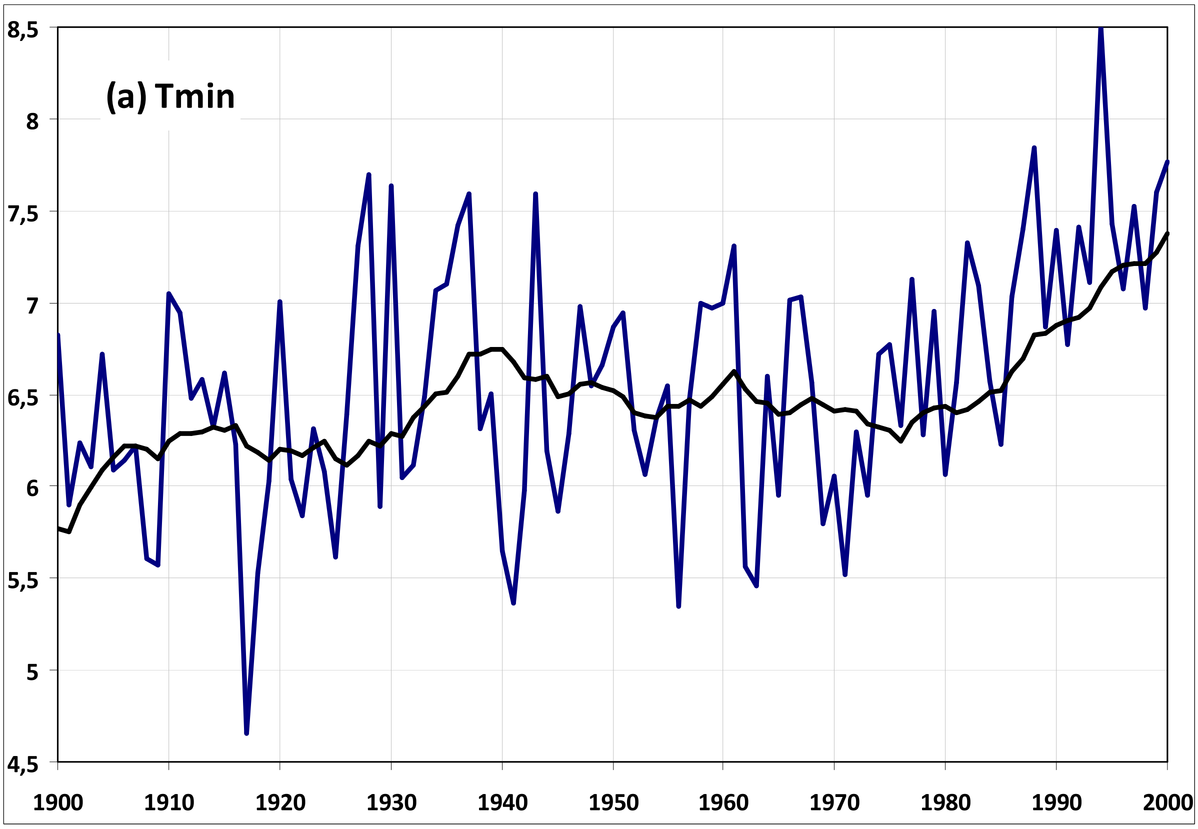


Figure III-21: Trends in climatic parameters at the Grenoble climatic station. Standardized data from Météo-France. (a): annual average of monthly minimum temperature, (b): annual average of monthly mean temperature and (c): annual thermal amplitude (difference between the monthly mean temperature of the warmest and the coldest months of the year). The interpolated line represents the moving average of the fifteen previous years.

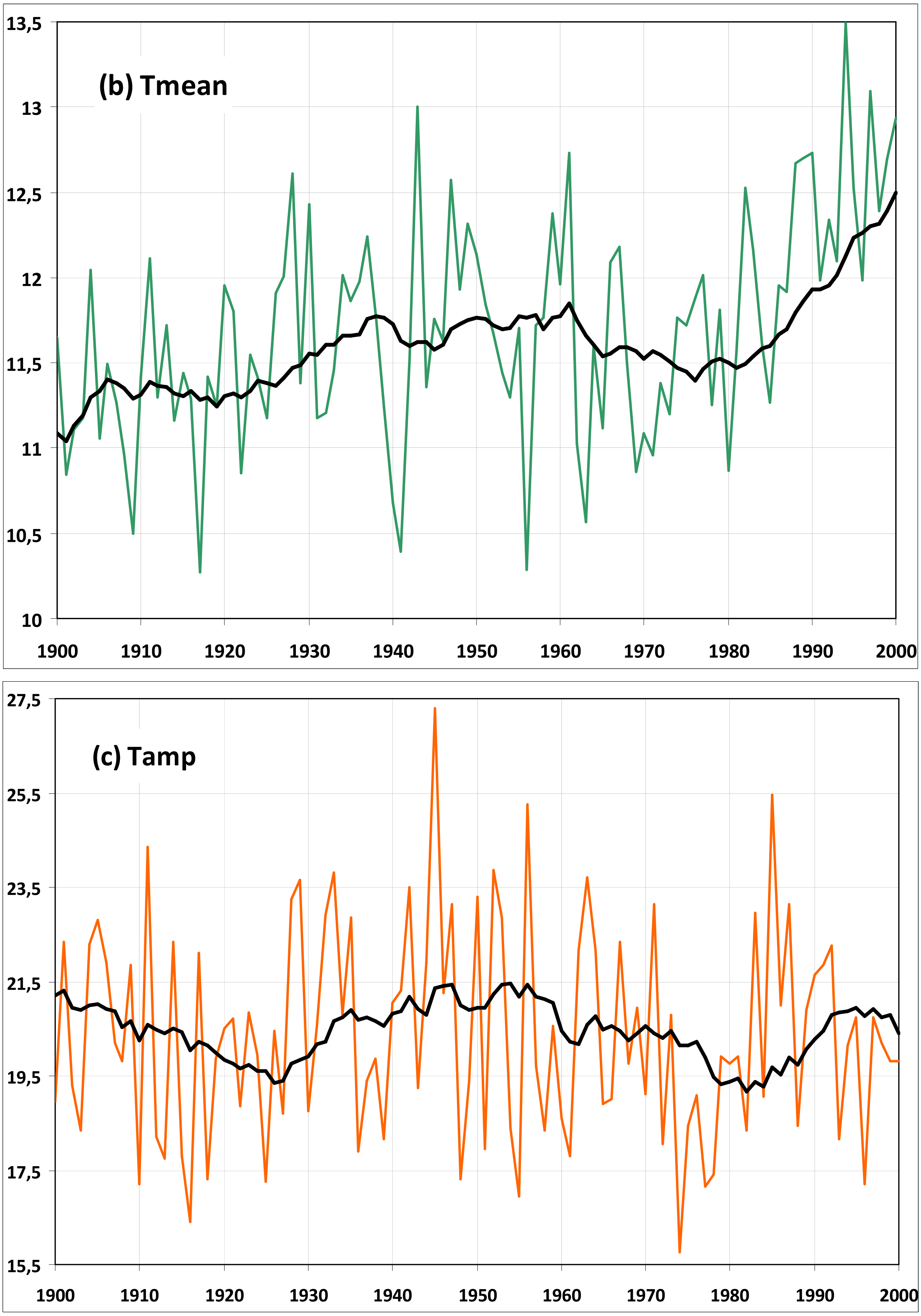


Figure III-21: (continued).

It appears clearly that temperatures have increased during the last 50 years of the XXth century, more for minimum than maximum temperatures. This trend also holds for the entire XXth century. Thermal amplitude, which is the main climatic indicator of continentality, did not show any clear centennial trend, but reached a maximum in the 1940s and 1950s. Considering a putative lag of fifteen years between a change in climate and the response of vegetation, we plotted the moving average of the last fifteen years for each parameter. The (15 years lagged average) minimum annual temperature increased by 1.0°C between 1955 and 2000, from 6.4°C to 7.4°C. The mean annual temperature increased by 0.8°C (0.16°C/decade, *i.e.* an equivalent increase in elevation of 28.8m/decade), from 11.7°C to 12.5°C and the annual thermal amplitude decreased by 0.9°C, from 21.3°C to 20.4°C. Although observed at a meteorological station located at 75 km from the heart of our study area, the previous climatic trends are in agreement with the observed shifts in vegetation.

The main change indicated by vegetation in Maurienne valley seemed to be a climate change. Two components of climate change appeared to be involved, in this inner-alpine valley: a temperature increase and a continentality decrease.

These results are in agreement with those obtained in southern-east France based on National Forest Inventory data (see previous chapter).

2. Changes in soil characteristics and nitrogen atmospheric deposition

The second observed vegetation change in Maurienne forests was an **eutrophication** as revealed by Ellenberg and Landolt indicator values. N Ellenberg indicator value, is known to be globally related with soil nitrogen availability (Ellenberg 1974). More recently, it has been more precisely shown to be correlated with percent nitrification and not ammonification (Andrianarisoa *et al.* 2009). This shift in vegetation was the second most significant after continentality shift for Ellenberg values and after temperature shift with Landolt values. The increase in mean nitrogen value of plant communities could be partly responsible for the large increase in species richness per plot between the two inventories. It has been shown in the literature that, at the intermediate levels of nitrogen availability usually observed in such areas, the increase in nitrogen supply promote an increase in species richness. The shift toward more nitrogen demanding communities was also highly significant on each bedrock type taken separately.

Because correlation between temperature and nitrogen indicator values were negative, either calculated on the set of species used in this study or on mean values per plot, the concomitant increase in nitrogen and Landolt temperature values represents two independent phenomena. Nitrogen increase indicated by vegetation could likely be caused by an increase in atmospheric nitrogen deposit in general, as *e.g.* intensified agricultural production (Vitousek *et al.* 1997, Galloway *et al.* 2008), and due to increase in road traffic (Paul 2000, Deletraz 2002, Laffray 2008) since opening of Fréjus Tunnel in particular. No direct measurements of nitrogen deposition were available in our study area. The closest site of the Level II European network of intensive forest monitoring (French Renecofor network) is located at St-Hugon, 50km to the north-west. There, the total bulk nitrogen deposition measured from 1993 to 2008 amounted to 7.4 kg-N.ha^{-1}.yr^{-1}. At the Boscodon Renecofor plot, 80 km to the south, the annual deposition was 4.4 kg-N.ha^{-1}.yr^{-1} between 1993 and 2008, one of the lowest observed in the French network. Thus the regional context of atmospheric nitrogen pollution suggests a rather low background level of deposition. However, this does not preclude locally high levels. Although emission of other pollutants, particularly sulphur dioxide, have decreased in Europe allowing recolonization by lichens (van Herk *et al.* 2002, Moning *et al.* 2009) or increase in basiphilous species (Hülber *et al.* 2008), N deposition in the Alps forests is still exceeding the estimated critical load (Rogora *et al.* 2006). Indeed, vegetation has already showed to be a sensitive bioindicator of increasing soil nitrogen availability in lowlands temperate forests close to emission sources (Becker *et al.* 1992, Thimonier *et al.* 1992, Thimonier *et al.* 1994, Diekmann & Dupré 1997, Brunet *et al.* 1998, Dupouey *et al.* 1999, Lameire *et al.* 2000, Gilliam 2006, Bernhardt-Romermann *et al.* 2007, Römermann *et al.* 2008), but also in presumably less impacted areas such as mountain forests (Dupouey *et al.* 1998, Økland *et al.* 2004, Schwabe *et al.* 2007, Hülber *et al.* 2008).

A strong industrial activity (aluminium industry) had occurred in the valley between the beginning of the 19th century and the end of the seventies, generating mainly fluorine pollution, which mostly caused leave necrosis (Fournier 1985) leading to decrease in forests yield (Fournier 1985, Garrec & Audigier 2007). This pollution has considerably diminished since the end of the seventies, leading to forest regeneration. This event has been recorded in fluorine content of lichens (Belandria *et al.* 1986). Nevertheless, recovering of the vegetation after this kind of pollution was not detected in our study since no tools were available for such detection.

As regard pH indicator value, no significant global trend over all plots was observed. But, when analysed separately between calcareous and non-calcareous bedrocks, it showed opposite shifts on each soil type between the two inventories, with vegetation indicating a very significant acidification on calcareous soils and basification on non-calcareous soils. One of the causes for this differential shift in pH indicator values between types of soils could be the strong link existing between the R indicator value and nitrogen availability. In our study, we observed the relationship between N and R indicators was not linear, with highest values of N found for intermediate values of R, a positive relationship on non-calcareous soils, and negative relationship on calcareous soils. Thimonier (1994) and Andrianarisoa *et al.* (2009), observed the same relationship between the N indicator value and direct soil pH measurements. Thus, R shifts could be explained by the increase in soil nitrogen level. Indeed, the intensity of the shift in R values decreased strongly when N values were taken into account in the explanatory model of R variations.

Decrease in sulphur dioxide during the last decades of the XXth century could also partly explain pH increase indicated by vegetation on non-calcareous soils.

Changes in soil structure (soil dispersion coefficient) and humus type were in agreement with variations of N and R coefficients, and did not brought any new information.

3. Forest development and structure

The decrease in light coefficient (L), especially on calcareous soils, could be the result of a closure of forest stands, as observed in the previous chapter. This effect was weak. Confrontation with stand characteristics (mean tree cover, mean number of stem per ha and mean basal area) confirmed a slight closure and maturation, but accompagnied by an increase in stand age. However, age was only recorded in even aged forests. In his publication of 1966, Bartoli mentioned the previous centennial lowering of the treeline and openings in the forest belt caused by human activities, including forest over-exploitation, pasturing and mowing. He already noted forest recolonization due to regression of such activities, especially mowing. Hence, decrease in anthropogenic pressure had perhaps occurred early enough to be only weakly visible in our study. However, S. Chauchard (pers. comm.) noted that some fir recruitments in upper Maurienne valley occurred later, *i.e.* between 1955 and 1990.

4. Sampling bias

Species number per plot had increased between the two inventories from 26.1 to 36.9 on average, as observed in the study presented in the previous chapter and in many other resampling studies. Indeed, the observation of an increase in species richness per plot is so common in resampling exercises that it is most probably, in our opinion, an effect of observer bias. The main bias is probably an increase in exhaustiveness of observations along successive inventories. While the objective of the first inventory in the Maurienne valley was to analyse spatial variations of vegetation and establish a site typology, a task which does not require a high exhaustiveness of vegetation censuses, we went back to study temporal changes in vegetation, with probably a greater concern for exhaustiveness. We were always two observers working together, whereas Bartoli probably worked sometimes alone. Minimal area is too fuzzy a concept to avoid bias in its operational delineation in the field.

It is unlikely that this bias could have played a role in our results. The main reason is that we worked with integrated properties of plant communities. For plant species richness and census exhautiveness to play a role on mean indicator values of plots would require that the species overlooked at the first inventory had indicator values systematically biased toward higher or lower values, which is very unlikely.

E. CONCLUSION

Understorey vegetation of Maurienne valley, in the inner French Alps, has shown two strong responses to environmental changes in the second part of the twentieth century. The first one is a response to climate change, expressed by a shift in plant communities toward more thermophilous species assemblages and by a retreat of vegetation characteristic of the continental climate occurring in the inner-alpine Maurienne valley. The second one, independent from the first, suggests a strong eutrophication induced by nitrogen atmospheric deposit, perhaps in relation with the large increase in road traffic increase which occurred in the valley. The clear bias observed in species number per plot should not have influenced our results.

F. REFERENCES

Andrianarisoa KS, Zeller B, Dupouey J, Dambrine E (2009) Comparing indicators of N status of 50 beech stands (*Fagus sylvatica* L.) in northeastern France. *Forest Ecology and Management*, **257**, 2241–2253.

Bartoli C (1966) *Etudes écologiques sur les associations forestières de la Haute-Maurienne*. .

Bassuel S (1976) *Etude écologique de la pertie septentrionale de la chaîne de Belledone*. Unpublished PhD thesis, Université Scientifique et Médicale de Grenoble, 66.

Becker M, Bonneau M, Tacon FL (1992) Long-term vegetation changes in *Abies alba* forest: natural development compared with response to fertilisation. *Journal of Vegetation Science*, **3**, 467-474.

Belandria G, Asta J, Garrec JP (1986) Diminutions of fluorine contents in lichens due to a regression of pollution in an alpine valley (Maurienne, Savoie, France) from 1975 to 1985. *Revue d'Ecologie Alpine*, **1**, 45-58.

Bernhardt-Romermann M, Kudernatsch T, Pfadenhauer J, Kirchner M, Jakobi G, Fischer A (2007) Long-term effects of nitrogen deposition on vegetation in a deciduous forest near Munich, Germany. *Applied Vegetation Science*, **10**, 399-406.

Brunet J, Diekmann M, Falkengren-Grerup U (1998) Effects of nitrogen deposition on field layer vegetation in south Swedish oak forests. *Environmental Pollution*, **102**, 35-40.

Deletraz G (2002) *Géographie des risques environnementaux lies aux transports routiers en montagne; Incidences des émissions d'oxydes d'azote en vallées d'Aspe et de Biriatou (Pyrénées)*. Unpublished PhD thesis, Université de Pau et des Pays de l'Adour.

Diekmann M, Dupré C (1997) Acidification and eutrophication of deciduous forests in northwestern Germany demonstrated by indicator species analysis. *Journal of Vegetation Science*, **8**, 855-864.

Dupouey J, Becker M, Bert D, Cadel G, Lefèvre Y, Picard J, Thimonier A (1998) Évolution récente des sols, de la végétation et de la productivité des forêts de montagne françaises. *Écologie*, **29**, 341-349.

Dupouey J, Thimonier A, Lebourgeois F, Becker M, Picard J, Timbal J (1999) Changements de la végétation dans les forêts du Nord-Est de la France entre 1970 et 1990. *Revue Forestiere Francaise*, **50**, 219-230.

Ellenberg H (1974) *Zeigerwerte der Gefäßpflanzen Mitteleuropas*. Erich Goltze KG, Göttingen.

Fournier J (1985) *Contribution à l'étude des Alpes intermédiaires françaises: la Moyenne-Maurienne*. Unpublished PhD thesis, Université Scientifique et Médicale de Grenoble, 88.

Galloway JN, Townsend AR, Erisman JW, Bekunda M, Cai Z, Freney JR, Martinelli LA, Seitzinger SP *et al.* (2008) Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions. *Science*, **320**, 889-892.

Garrec JP, Audigier C (2007) The relationship between fluoride content of needles and decrease in yield in conifer forests subject to fluorine pollution. *European Journal of Forest Pathology*, **10**, 432-438.

Gilliam FS (2006) Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *Journal of Ecology*, **94**, 1176-1191.

Grabherr G, Gottfried M, Pauli H (2000) GLORIA: A Global Observation Research Initiative in Alpine Environments. *Mountain Research and Development*, **20**, 190-191.

Hülber K, Dirnböck T, Kleinbauer I, Willner W, Dullinger S, Karrer G, Mirtl M (2008) Long-term impacts of nitrogen and sulphur deposition on forest floor vegetation in the Northern limestone Alps, Austria. *Applied Vegetation Science*, **11**, 395-404.

Jackson ST, Overpeck JT (2000) Responses of plant populations and communities to environmental changes of the Late Quaternary. *Paleobiology*, **26**, 194-220.

Laffray X (2008) *Pollution atmosphérique dans la vallée de l'Arc (Maurienne, Savoie); Nouvelles approches en biosurveillance végétale*. Unpublished PhD thesis, Université Henri Poincaré, Nancy.

Lameire S, Hermy M, Honnay O (2000) Two decades of change in the ground vegetation of a mixed deciduous forest in an agricultural landscape. *Journal of Vegetation Science*, **11**, 695-704.

Landolt E (1977) *Ökologische Zeigerwerte zur Schweizer Flora*. Stiftung Rübel, Zürich.

Moning C, Werth S, Dziock F, Bassler C, Bradtka J, Hothorn T, Muller J (2009) Lichen diversity in temperate montane forests is influenced by forest structure more than climate. *Forest Ecology and Management*, **258**, 745-751.

Økland T, Bakkestuen V, Økland RH, Eilertsen O (2004) Changes in forest understorey vegetation in Norway related to long-term soil acidification and climate change. *Journal of Vegetation Science*, **15**, 437-448.

Ozenda P (1985) *La végétation de la chaîne alpine dans l'espace montagnard européen*. Masson, Paris.

Ozenda P, Borel J (1995) Possible responses of mountain vegetation to a global climatic change: The case of the Western Alps. In: *Potential ecological impacts of climate change in the Alps and Fennoscandian mountains* (eds Guisan A, Holten JI, Spichiger R, Tessier L), pp. 137-144. Conservatoire et Jardin Botaniques de Genève.

Paul E (2000) *Pollution azotée et circulation automobile dans les vallées de la Maurienne et de Chamonix*. Unpublished PhD thesis, Université de Grenoble 1, Saint-Martin-d'Hères, FRANCE, 193 p.

Rogora M, Mosello R, Arisci S, Brizzio M, Barbieri A, Balestrini R, Waldner P, Schmitt M *et al.* (2006) An overview of atmospheric deposition chemistry over the Alps: Present status and long-term trends. *Hydrobiologia*, **562**, 17-40.

Römermann C, Tackenberg O, Jackel AK, Poschlod P (2008) Eutrophication and fragmentation are related to species ' rate of decline but not to species rarity: results from a functional approach. *Biodiversity and Conservation*, **17**, 591-604.

Schwabe A, Kratochwil A, Pignatti S (2007) Plant indicator values of a high-phytodiversity country (Italy) and their evidence, exemplified for model areas with climatic gradients in the southern inner Alps. *Flora*, **202**, 339-349.

Thimonier A, Dupouey J, Timbal J (1992) Floristic changes in the herb-layer vegetation of a deciduous forest in the Lorraine plain under the influence of atmospheric deposition. *Forest Ecology and Managment*, **55**, 149-167.

Thimonier A. (1994) Changements de la végétation et des sols en forêt tempérée européenne au cours de la période 1970-1990 Rôle possible des apports atmosphériques. Université Paris XI Orsay en Sciences de la Vie.

Thimonier A, Dupouey J, Bost F, Becker M (1994) Simultaneous eutrophication and acidification of a forest ecosystem in northeast France. *New Phytologist*, **126**, 533-539.

Tutin TG, Heywood VH, Burges NA, Valentine DH, Moore DM (1968-1993) *Flora Europaea, 5 vol.*. Cambridge University Press.

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG (1997) Human alteration of the global nitrogen cycle: Sources and consequences. *Ecological Applications*, **7**, 737-750.

van Herk C, Aptroot A, van Dobben H (2002) Long-term monitoring in the Netherlands suggests that lichens respond to global warming. *Lichenologist*, **34**, 141-154.

G. ANNEX OF THE CHAPTER THREE

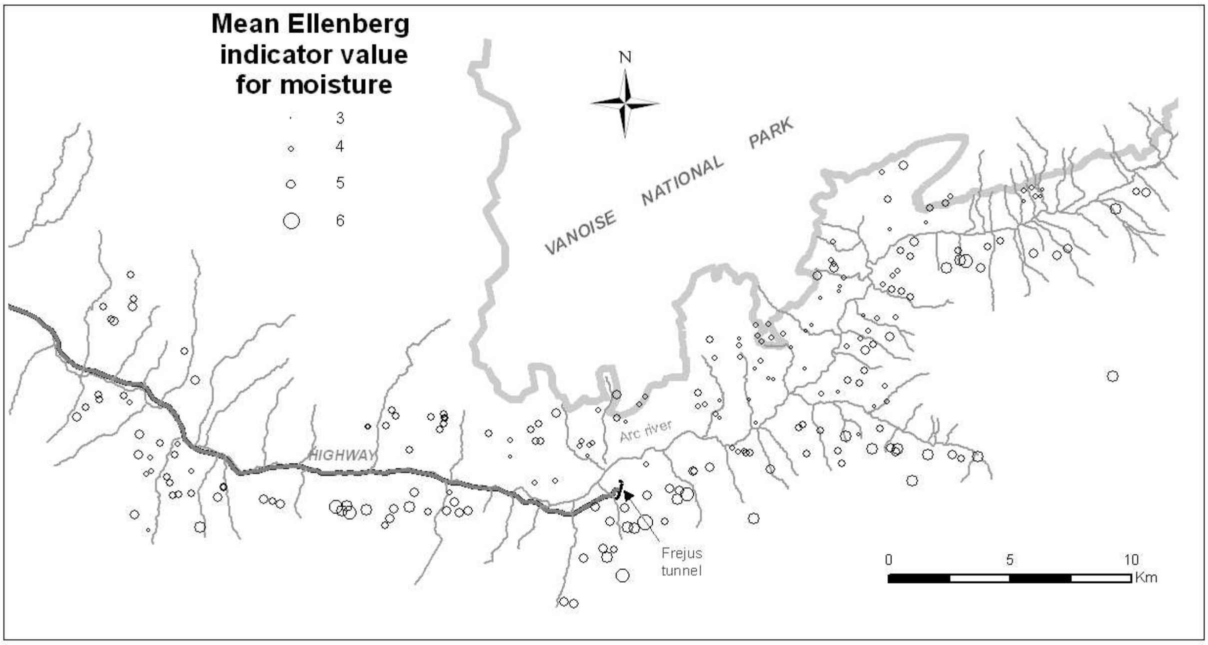


Figure III-A1: Map of mean Ellenberg indicator value per plot for moisture.

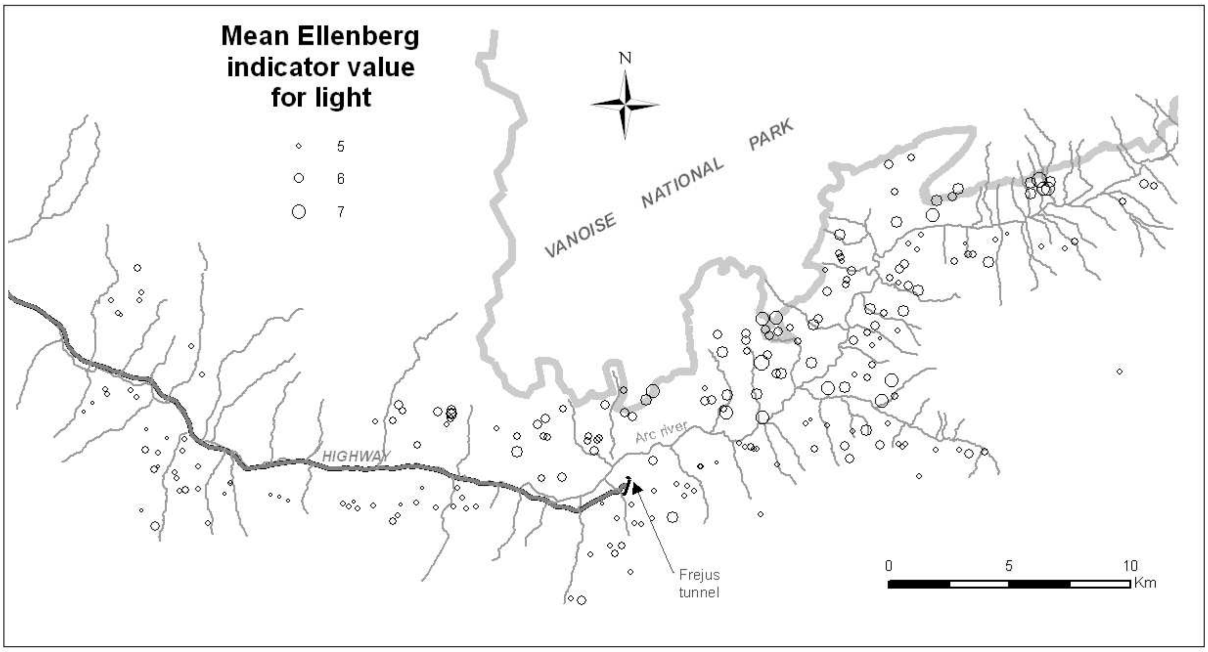


Figure III-A2: Map of mean Ellenberg indicator value per plot for light.

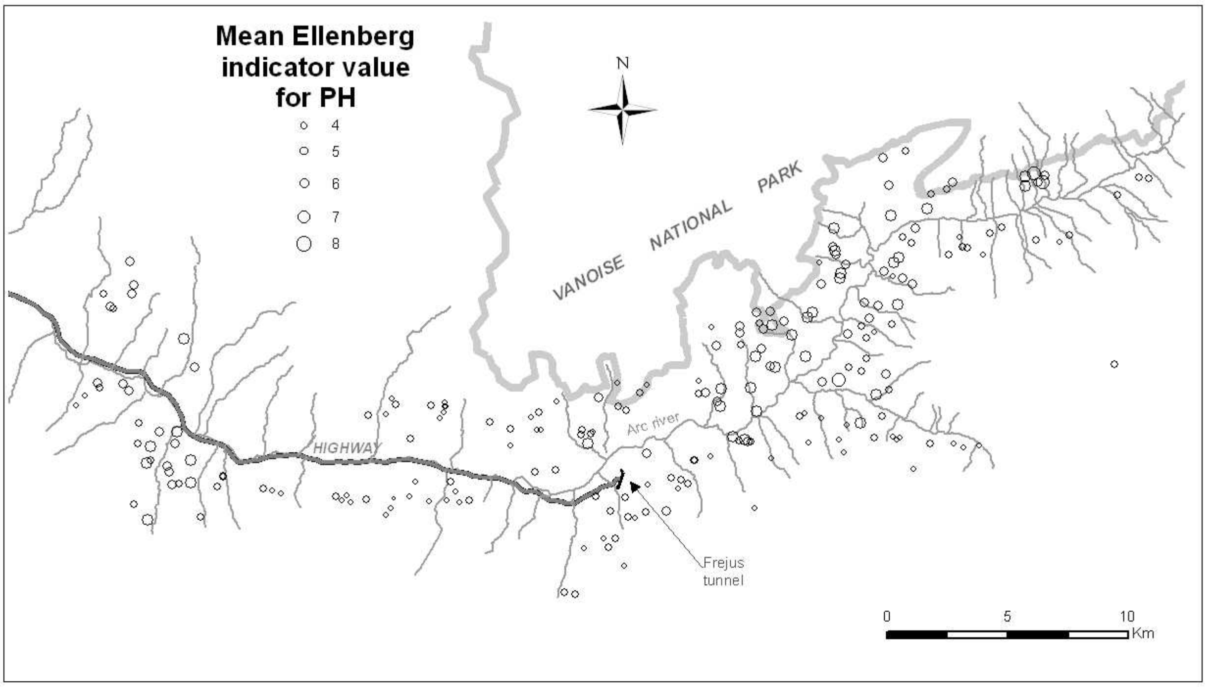


Figure III-A3: Map of mean Ellenberg indicator value per plot for reaction (pH).

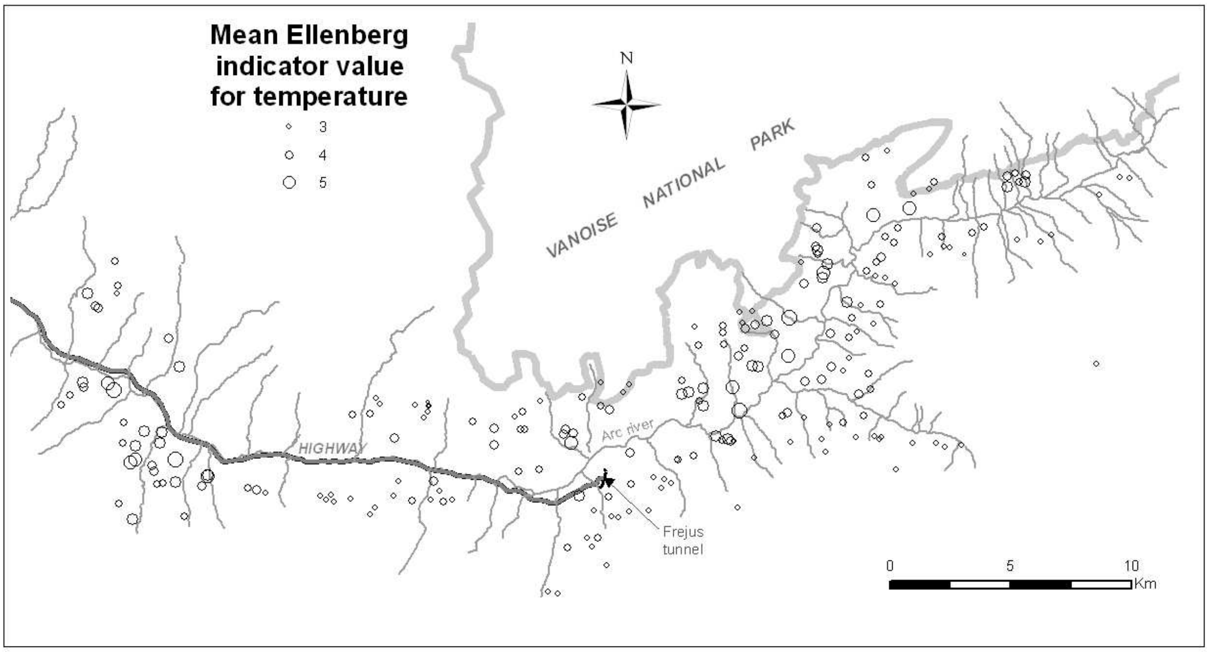


Figure III-A4: Map of mean Ellenberg indicator value per plot for temperature.

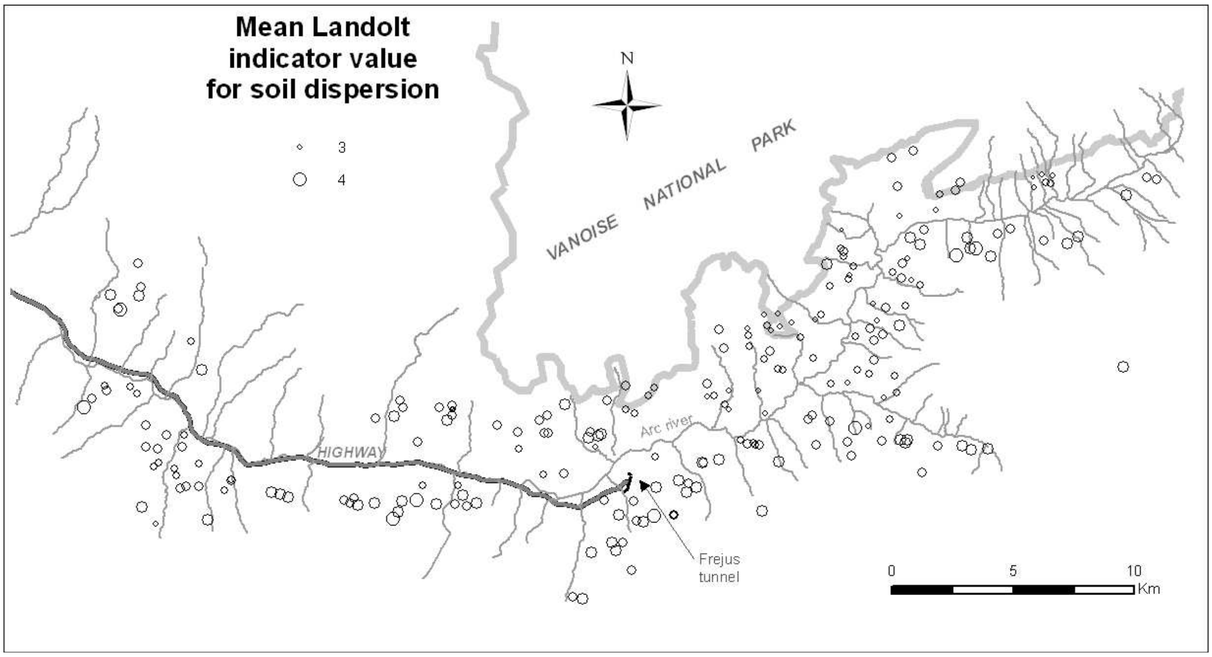


Figure III-A5: Map of mean Landolt indicator value per plot for soil dispersion.

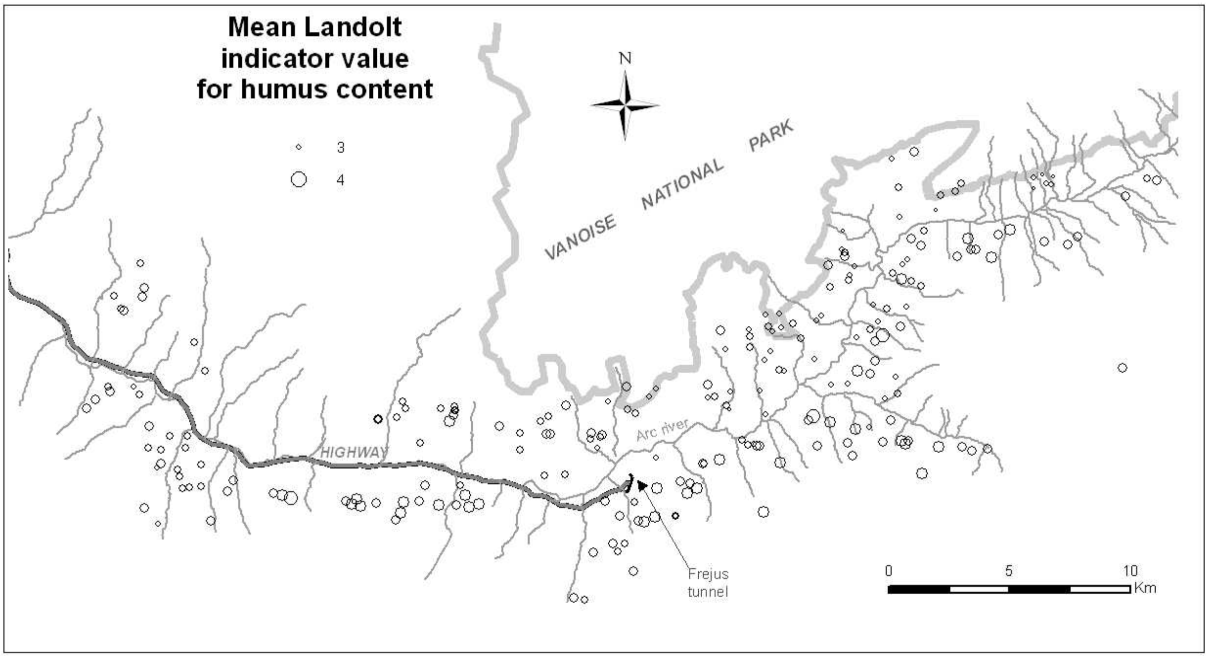


Figure III-A6: Map of mean Landolt indicator value per plot for humus content.

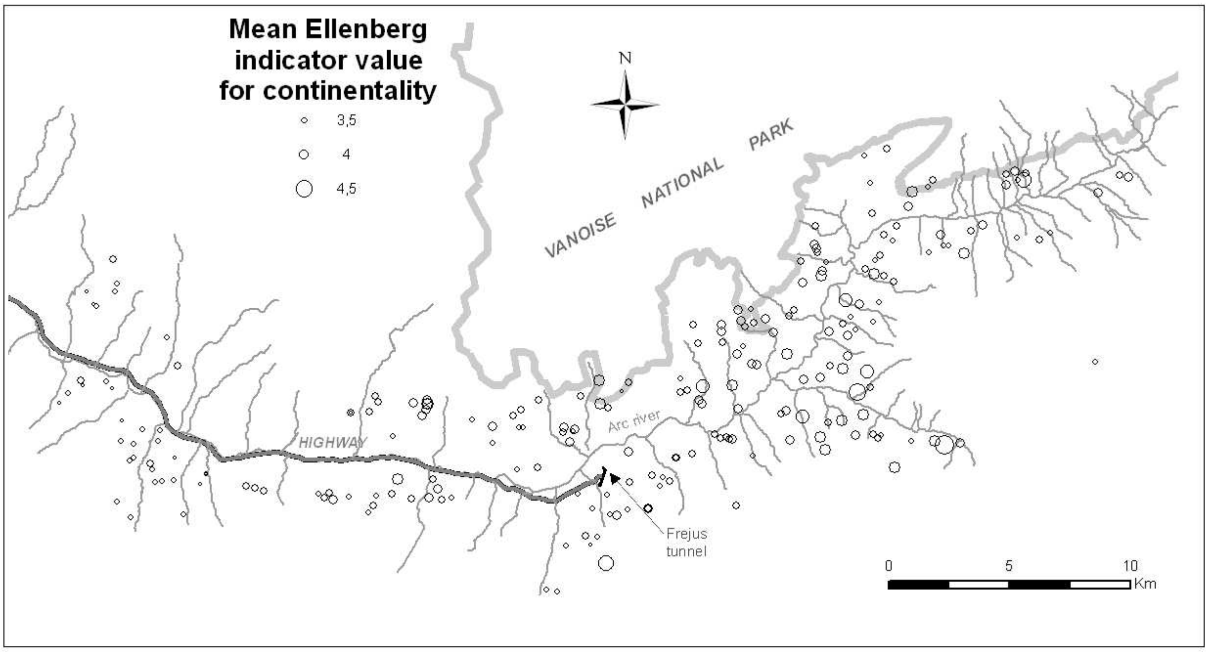


Figure III-A7: Map of mean Ellenberg indicator value per plot for continentality.

IV. PLANT SPECIES' RANGE SHIFTS IN MOUNTAINOUS AREAS – ALL UPHILL FROM HERE?

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Important note: This chapter compiles several studies focusing on shift of species at their upper and lower limit. Only the study of species response at their lower limits is my own work as a part of my PhD.

A. ABSTRACT

Species from many different habitats are responding to recent climate change. Mountainous areas are of particular interest as they provide pronounced gradients and have experienced above-average temperature increases. Data from the beginning of the 20th century of both the upper and lower range limits of plants of the European Alps were updated a century later and analyzed in order to identify common trends and deviating patterns of shifts at opposing ends of species' ranges. At the upper limit, the vast majority of species experienced a consistent upward shift, in some cases exceeding 100 elevational meters, and almost half of the investigated species shifted upwards to a present altitude which is higher than any reported occurrence in the region one century ago. The response at the lower range limit was more heterogeneous and suggests species-specific differences in responsiveness and response patterns. With this approach of the combined analysis of upper and lower range limits along elevational gradients, it is possible to identify candidate species that might not keep pace with climate change, and thus, might face an increased risk of extinction with continued global warming.

Key words: alpine, range margin, monitoring, ecology, biogeography, Switzerland

B. INTRODUCTION

Ecological ‘fingerprints’ of climate change (Walther *et al.* 2001; Parmesan and Yohe 2003; Root *et al.* 2003) appear across a wide range of taxonomic groups and geographic regions (Walther *et al.* 2002; Rosenzweig *et al.* 2007) and are being identified with increasing frequency (Walther *et al.* 2005; Parmesan 2006). In this context, mountain ranges are of particular interest. Mountainous regions tend to warm more rapidly (Rebetez and Reinhard 2008) and the projected rate of warming in mountain systems is expected to be up to three times higher than the global average rate of warming recorded during the 20th century (Nogues-Bravo *et al.* 2007). Furthermore, mountain ecosystems sustain centers of endemism for biodiversity and provide important ecosystem services for erosion control and water supply beyond their geographical limits including also the surrounding lowlands (Körner 2003; Becker *et al.* 2007).

The European Alps provide a long history of ecological data collection. Historical inventories of the Alpine flora proved to be a useful reference for detecting effects of climate change of the recent past and present (Hofer 1992; Grabherr *et al.* 1994, 2001; Camenisch 2002; Walther *et al.* 2005; Holzinger *et al.* 2008; Parolo and Rossi 2008; Vittoz *et al.* 2008). The comparison of recent and past inventories showed striking increases in species richness on mountain tops, and also suggested an increase of the floristic similarity of the summits (Jurasinski and Kreyling 2007). Hence, there is evidence for a widespread upward movement of species along elevational gradients (Krajick 2004), but are there also species with opposing trends, *e.g.* resisting this widespread behavior and remaining in place or even moving downwards?

We here compile and synthesize data of plant distributions on 25 summits of the Alps, which were re-inventoried recently. We compare the altitude of the present occurrences on mountain tops with information of their upper distributional limits at the beginning of the 20th century, to quantify their responsiveness to environmental change. Whereas these shifts reflect changes at the upper limit of plant elevational distributions (Walther *et al.* 2005), we also analyze data of the same region for potential shifts at the lower-elevational range limit. Thus, we are able to compare findings from the upper range margins with those from the lower range margins of species in the same area, in order to find common trends and deviating patterns of shifts at opposite ends of species’ elevational distributions.

C. MATERIAL & METHODS

Rübel (1912) and Braun (1913) published data on the distribution of the alpine and nival flora in the region of Engadine valley in south-eastern Switzerland. These historical sources provide information on both the species’ upper range limits and localities of lowest detected occurrences in the past. These publications also served as historical source and baseline data for comparison with recent re-inventories of high-mountain summit vegetation (Grabherr *et al.* 2001; Camenisch 2002; Walther *et al.* 2005). We here combine and analyze available data from the literature (Grabherr *et al.* 2001; Camenisch 2002), our own published data (Walther *et al.* 2005), and new data from Piz Languard regarding the upper limit of species distribution on mountain summits in the Swiss Alps. Furthermore, we gathered new data for the species‘ lower elevational limit in the same region in summer 2006, resurveying the surrounding area of the localities where the species’ lowermost occurrences were described in the historical literature (Rübel 1912). This allows us to study shifts at both the upper and lower ends of species‘ distributions that have occurred since the beginning of the 20th century along elevational gradients. The altitudes of recent occurrences of the species were measured using barometric altimeters (Thommen pocket altimeter, Revue Thommen

AG, Switzerland, and Suunto Vector altimeter, Suunto Oy, Finland), which were calibrated against the relevant topographic map during field work. Given the precision of the altimeter and considering the discrepancy of a few meters in summit heights provided in the maps at the beginning and the end of the 20th century, differences between historic and present altitudes of the same species of < 15 meters were considered as to be within the range of uncertainty. We tested mean shifts for statistical significance by one sample t-tests using SAS for Windows 9.1. The nomenclature for species' names in all records was standardized and updated following Aeschimann *et al.* (2004).

1. Shifts at the upper range margin

Usually, the summit area for investigation was defined as the uppermost 10 elevational meters (Rübel 1912), and the same delimitation was applied for all the recent re-inventory data. On Piz Languard (3262 m at the summit), the uppermost 30 meters were investigated, in agreement with the historical survey. In total, we compiled available data of the floras of 25 summits with altitudes between 2836 m and 3418 m a.s.l., including 17 siliceous peaks and 8 calcareous peaks. Differences in the number of summits colonized by each species in the past compared to the present were calculated in order to identify changes in species' frequency on summits. Furthermore, for all species recorded on a summit in a recent inventory, we searched the historical literature for information on the historic highest detected occurrences of the same species in order to quantify range shifts that occurred in the course of the last century. These range shifts were analyzed at both the local scale, i.e. the difference between present and past species‘ upper limit on the same mountain (provided that information on the highest detected occurrence of the same species on the slope of the particular mountain was available in the historical literature), and the regional scale, i.e. the difference between the present and past uppermost limit of the same species on any mountain in the entire region (i.e. the Engadine).

The aforementioned analyses were restricted for methodological reasons to species that succeeded in reaching the defined summit area (usually the 10 uppermost elevational meters of each summit) in any of the recent inventories, but for Piz Languard (3262 m a.s.l.), additional information is available for the uppermost occurrence of all species detected between 3000 m a.s.l. and the summit (Braun-Blanquet 1955). Hence, we updated this data in summer 2005 by screening the area from 3000 m a.s.l. to the summit, and recording the uppermost present occurrence of each species found in the resurvey.

2. Shifts at the lower range margin

For the lower range limits, information on the locality and altitude was taken from Rübel (1912) for a set of 57 species in the study region. The species were selected based on the precision of the records from the historical data set and the phenological status during the period of field work (if possible, while in flower). The surrounding area of the localities mentioned for lowest occurrences of these species in the past (Rübel 1912) were resurveyed at elevations of 1715-2700 m in summer 2006. As one species could be present in several localities within the investigated region, and several species could be present in the same locality, 81 species-locality pairs resulted. As we did for the upper limit, we calculated species shifts separately for the local and regional scales. On the local scale, they resulted from differences between present and past lower limits for species found at the same locality (*e.g.* on the slope of the same mountain or in the same valley) as reported in the past. When a species was not found at the same locality as reported in the historical literature, but elsewhere in the region, the lowest site was used to calculate species shifts at the regional scale, i.e., the difference between present and past lowest occurrence of a species in the entire region.

Table IV-1. List of species with new uppermost elevational records [m a.s.l.] in descending order according to the elevational shift for the region.

Species name	Highest record in the past (Rübel 1912 / Braun 1913) in the region	Highest record in the past (Rübel 1912 / Braun 1913) on the same mountain	Altitude of new highest record	Locality	Upward shift at the same mountain	Elevational difference for the region
Species with new record on the same mountain as in the past:						
Botrychium lunaria	3000	3000	3215	Piz Languard	215	215
Cerastium latifolium	3130	3130	3268	Piz Üertsch	138	138
Agrostis rupestris	3260	3260	3350	Piz Julier	90	90
Luzula spicata	3300	3300	3382	Piz Linard	82	82
Juniperus communis	3180	3180	3245	Piz Languard	65	65
Juncus jacquinii	3180	3180	3215	Piz Languard	35	35
Juncus trifidus	3180	3180	3210	Piz Languard	30	30
Pritzelago alpina	3240	3240	3268	Piz Üertsch	28	28
Saxifraga exarata	3380	3380	3407	Piz Kesch	27	27
Linaria alpina	3200	3200	3225	Piz Languard	25	25
Species with new record on a different mountain than reported from the past:						
Avenella flexuosa	2600		3043	Piz Forun		443
Hieracium villosum	2650	2600	2965	Piz Alv	365	315
Adenostyles leucophylla	2940	2700	3230	Piz Languard	530	290
Arnica montana	2800	2500	3065	Piz Languard	565	265
Agrostis alpina	3010	3000	3245	Piz Languard	245	235
Trollius europaeus	2600		2820	Piz Murtèr		220
Carduus defloratus	2600		2814	Piz Murtèr		214
Artemisia umbelliformis	3020	2700	3230	Piz Languard	530	210
Leontodon hispidus	2620		2827	Piz Murtèr		207
Potentilla frigida	3200	3000	3405	Piz Kesch	405	205
Gnaphalium hoppeanum	2762	2650	2965**	Piz Alv	315	203
Artemisia genipi	3208	3000	3407	Piz Kesch	407	199
Anthoxanthum alpinum	3045	3000	3235	Piz Languard	235	190
Draba dubia	3206		3392	Piz Kesch		186
Lloydia serotina	3050	2850	3230	Piz Languard	380	180
Solidago virgaurea	2790	2650	2965**	Piz Alv	315	175
Crepis kerneri	2650		2820	Piz Murtèr		170
Selaginella selaginoides	2650		2810	Piz Murtèr		160
Sedum atratum	3000		3153	Piz Tavrü		153
Arabis bellidifolia	3009*		3158	Piz Tavrü		149
Nardus stricta	2900		3041	Piz Forun		141
Antennaria dioica	3020	2590	3150	Piz Languard	560	130
Phyteuma hemisphaericum	3098*	3000	3215	Piz Languard	215	117
Helianthemum alpestre	2850	2600	2965**	Piz Alv	365	115
Cardamine resedifolia	3280	3060	3395	Piz Linard	335	115
Geum montanum	3120	3000	3235	Piz Languard	235	115
Cirsium spinosissimum	2985	2980	3100	Piz Languard	120	115
Poa alpina	3300		3405	Piz Kesch		105
Taraxacum alpinum	3150	3030	3250	Piz Languard	220	100
Trisetum distichophyllum	3072*		3156	Piz Tavrü		84
Saxifraga caesia	3010*		3087	Piz Foraz		77
Elyna myosuroides	3010	2980	3085	Piz Stretta	105	75
Minuartia verna	3200		3268	Piz Uertsch		68
Moehringia ciliata	3100		3158	Piz Tavrü		58
Campanula cochleariifolia	*3020*		*3069*	Piz Foraz		*49*
Achillea atrata	2980		3025	Piz Laschadurella		45
Arabis caerulea	3130		3159	Piz Tavrü		29
Cerastium cerastoides	3000	2600	3025	Piz Languard	425	25
Salix herbacea	3230	2980	3255	Piz Languard	275	25

* highest occurrence in the past according to the information provided in Grabherr *et al.* (2001)

** no precise altitude within investigated summit area is available, therefore the lower limit of the investigated area is used for the calculation of the upward shift.

3. Comparing range shifts at the lower and upper limit of the same species

Despite the fact that the re-inventories on upper and lower range limits were carried out independently, a set of 14 species resulted with information on both range margins at the local scale, and for 28 species on the coarser regional scale, which then could be compared in terms of common trends and deviating patterns of shifts at opposing ends of elevational species' ranges.

D. RESULTS

1. Shifts at the upper range margins of species reaching the summit areas

Across all the investigated summits, there was a strong trend towards an increase in species richness per summit (Fig. 1), but also a significant increase in the mean number of summits colonized by each species (+ 1.75, SD = 1.66, $p < 0.0001$, n = 125 species) in the course of the 20th century. Furthermore, several species with historical information on their uppermost occurrence on the same mountain, but at that time not occurring on the summit, succeeded in reaching the top and underline the upward trend of upper range margins (Fig. 2); among them, 33 species were recorded for the first time on any of the investigated summit areas.

For the species with range shifts > 15 m in either direction, there is a significant mean upward shift of +145.3 m (SD = 156.4 m, n = 172 species) for the species on all summits; when excluding Piz Languard from the summit set (due to different delimitation of the summit area, see Material & Methods): +138.4 m (SD = 120.4 m, n = 119 species), and for Piz Languard only: +161 m (SD = 217.3 m, n = 53 species) (in each case $p<0.0001$). For several species, reaching the top of one of the investigated higher-elevation summits also means a new uppermost elevational record for the entire region (Table 1).

Table IV-2. Species occurring on the same number or fewer summits than in the historical survey (for details see text)

Species name	Number of summits where species was recorded either in the past or present		
	new (recorded only in the present)	stable (recorded in past and present)	missing (recorded only in the past)
fluctuating species:			
Cardamine resedifolia	1	7	1
Cerastium pedunculatum	1		1
Elyna myosuroides	1		1
stable species:			
Androsace alpina		12	
Saxifraga aphylla		6	
Primula hirsuta		4	
Sempervivum montanum		3	
Androsace helvetica		3	
Juncus trifidus		1	
Sesleria caerulea		1	
declining species:			
Luzula alpinopilosa		1	1*
Achillea erba-rotta ssp. *moschata*		2	1+1*
Achillea nana			1*

* missing within the investigated summit area, but recorded on the same mountain below the summit area.

However, not all the species followed this trend towards higher altitudes and increasing numbers of summit colonizations. Three species fluctuated in the number of summits on which they were found, and experienced an equal number of losses and gains (= ‘fluctuating species’ in Table 2); 7 species did not change at all their number of summit occurrences (= ‘stable species’ in Table 2); and finally, there were also 3 species with a declining trend in the number of summits on which they are occurring, relative to the first survey at the beginning of the 20th century (= ‘declining species’ in Table 2).

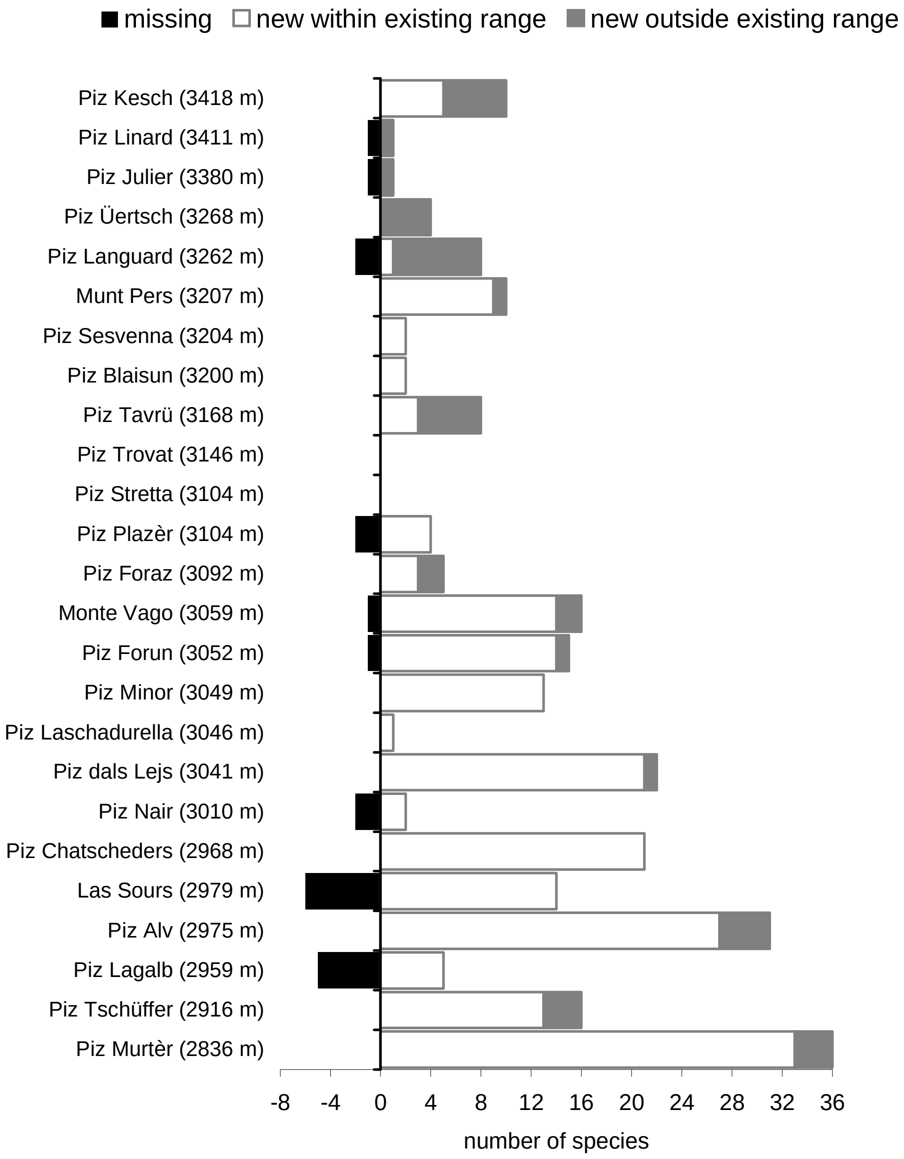

Figure IV-1. Change in species richness of each investigated summit; new species are differentiated between those occurring on summits of lower altitudes than the species’ historical upper limit (i.e. within existing range) and those above the former upper-elevational limit (outside existing range).

2. Shifts of the upper range margins along the upper slopes of Piz Languard (3000 - 3262 m a.s.l.)

Whereas the previous analyses are based on the species which successfully reached the top of the mountains, the more comprehensive historical data set for Piz Languard (3262 m a.s.l.) offers the possibility to analyze all species occurring above an altitude of 3000 m (Fig. 2). On this mountain, 10 species descended slightly (-15 m to -35 m) in the upper part of the investigated range, whereas 3 species descended to considerably lower areas (*Luzula alpinopilosa*: -215 m; *Achillea nana*: -90 m; *Androsace obtusifolia*: -70 m). *Festuca violacea* was recorded in the past above 3000 m, but was not detected in the latest survey. 73 species were observed either at the same altitude or higher than reported in the past. Among them, 27 species were recorded for the first time above 3000 m on this mountain and 18 species at higher altitudes than ever recorded in the past in the entire region.

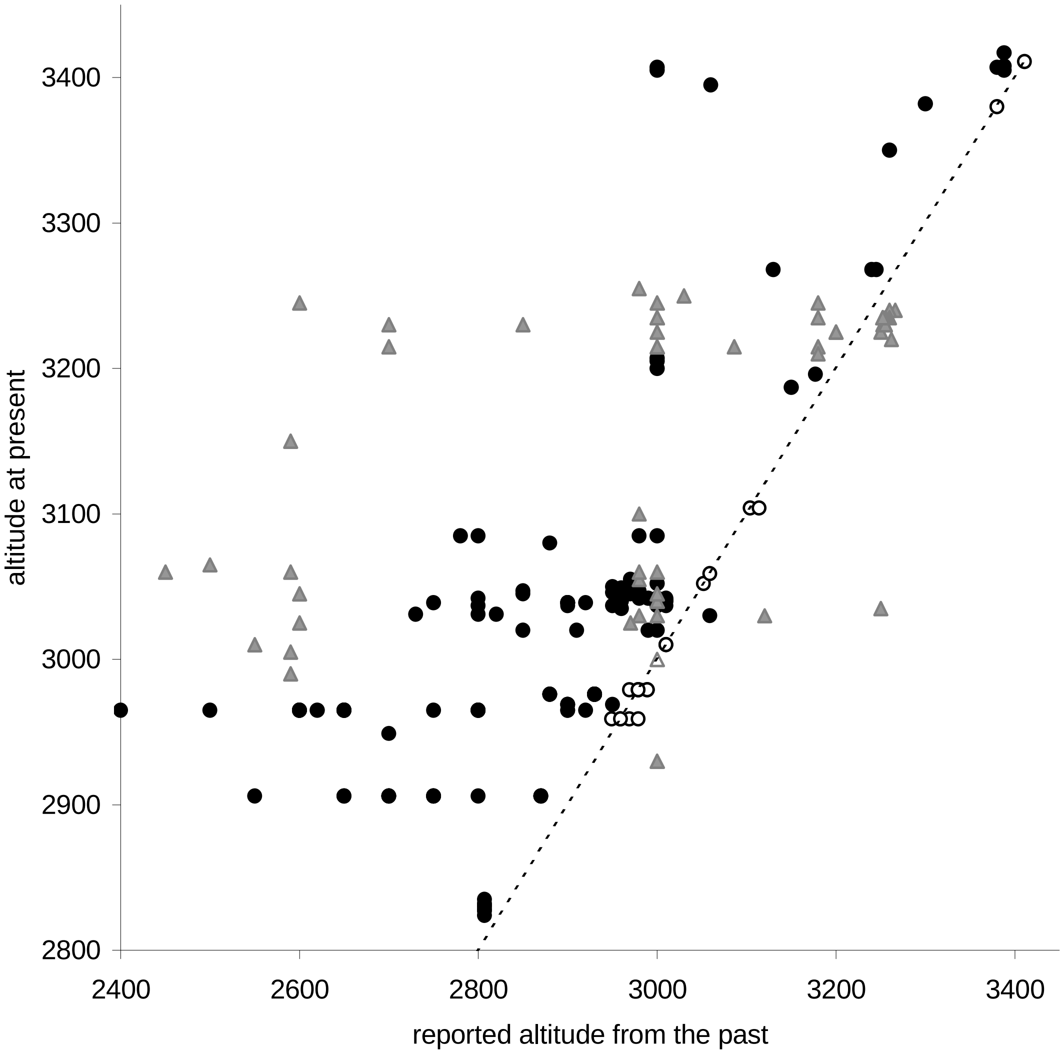

Figure IV-2. Elevational range shifts of the species with information on their historical occurrence at the same mountain (only species with shifts > 15 elevational meters are shown). In general, the investigated summit area at present was delimited to the uppermost 10 meters of elevation, except Piz Languard, where information from 3000 m to the summit (3262 m a.s.l.) was available. Grey symbols show the data from Piz Languard and black symbols from all the other summits excluding Piz Languard, open symbols show the historical altitude of the species that were not found in the investigated area of the same mountain in the resurveys, the broken line indicates the line of equal altitude.

3. Shifts at the lower range margin

At the lower range limit, 35 out of the 57 resurveyed species were found at the same localities but sometimes at different altitudes than reported in the past (Table 3 and Fig. 3) and resulted in 46 species-locality pairs. Overall, there was no significant difference in elevation (mean shift = -2.4 m; SD = 68.6 m; p = 0.82; n = 46 species-locality pairs) for the resurveyed species at their lower-elevation boundary (Fig. 4). However, when splitting the dataset into two groups, species that were found at an altitude lower than 2250 m revealed a positive but non-significant upward trend (mean shift = +14.2 m; SD = 59.4 m, p = 0.17, n = 35 species-locality pairs), while for species with a lower elevational limit at higher (> 2250 m) altitudes, there was a significant, but downward shift (mean shift = -55.0m; SD = 72.2 m, p = 0.03, n = 11 species-locality pairs).

When a species was not found near the same locality but, for example, in a neighboring valley or on the slope of a different mountain than reported in the past, the range shift was interpreted on a regional scale. This approach resulted in data for 45 species and a mean shift on the regional scale that was significantly positive: +55.8 m (SD = 161.0 m, p = 0.0254, n = 45 species).

Table IV-3. Comparison of lowest-elevation occurrences of plant species in recent (2006) and historical (Rübel 1912, Braun 1913) surveys (the same species may show different trends at different localities).

	Same locality (35 species, 46 species-locality pairs)	**Region** (in total: 45 species)
Shift towards lower altitudes	11 species at 12 localities	7 species
Change only within range of uncertainty (+/- 15 m)	20 species at 22 localities	17 species
Shift towards higher altitudes	11 species at 12 localities	21 species

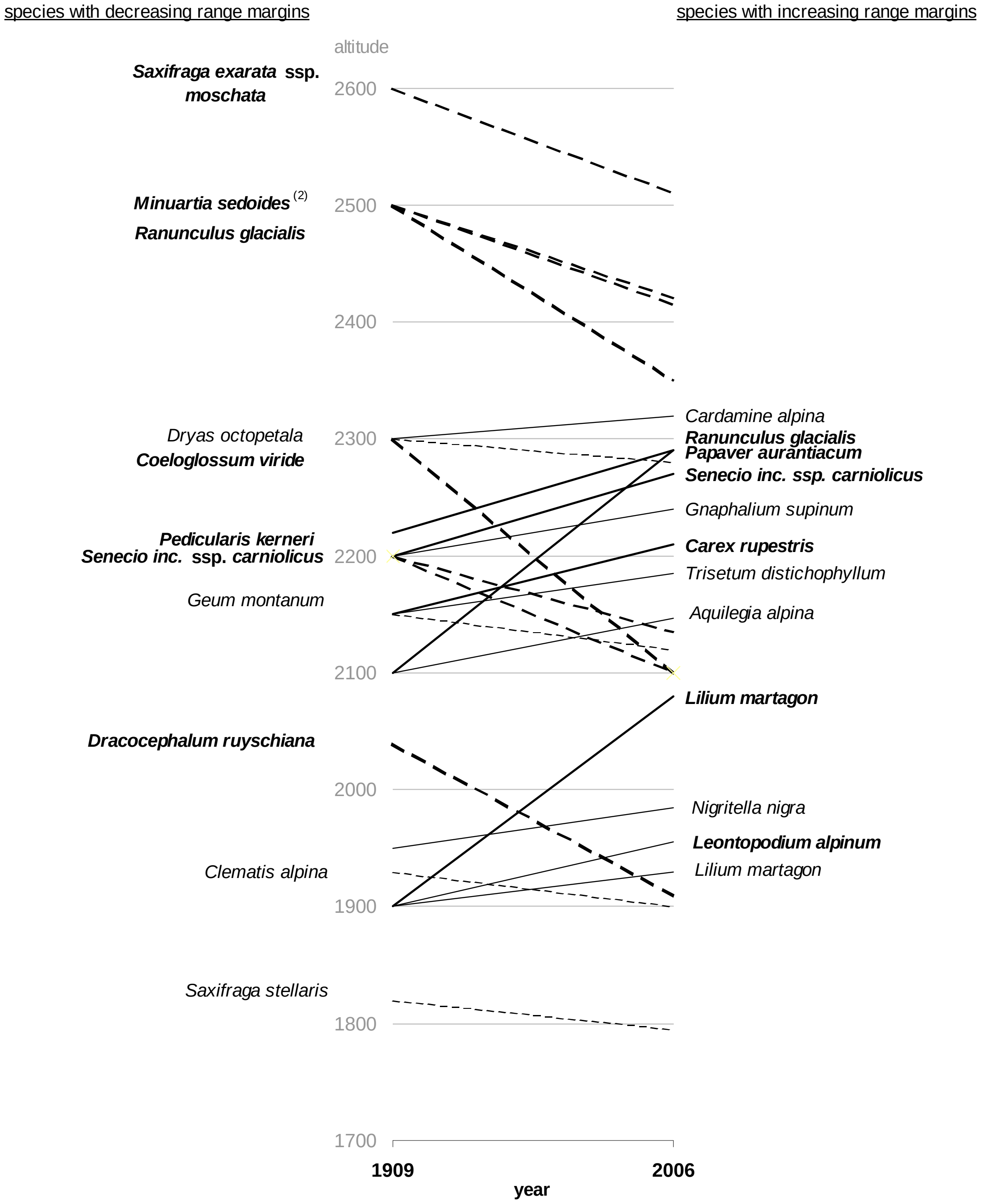

Figure IV-3. Shifts at the lower distribution limit of species found at the same locality as reported in the past (only species with differences > 15 m are shown; dashed lines = decreases in altitude of range margin and solid lines = increases in range margin, bold: species with shifts > 50 m. For *Minuartia sedoides*, information for two localities is available).

Table IV-4. Matrix for the comparison of the directions of range shift at opposite range margins of the same species found at the same localities as reported in the past (for details see text).

		upper range margin	
		upward shift	within range of uncertainty (< 15 m)
lower range margin	upward shift	*Gnaphalium supinum*	*Trisetum distichophyllum*
	within range of uncertainty (< 15 m)	*Geum montanum,* *Gentiana punctata,* *Phyteuma globulariifolium,* *Carex sempervirens,* *Carex firma,* *Juncus trifidus*	*Androsace alpina*
	downward shift	*Senecio incanus* ssp. *carniolicus,* *Ranunculus glacialis,* *Dryas octopetala,* *Pedicularis kerneri*	*Minuartia sedoides*

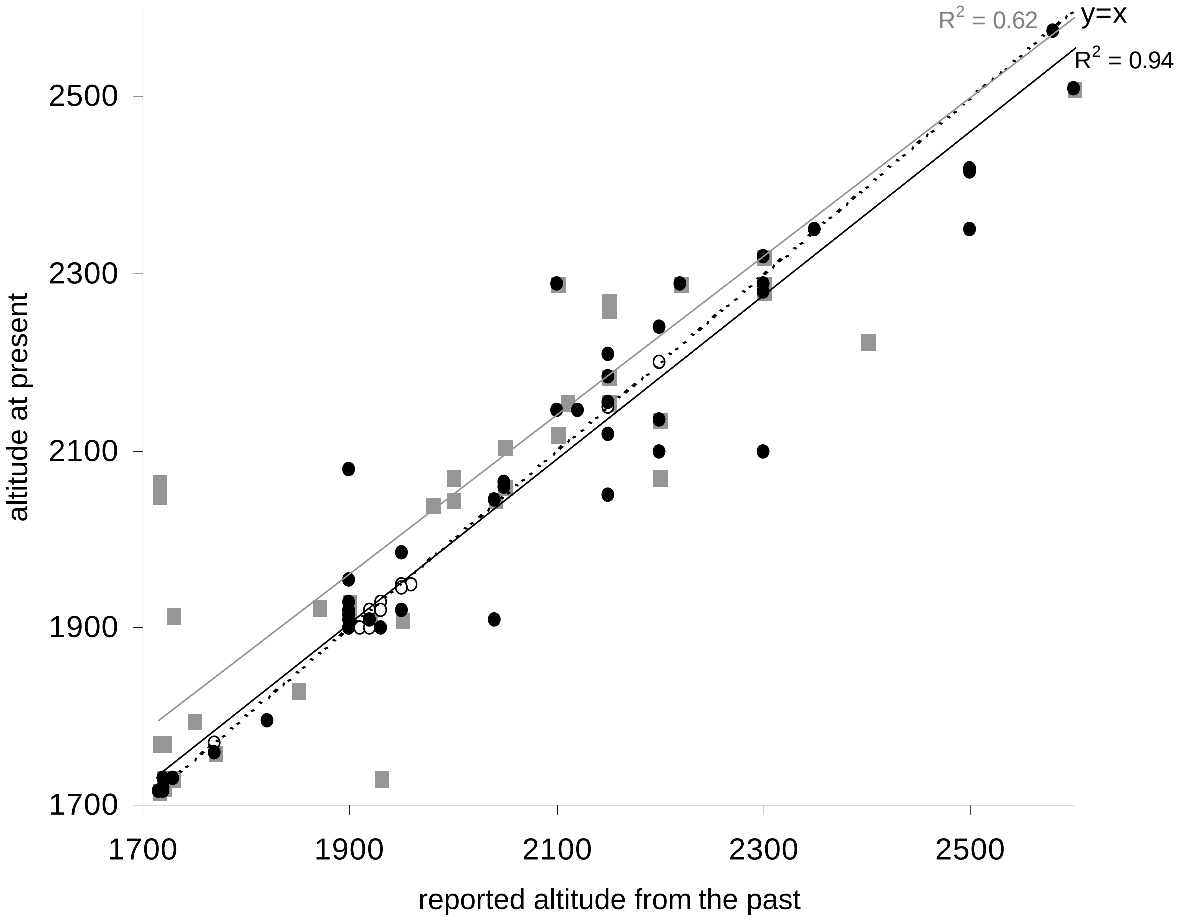

Figure IV-4. Elevational shifts of the species at their lower range margins for species found at the same localities as reported in the past (black symbols and linear trendline) and on the regional scale (grey symbols and linear trendline). Open symbols show the historical altitude of the species that were not found in the resurvey, the broken line indicates the line of equal altitude.

4. Shifts at opposite range margins of the same species

For 14 species, data are available to analyze trends on both upper and lower range margins of the same species at the local scale (Table 4). Again, shifts at the upper range limit showed a more consistent trend (11 species with a marked upward shift, 3 species within the range of uncertainty), whereas at the lower range limit the pattern was more heterogeneous and included all three options (2 upward, 7 no shift, 5 downward).

On the regional scale, the comparison of the direction of range shifts at upper and lower range limits is possible for 28 species. At this coarser resolution, the parallel upward shift of both range margins is more frequent than on the local scale (11 species, 39%), followed by species exhibiting an upward shift of the upper range boundary but with a stable (7 species, 25%) or downward trend (5 species, 18%) at the opposite, lower end of the elevational range. The remaining 5 species showed no shift at the upper limit whereas the lower limit shifted upwards for 3 species (11%), remained stable for 1 species (3.5%) and showed a downward shift for 1 species (3.5%). For the species that showed a downward shift at their upper limit on Piz Languard, no information is available so far for their lower range limit.

E. DISCUSSION

Although the historical data (Rübel 1912; Braun 1913) used in this study were not primarily intended to serve as baseline data for later resurveys, they have already proven to provide valuable information for analyses of floristic changes (Hofer 1992; Grabherr *et al.* 1994; Camenisch 2002; Walther *et al.* 2005; Vittoz *et al.* 2008). As in many other cases (for reviews see *e.g.* Walther *et al.* 2001, 2002; Parmesan and Yohe 2003; Root *et al.* 2003; Parmesan 2006; Rosenzweig *et al.* 2007), we depend upon these detailed historical records or long-term monitoring series, dating as far back as before the increase in global average temperature of the recent past, in order to detect changes due to recent global warming.

For the upper range limit, the upward shift of alpine plant species was not only reflected in the increasing species richness on the summits as reported in previous studies (Hofer 1992; Grabherr *et al.* 1994; Camenisch 2002; Walther *et al.* 2005), but also in the colonization of on average nearly two more summits per species within a century among the investigated species. However, it has been questioned to what degree this floristic enrichment should be interpreted as upward migration due to recent climate change or simply as re-colonization after the end of the Little Ice Age (Kammer *et al.* 2007). Nonetheless, Kammer *et al.* (2007) also considered species that were discovered at elevations higher than their former uppermost occurrences as the first signs of an upward migration due to recent climate change. In this regard, the data set analyzed here identified 10 species that were found on the same mountain at higher altitudes than their highest-elevation record in the past, and another 39 species that reached the peak of a mountain with an altitude that is higher than the uppermost occurrence of the species reported historically for the region. Furthermore, 33 species were recorded for the first time on any summit within the investigated range. Overall, there was a significant mean upward shift of ca. 150 elevational meters (depending on the specific data set used for calculation) of the upper end of species' distribution compared to the occurrences reported one century ago. From this perspective, alpine/nival plants, although considered as slow-growing and facing constraints of sexual reproduction (Krajick 2004; Cannone *et al.* 2007) are responding surprisingly fast to the recently changing environmental conditions.

However, focusing only on species that reach the top does not cover those that do not successfully move upwards until the summit areas. In this regard, the results from Piz Languard, where data are available on a much larger elevational range than just the summit area, provide a more-balanced picture of the situation at the upper range limit. Within this extended dataset, only a few species show a downward shift, while the general upward shift of the species' upper range limit is as strongly pronounced on this mountain as on all the other summits.

Not all species seem equally responsive. From the 125 species analyzed here at their upper range limit, 5 species (*Androsace alpina*, *Saxifraga aphylla*, *Sempervivum montanum*, *Androsace helvetica* and *Sesleria caerulea*) retained stable distributions in terms of both maximum altitude and number of summits they had colonized. *Androsace alpina* is also listed among the species with decreasing species cover between 1994 and 2004 in a recent analysis of permanent plots along an elevational gradient at the Schrankogel (Austria) (Pauli *et al.* 2006). Further candidate species that suggest a response in the downward direction, and thus, contrary to the general trend, include *Luzula alpinopilosa*, found on the same mountains but partly at considerably lower altitude (-215 m on Piz Languard) than in the past, and in particular *Achillea erba-rotta* ssp. *moschata* and *Achillea nana*, which both decreased in the number of summits they occupied as well as their altitude of occurrence on particular mountains.

At the lower-elevation limit, the species differ much more in terms of the direction of range shifts and their responsiveness to climate change than at the upper-elevation boundary. On the coarse, regional scale, there is a trend towards higher altitudes, which is in concert with the observed recent decline of arctic-alpine plants at or near the southern periphery of their continuous geographic range in northwest Montana (Lesica and McCune 2004). Furthermore, the species that were not found in our survey, may have left the investigated range towards even higher altitudes. However, not finding them may also simply be a consequence of the problem of re-spotting a particular species in difficult terrain. In contrast to the well-defined summit area, the localities of the lower range limits were much larger. For this reason, the results from the lower range limit must be interpreted more cautiously, and factors such as different time periods and sampling efforts (cf. Miller-Rushing and Primack 2008) play a more important role. In any case, the positive mean shift of the species' lower occurrences supports the hypothesis of a parallel upward shift of both lower and upper range limits (cf. Hampe and Petit 2005). However, the variability in species' range shifts is revealed when looking at the responses in more detail, i.e. comparing corresponding localities in the past and present, or comparing upper and lower range limits of the same species. This approach suggests highly species-specific behavior depending on the ecophysiology, habitat preferences, and dispersal capacity of the individual species. Almost all combinations of upward, stable and downward shift are represented, except those with downward shifts of the upper limit (cf. Table 4). For the few species that showed this downward movement at their upper limit on Piz Languard, no data are available (so far) for their lower limit, as they were not included in the initial set of species selected for resurveying the lower limit.

In general, the (up to now) less-responsive lower range limit might also be a consequence of lagged impacts of climate change, given the fact that at the lower limit, effects due to climate change are expressed first in the species' demography rather than in their biogeography (Walther *et al.*, in press). Furthermore, both abiotic environmental conditions and biotic interactions may affect alpine plant population dynamics (Klanderud 2005). In this regard, simulations of climatic warming in arctic zones suggested an increase in shrub biomass at the expense of other plant functional types (Epstein *et al.* 2000), a process that might also be expected in the longer term in alpine areas. Hence, with continued global warming, alpine species may face more competition from other plants and exposure to 'new' animal species migrating upwards from lower altitudes (Kullmann 2002, but see Price and Waser 2000), and thus, a diminished available area for alpine species – even species with expanding elevational ranges (cf. also Breshears *et al.* 2008).

Future research should continue searching the limits of the species not detected here and monitoring the candidates identified here as less-responsive species not only at their range limits but also populations at localities within their range in order to verify the trends presented at their limits of distribution. Furthermore, we should strive to substantially extend the list of species, resurveyed in parallel at both their upper and lower range margins, in order to broaden the spectrum of species and the information for general trends at opposite range limits. Elevational gradients are powerful ‘natural experiments’ for testing ecological responses to environmental change (Körner 2007), and the combined analysis of upper and lower range limits along elevational gradients is an effective tool to identify candidate species that might not keep pace with global warming.

F. ZUSAMMENFASSUNG

Tier- und Pflanzenarten aus den verschiedensten Lebensräumen zeigen bereits Reaktionen auf den Klimawandel. Gebirgslebensräume sind in diesem Zusammenhang von besonderem Interesse, da sie ausgeprägte Gradienten aufweisen und eine im Vergleich zum globalen Durchschnitt stärkere Erwärmung erfahren haben. Detaillierte Angaben zu den höchst- und tiefstgelegenen Vorkommen von Pflanzenarten in den Alpen liegen von anfangs des 20. Jahrhunderts vor. Diese Angaben dienten als Grundlage für die vorliegende Arbeit. Sie wurden ein Jahrhundert später aktualisiert und im Hinblick auf gemeinsame Trends bzw. divergierende Veränderungsmuster an den jeweiligen Arealgrenzen ausgewertet. An der Arealobergrenze zeigt die überwiegende Mehrheit der Arten eine deutliche Aufwärtsverschiebung, die in manchen Fällen mehr als 100 Höhenmeter betragen kann. Fast die Hälfte aller untersuchten Arten kommt mittlerweile in einer Höhe vor, die oberhalb der früher dokumentierten regionalen Höchstgrenze liegt. Die Veränderungen an der Untergrenze zeigen hingegen ein deutlich heterogeneres Bild und weisen auf unterschiedliche, artspezifische Reaktionsgeschwindigkeiten und –muster hin. Mit dem Ansatz der kombinierten Analyse der Veränderungen an der Arealober- und untergrenze lassen sich Kandidaten für Arten erkennen, welche möglicherweise nicht mit dem Klimawandel Schritt halten können und damit einem erhöhten Aussterberisiko im Zusammenhang mit der fortschreitenden Erderwärmung ausgesetzt werden.

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*G. R*EFERENCES

Aeschimann D, Lauber K, Moser D M. and Theurillat J-P (2004) *Flora alpina*. Haupt, Bern.

Becker A, Körner C, Brun JJ, Guisan A and Tappeiner U (2007) Ecological and land use studies along elevational gradients. *Mountain Research and Development,* **27**, 58–65.

Braun J (1913) *Die Vegetationsverhältnisse der Schneestufe der Rätisch-Lepontischen Alpen – Ein Bild des Pflanzenlebens an seinen äussersten Grenzen*. Denkschr. Schweiz. Nat.forsch. Ges, **48**.

Braun-Blanquet J (1955) Die Vegetation des Piz Languard, ein Massstab für Klimaänderungen. *Svensk Botanisk Tidskrift* **49**, 1–9.

Breshears DD, Huxman TE, Adams HD, Zou CB and Davison JE (2008) Vegetation synchronously leans upslope as climate warms. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 11591–11592.

Camenisch M (2002) Veränderungen der Gipfelflora im Bereich des Schweizerischen Nationalparks: Ein Vergleich über die letzten 80 Jahre. *Jahresbericht der Naturforschenden Gesesllschaft Graubünden* **111**, 27–37.

Cannone N, Sgorbati S and Guglielmin M (2007) Unexpected impacts of climate change on alpine vegetation. *Frontiers in Ecology and the Environment*. **5**, 360–364.

Epstein HE, Walker MD, Chapin FS and Starfield AM (2000) A transient nutrient-based model of Arctic plant community response to climatic warming. *Ecological Applications* **10**, 824–841.

Grabherr G, Gottfried M and Pauli H (1994) Climate effects on mountain plants. *Nature* **369,** 448.

Grabherr G, Gottfried M and Pauli H (2001) Long-term monitoring of mountain peaks in the Alps. In: Burga CA and Kratochwil A (eds.). *Biomonitoring: General and applied aspects on regional and global scales*. Tasks for vegetation science 35. Kluwer Academic Publishers, Dordrecht, 153–177.

Hampe A and Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecological Letters* **8**, 461–467.

Hofer HR (1992) Veränderungen in der Vegetation von 14 Gipfeln des Berninagebietes zwischen 1905 und 1985. *Ber. Geobot. Inst. Eidgenöss. Tech. Hochsch., Stiftung Rübel* **58**, 39–54.

Holzinger B, Hülber K, Camenisch M and Grabherr G (2008) Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates. *Plant Ecology* **195**, 179–196.

Jurasinski G and Kreyling J (2007) Upward shift of alpine plants increases floristic similarity of mountain summits. *Journal of Vegetation Science* **18**, 711–718.

Kammer PM, Schob C and Choler P (2007) Increasing species richness on mountain summits: Upward migration due to anthropogenic climate change or re-colonisation? *Journal of Vegetation Science* **18**, 301–306.

Klanderud K (2005) Climate change effects on species interactions in an alpine plant community. *Journal of Ecology* **93**, 127–137.

Körner C (2003) *Alpine plant life: functional plant ecology of high mountain ecosystems*. Springer, Berlin Heidelberg.

Körner C (2007) The use of ‘altitude’ in ecological research. *Trends in Ecology and Evolution* **22**, 569–574.

Krajick K (2004) All Downhill From Here? *Science* **303**, 1600–1602.

Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology* **90**, 68–77.

Lesica P and McCune B (2004) Decline of arctic-alpine plants at the southern margin of their range following a decade of climatic warming. *Journal of Vegetation Science* **15**, 679–690.

Miller-Rushing AJ and Primack RB (2008) Global warming and flowering times in Thoreau’s Concord: a community perspective. *Ecology* **89**, 332–341.

Nogués-Bravo D, Araújo MB, Martinez-Rica JP and Errea MP (2007) Exposure of global mountain systems to climate change. *Global Environmental Change-Human and Policy Dimensions* **17**, 420–428.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* **37**, 637–669.

Parmesan C and Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.

Parolo G and Rossi G (2008) Upward migration of vascular plants following a climate warming trend in the Alps. *Basic and Applied Ecology* **9**, 100–107.

Pauli H, Gottfried M, Reiter K, Klettner C and Grabherr G (2006) Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994–2004) at the GLORIA master site Schrankogel, Tyrol, Austria. *Global Change Biology* **12**, 1–10.

Price MV and Waser NM (2000) Responses of subalpine meadow vegetation to four years of experimental warming. *Ecological Applications* **10**, 811–823.

Rebetez M and Reinhard M 2008. Monthly air temperature trends in Switzerland 1901–2000 and 1975–2004. *Theoretical and Applied Climatology* **91**, 27–34.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C and Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60.

Rosenzweig C, Casassa G, Karoly DJ, Imeson A, Liu C, Menzel A, Rawlins S, Root TL, Seguin B and Tryjanowski P (2007) Assessment of observed changes and responses in natural and managed systems. In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ and Hanson CE (eds.). *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, 79–131

Rübel E (1912) *Pflanzengeographische Monographie des Berninagebietes*. Engelmann, Leipzig.

Vittoz P, Bodin J, Ungricht S, Burga CA and Walther G-R (2008) One century of vegetation change on Isla Persa, a nunatak in the Bernina massif in the Swiss Alps. *Journal of Vegetation Science* **19**, 671–680.

Walther G-R, Beißner S and Burga CA (2005) Trends in the upward shift of alpine plants. *Journal of Vegetation Science* **16**, 541–548.

Walther G-R, Burga CA and Edwards PJ (eds.) (2001) *‘Fingerprints’ of climate change – Adapted behaviour and shifting species ranges*. Kluwer/Plenum, New York/London.

Walther G-R, Hughes L, Vitousek P and Stenseth NC (2005) Consensus on climate change. *Trends in Ecology and Evolution* **20**, 648–649.

Walther G-R, Nagy L, Heikkinen RK, Penuelas J, Ott J, Pauli H, Pöyry J, Berger S, Hickler T in press. Observed climate-biodiversity relationships. In: Settele J *et al.* (eds.). *Atlas of*

Biodiversity Risks – from Europe to the Globe and from stories to maps. Pensoft Publishers, Sofia.

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O and Bairlein F (2002) Ecological responses to recent climate change. *Nature* **416**, 389–395.

V. ONE CENTURY OF VEGETATION CHANGE ON ISLA PERSA, A NUNATAK IN THE BERNINA MASSIF IN THE SWISS ALPS

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A. ABSTRACT

Question: How did the vascular plant species composition of a nunatak in the alpine vegetation belt change over a time span of one century?
Location: A 0.056-km^2 nunatak, Isla Persa in the Swiss Alps, that remained ice free during the last maximum glacier advance in the 1850s and is today partly covered with climactic alpine grassland and dwarf heath shrubs.
Methods: Floristic inventories in 1906, 1927, 1972, 1995, 2003 and 2004 and a comparative analysis of the species composition over the period 1906–2004.
Results: Thirty-one species that were not recorded in the first inventory were found in the following surveys. However, among them only six were common by 2004. On average, the new species prefer warmer conditions than those previously present and most newcomers are associated with montane or subalpine grasslands and woodlands. In particular, the observed increase of *Vaccinium myrtillus* and the arrival of shrub and tree species further substantiate a trend towards vegetation composition of the lower altitudinal belt. Ferns represented 24% of the newcomers, probably due to the high dispersal ability of their lightweight spores. The observed species enrichment was globally small compared to previously inventoried summits.
Conclusion: Floristic change strongly suggests warmer climatic conditions as the main factor contributing to species compositional change. The relative stability of species richness may be explained by several factors: the isolation of the nunatak and the difficulties for plants to reach the site, the colder local climate, a limited available species pool and interactions of established alpine plants with newly immigrating taxa. Supplementary data collected at about the same altitude would be necessary to better understand the influence of climate change on alpine grasslands.

Keywords: Alpine vegetation, Global warming, Long-term monitoring, Plant traits, Species diversity, Switzerland

B. INTRODUCTION

Climate warming induces upward range shifts of plant species in mountain areas. This trend was predicted by numerous studies (*e.g.* Gottfried *et al.* 1998; Guisan & Theurillat 2000; Dirnböck *et al.* 2003) and it has also been substantiated by observations on many high alpine, rocky summits (Braun-Blanquet 1957; Hofer 1992; Grabherr et al. 1994, 1995; Burga *et al.* 2004; Walther et al. 2005a; Vittoz *et al.* 2006; Parolo & Rossi 2008), by single species re-surveys (Dobbertin *et al.* 2005; Walther *et al.* 2005b), and by altitudinal shifts of the treeline ecotone (Kullman 1986; Taylor 1995; Moiseev & Shiyatov 2003; Camarero & Gutiérrez 2004; Vittoz *et al.* 2008; for a review see Walther 2004). However, data for long-term vegetation changes in subalpine or alpine grasslands are lacking (for shorter time scales see Kudernatsch 2005). Sufficiently long time series of permanent plots are few or unavailable for studying upward range shifts of mountain plants due to anthropogenic disturbances.

In the Alps, the glaciers reached their last maximum extent in the 1850s (see references in Burga 1999) and have since then been shrinking. The rate of glacier retreat has increased further in the last few decades (Paul *et al.* 2004). In previous centuries throughout the Holocene period, the extent of the glaciers of the Alps is assumed to have reached the 1850 maximum but never substantially exceeded this level (Maisch *et al.* 1999). Hence, isolated rocks surrounded by glaciers in 1850, called nunataks, may at least be partly covered with ancient soils and with vegetation in climax states.

Isla Persa (literally the “lost island” in Rhaeto-Romanic) in the Eastern Swiss Alps is such a nunatak in the alpine belt. It remained ice-free during the last maximum of the local glaciers (Fig. 1; Lechner 1858) and is covered with large patches of climactic alpine grasslands. The nunatak is an interesting area for vegetation studies due to its isolation from intensive anthropogenic disturbance, and has therefore attracted the interest of botanists since the early 20th century.

The first floristic inventory of this nunatak was published in Rübel's monograph (1912) on the vegetation of the Bernina region, named after the highest mountain peak (Piz Bernina 4049 m a.s.l.) of the Eastern Alps. The nunatak was revisited three times in 20th century but the inventories remnained partly unpublished (Flütsch *et al.* 1930; De Haas 1973; Ungricht 1995). With the present article, we wish to compile all of this previous historic data and integrate two recent inventories. Altogether, these inventories provide a rare opportunity for the analysis of vegetation change in alpine grasslands during the course of one century. Specifically, we address the following questions: (i) how much has the floristic species richness changed through time, (ii) is climate change likely to be responsible for the observed development, and (iii) which are the biological traits linked to the observed colonization process?

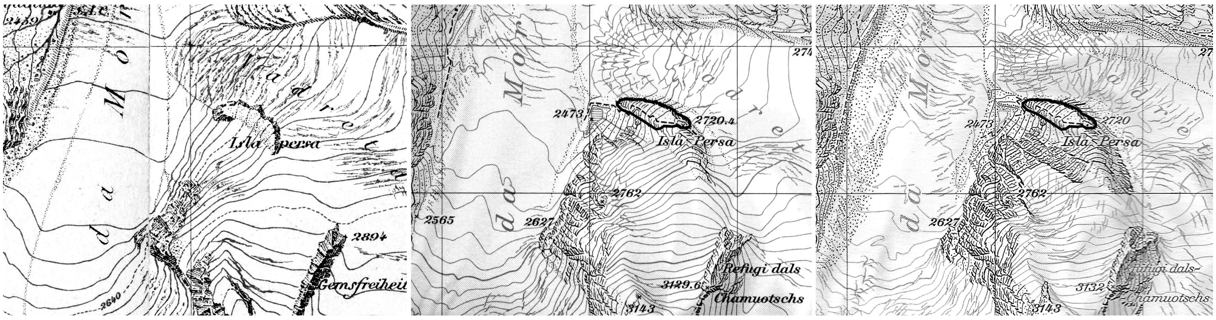

Figure V-1. Glacier retreat around Isla Persa between 1876 (left), 1965 (centre) and 1991 (right). Rübel area is delimited by the Morteratsch glacier to the West, the Pers glacier to the North and East, and the Fortezza glacier to the South in 1876 and by the black line in 1965 and 1991. Swisstopo, Siegfried map n°521 at 1:50'000 in 1896, Landeskarte n° 268 in 1965 and 1991 at 1:50'000 with a grid size of 1 km. Reproduced by permission of swisstopo (BA071283). Isla Persa extends now on the whole rocky area (grey part in the south of the Rübel area).

C. STUDY AREA

The investigation area, a nunatak named Isla Persa (46°24' N, 9°56' E), is delimited to the West by the Morteratsch glacier, to the North and East by the Pers glacier and to the South by the Fortezza glacier (Fig. 1). At present, the altitudinal range of the Isla Persa spans 400 m, between 2450 m and 2850 m a.s.l., which is entirely within the alpine belt (2300–3000 m in the region). Isla Persa is isolated from the surrounding ice-free areas by 500 m to the North and 900 m to the West. It is very unlikely that it was ever permanently inhabited and grazed by domestic cattle or sheep. However, the nunatak is now frequently visited by hikers crossing the ice-free area between the two adjoining glaciers.

The nunatak belongs to the lower Eastern-Alpine Bernina nappe *s.l.* The rocks consist mainly of granites, granodiorites, diorites, and gabbros (Büchi 1994). A large part of the Isla Persa represents a granitic rock outcrop partly covered with screes. The vegetation consists of scattered alpine grasslands and some heath dwarf shrubs on well-developed alpine regosols and leptosols, especially on the southern foot area of the nunatak.

At the time when it was first investigated in 1906 by Rübel (1912), the Isla Persa covered about 0.056 km^2 and comprised altitudes between 2510 and 2720 m a.s.l. Since then, the ice-free surface has increased to ca. 0.68 km^2 as a consequence of a rapid glacier retreat (Fig. 1). However, since the 1940s, the total area of the nunatak can no longer be clearly delimited because another ice-free rocky area merged at its southwestern corner making it extend to 3143 m a.s.l.

The closest meteorological station is located in Sils-Maria, at 1802 m a.s.l., 15 km to the West of Isla Persa. Both sites are located in the Inner Alps, which have low precipitation and air humidity. Mean annual temperature (± 1SD) for the 1961–90 period was 1.6 ± 0.5°C (–7.2 ± 1.9°C in January and 10.4 ± 1.2°C in July) and the average annual precipitation was 978 ± 168 mm, with drier winters (mean of the sum for December to February 143 ± 61 mm) than summers (June to August 335 ± 98 mm). During the 20th century, a general temperature increase during the growth season (May-September) occurred between 1918 and 1951, a decrease was observed till 1974, and since then an increase has again been observed (Fig. 2) in accordance with other regions in Switzerland (Bader & Bantle 2004). However, the temperature increase was altogether lower in Sils-Maria than in other Swiss regions: +0.4°C/100 years in summer for the period 1864–2001 compared with +0.6–0.9°C/100 years for the lowland and Northern Alps (Bader & Bantle 2004). Like in all other regions, most of this increase took place in the last decades and the mean annual increase was similar to records for the Northern Hemisphere (Rebetez & Reinhard 2008).

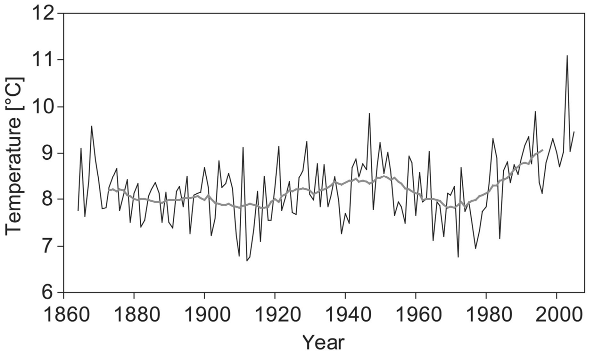

Figure V-2. Average growth season (May-September) temperature in Sils-Maria (1802 m a.s.l., 15 km from Isla Persa; data MeteoSwiss). The grey line is the 20-yr mobile average.

D. METHODS

1. Field plant inventories

A set of six consecutive plant species inventories of the Isla Persa area was available, spanning the period of one century (Tab. 1). Two inventories were made in the first half of the 20th century by Rübel (1912) in 1906 and Braun-Blanquet in 1927 (Flütsch 1930), followed by two inventories in the second half of the 20th century (De Haas 1973; Ungricht 1995). In 2003 the full ice-free area was again inventoried by two of the authors (Walther, Burga and collaborators). In 2004, a further inventory took place by another author (Vittoz), which was restricted to the originally ice-free core area of the nunatak, i.e., the same area as originally inventoried by Rübel (here designated as Rübel area, Tab. 1). The different inventories were accomplished by varying numbers of observers over varying numbers of days, hence with different levels of assessment effort. However, all included the most favourable period as judged by the phenology of alpine plants. At all inventories only the presence of the species was recorded, with occasional indications for rare species, except the last inventory (2004) by which abundance estimates to classes were provided (Tab. 2; cf. Grabherr *et al.* 2001) and data about plant location and substrate was recorded for most of the rarest species.

Table V-1. Authors, dates, assessment areas, number of observers, assessment time and recorded species numbers of the six inventories on Isla Persa (Swiss Alps). All but the last author inventoried the complete ice-free area, which increased through time. The area inventoried by Rübel in 1906 is here defined as the "Rübel area" and used for the analyses in this paper. The corrected number of species incorporates the potentially overlooked species observed by a previous and the following inventory. The two last inventories were merged as they were separated only by one year.

Author	Date of publication	Date of inventory	Inventoried area	Number of observers	Time used	Number of recorded species		
						inventoried area	Rübel area	corrected for Rübel area
Rübel	1912	1906	Ice-free area = Rübel area	1 ?	?	98	98	98
Flütsch	1930	1927	Ice-free area	27	1 day	103	99	106
De Haas	1973	1971-72	Ice-free area	several	44 days	134	116	118
Ungricht	1995	1994-95	Ice-free area	1-4	40 hours	110	99	117
Walther & Burga		2003	Ice-free area	3-4	7 days	136	115	126
Vittoz		2004	Rübel area	2	3 days	122	122	

By comparing the two last inventories and previous indications of species location, we established a comparative species list for the Rübel area and a list of additional species from the newly deglaciated area (App. 1, supplementary archives). For each inventory it was possible to obtain a comprehensive species list for the Rübel area, but the data were inadequate to get species lists for the newly ice-free area. Therefore, we limited our study to the Rübel area.

The species names follow Aeschimann *et al.* (2004). From the different species lists, the following species were merged because of suspected misidentifications: *Avenella flexuosa-Deschampsia caespitosa*; *Adenostyles leucophylla-A. intermedia*; *Carex frigida-C. ferruginea*; *Galium anisophyllon-G. pumilum*; *Poa supina-P. annua-P. badensis*; *Poa laxa-P. minor* and *Sagina saginoides-S. glabra*.

2. Analyses

It is likely that some rare and/or inconspicuous species were overlooked in all inventories (Vittoz & Guisan 2007). Hence, species present in an earlier inventory that lacked confirmation in an intermediate inventory, but were “rediscovered” in a later survey were considered present throughout the entire interval. It is more likely for a missed species to have been overlooked in the intermediate inventory than for it to have disappeared and re-colonized the area in the given time interval. For the same reason, we assumed that no species disappeared or appeared between 2003 and 2004 and we merged these last two inventories (Tab. 1).

We used biological traits to assess if newcomer species (i.e. species that were found for the first time after 1906) differed from the original species (already present in 1906). Five of the recorded traits were indicative of the ecological conditions under which the species occur. The ecological indicator values (Landolt 1977) vary between 1 and 5 and are available for each Swiss species following its ecological preferences. The soil texture (1, stony – 5, clayey), soil humus content (1, no humus – 5, peaty), soil nutrients content (1, oligotrophic – 5, eutrophic) and temperature (1, alpine-nival belt – 5, collinean belt) were used. The sociological classification of species simplified from Ellenberg *et al.* (1991) – or Aeschimann *et al.* (2004) in case the species is not listed in the former – was completed with a more integrative view of the species ecological preferences. The nomenclature for plant sociological units follows Ellenberg *et al.* (1991). The growth forms were simplified from Pignatti (2005) (therophytes, non-graminoid hemicryptophytes, graminoid hemicryptophytes, geophytes, creeping chamaephytes, chamaephytes in cushions, succulent chamaephytes, woody chamaephytes, phanerophytes). Four traits were related to reproduction. The respective importance of sexual and clonal reproduction was assessed following the BIOLFLOR databank (Klotz *et al.* 2002) in three categories: sexual reproduction only, sexual and clonal reproduction possible and mainly clonal reproduction. The same reference was used for the fertilization type in five categories: only self-fertilization, wind as vector, insects, mainly insects but possible self-fertilization and fern gametophyte fertilization. Data on seeds or weight of other diaspores were taken from Klotz *et al.* (2002) and Müller-Schneider (1986). Since values were still missing for 29% of the species, we used seven categories for which unknown species were attributed on the basis of the closest relative species: 1, diaspore < 0.05 mg; 2, 0.06–0.2 mg; 3, 0.21–0.5 mg; 4, 0.51–1 mg; 5, 1.01–2 mg; 6, 2.01–10 mg; 7, diaspore > 10 mg. Dispersal vector of the seeds followed Müller-Schneider (1986) and dispersal distance of the diaspores was simplified in 7 types following Vittoz & Engler (2007), which takes into account the main dispersal vector and important species traits influencing dispersal. The types chosen were: 1 when 99% of the seeds fall <1 m; 2, <5 m; 3, <15 m; 4, <150 m; 5, <500 m; 6, <1500 m; 7, <5000 m. $\chi 2$-tests were used in statistical analyses of trait differences.

E. RESULTS

During the assessment window of nearly one century, the number of species increased almost continuously in the Rübel area from 98 in 1906 (Rübel 1912) to 126 in 2004 (Tab. 1). However, most of the newly recorded species were rare in 2004 and only some species, which arrived between 1906 and 1927, were locally common in 2004 (Tab. 2). The abundance of *Vaccinium myrtillus*, *Elyna myosuroides* and *Cerastium uniflorum* was relatively high at the last inventory and these species have never been overlooked since their first record (in 1927) making it likely that they immigrated after 1906. *Pinguicula leptoceras*, *Soldanella alpina* and *Primula integrifolia* were present in a particular sector of the nunatak only. These species were also recorded for the first time in 1927. We assumed that although present, they may have been overlooked in the 1906-inventory but nonetheless they are considered to have colonized the nunatak when observed for the first time in 1927.

Among the 31 new species, 10 species were found at a higher altitude in 2004 (Tab. 2) than reported for the whole Bernina region at the beginning of the 20th century (Rübel 1912). These altitudinal shifts were particularly pronounced for *Athyrium distentifolium* (+470 m), *Diphasiastrum alpinum* (+340 m), *Pinguicula leptoceras* (+260 m) and *Poa supina* (+120 m) (identification was uncertain for two poorly developed, supplementary species: *Dryopteris dilatata* and *Leontodon autumnalis*).

Some species disappeared or were not found after the first observation (Tab. 2). Misidentifications cannot be discounted, but they were rather unlikely. Three of these species (*Euphrasia rostkoviana*, *Gentiana campestris*, *Thymus serpyllum*) occurred close to their highest altitudinal range in the region (Rübel 1912).

None of the ecological indicator values (Landolt 1977) for soil conditions showed differences between species that had recently colonized Isla Persa compared to those present in 1906 (Tab. 3). The mean values (± 1 SD) for 1906-species and colonizing species, respectively, were 3.31 ± 0.91 and 3.42 ± 1.15 for soil texture, 3.27 ± 0.71 and 3.42 ± 0.87 for soil humus content, and 2.19 ± 0.71 and 2.39 ± 0.79 for soil nutrient content. In contrast, the temperature indicator value showed a highly significant difference between inventories, with means 1.53 ± 0.58 for the 1906 inventory compared to 2.09 ± 0.53 for the new species (Tab. 3). This corresponded with a continuously decreasing proportion of alpine and nival species (value 1, represented only 9.1% of the new species) in the inventories and a corresponding increase in subalpine species (value 2, 72.7% of the new species) and montane or indifferent species (value 3, 21.2% of the new species; Fig. 3).

Table V-2. Species that have disappeared or were newly recorded on Isla Persa between 1906 and 2004. 1 species present without abundance estimation; * species probably overlooked because present in the previous and following inventory; r! very rare; r rare; s scattered; r-lc rare but locally common; s-lc scattered but locally common (for a complete species list see App. 1 in Supplemental archives). The highest altitudes are the recorded altitudinal limit for the whole Bernina regions in 1906 (Rübel 1912) and for the Isla Persa in 2004. Species sociology is simplified from Ellenberg et al. (1991) or Aeschimann et al. (2004) and the occupied substrate refers to the conditions where the individuals were recorded in 2004.

Plant species	1906	1927	1972	1995	2004	Highest altitude [m]		Sociology	Occupied substrate
						1906	2004		
Disappeared species									
Veronica bellidioides	1	1	1			3260		Alpine grasslands	
Euphrasia rostkoviana	1					2600		Lowland meadows	
Gentiana campestris	1					2700		Lowland meadows	
Thymus serpyllum		1				2700		Others	
Festuca halleri			1			3400		Alpine grasslands	
New species									
Vaccinium myrtillus		1	1	1	s-lc	2750	2520	Shrubs and forests	Grassland and heathland
Elyna myosuroides		1	1	1	s	3090	2520	Alpine grasslands	
Soldanella alpina		1	1	*	s	2700	2510	Alpine grasslands	Grassland
Pinguicula leptoceras		1	1	*	s	2260	2520	Others	Grassland
Primula integrifolia		1	1	*	r-lc	3010	2510	Alpine grasslands	
Cerastium uniflorum		1	1	1	r-lc	3400	2660	Rocks, cliffs, screes	Stones and/or gravel
Gentiana brachyphylla		1	1	1	r	3260	2560	Lowland meadows	Grassland
Trichophorum cespitosum		1	*	*	r	2450	2510	Others	Grassland
Antennaria dioica		1	1	*	r!	3010	2560	Lowland meadows	Grassland
Phleum alpinum			1	*	r	2830		Alpine grasslands	
Sagina saginoides / S. glabra			1	*	r	2550	2540	Alpine grasslands	Stones and/or gravel
Asplenium septentrionale			1	*	r	2470	2530	Rocks, cliffs, screes	Cliff
Cryptogramma crispa			1	1	r	2730	2560	Rocks, cliffs, screes	Stones and/or gravel
Polystichum lonchitis			1	1	r	2550	2540	Rocks, cliffs, screes	Stones and/or gravel
Coeloglossum viride			1	*	r	2650	2520	Lowland meadows	Grassland
Trifolium alpinum			1	1	r	2730		Lowland meadows	
Athyrium distentifolium			1	1	r	2230	2700	Shrubs and forests	Stones and/or gravel
Poa supina / P. annua / P. badensis			1	*	r	2600	2720	Others	Track
Diphasiastrum alpinum			1	*	r!	2630	2700	Lowland meadows	Grassland
Ribes petraeum			1	*	r!	2450	2530	Shrubs and forests	Heathland
Salix helvetica			1	1	r!	2500	2510	Shrubs and forests	Stones and/or gravel
Gymnocarpium dryopteris				1	r!	2570	2540	Shrubs and forests	Stones and/or gravel
cf Aster bellidiastrum					r!	2600	2540	Alpine grasslands	
Gentiana verna					r!	2900	2560	Alpine grasslands	Grassland
Leontodon cf autumnalis					r!	2320	2720	Lowland meadows	Track
Pulsatilla alpina s.l.					r!	2730	2710	Lowland meadows	Grassland
Arctostaphylos uva-ursi					r!	2550	2500	Shrubs and forests	Stones and/or gravel
Dryopteris filix-mas					r!	2540	2540	Shrubs and forests	Stones and/or gravel
Larix decidua					r!	2660	2510	Shrubs and forests	Stones and/or gravel
Dryopteris cf dilatata					r!	2260	2520	Shrubs and forests	Stones and/or gravel
Festuca rubra aggr.					r!	2650	2540	Others	Grassland

The sociology of original and recent plant species differed significantly (Tab. 3). The newly arrived species were associated in similar proportions with forests (*Vaccinio-Piceetea*, *Erico-Pinetea*, *Querco-Fagetea*), alpine grasslands (*Salicetea herbaceae*, *Juncetea trifidi*, *Seslerietea albicantis*, *Carici rupestri-Kobresietea*, *Loiseleurio-Vaccinietalia*, *Poion alpinae*) or montane and/or subalpine grasslands (*Nardo-Callunetea*, *Molinio-Arrhenatheretea*) (Tab. 2; Fig. 4). Altogether, forests and montane-subalpine grassland species represented 23% of the 1906 floristic composition but 45% of the new species. By contrast, alpine grassland and rock/scree species (*Asplenietea trichomanis*, *Thlaspietea rotundifolii*, *Sedo-Scleranthetea*) comprised only 36% of the new species, while they comprised 70% of the 1906 composition (Fig. 4).

Table V-3. P values for the comparisons of biological traits between the species present in the 1906-inventory on Isla Persa and those that arrived later are obtained by χ^2-tests (see Methods for the description of traits).

Biological trait	p-value
Soil texture	0.134
Soil humus content	0.130
Soil nutrients content	0.257
Temperature	**<0.0001**
Sociology	**0.009**
Growth form	0.243
Reproduction type	0.288
Fertilization type	**0.006**
Fertilization type (without ferns)	0.351
Diaspore weight	**0.017**
Diaspore weight (without ferns)	0.497
Dispersal distance	0.240

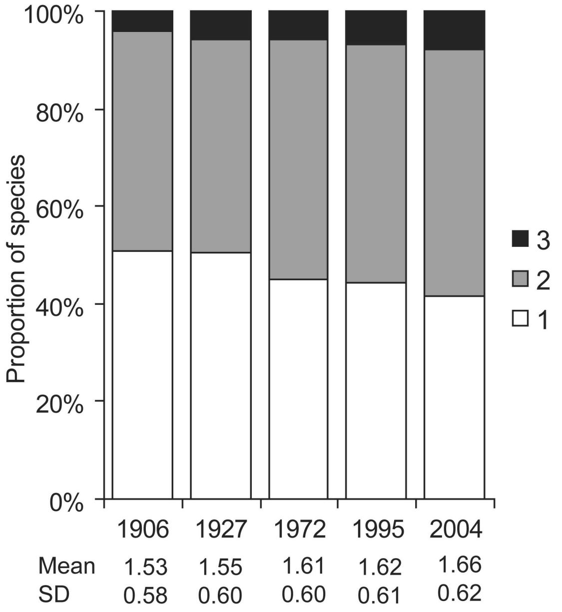

Figure V-3. Proportion of species corresponding to the different temperature indicator values following Landolt (1977) in the floristic inventories on Isla Persa: 1 species typically distributed in alpine and nival belts, 2 subalpine species, 3 montane or indifferent species. Mean and standard deviation (SD) for the complete inventories are given for the individual years.

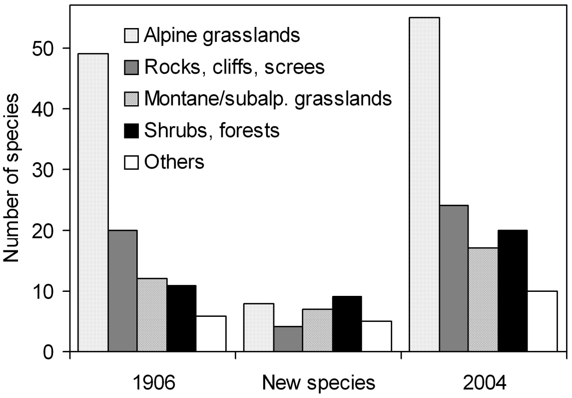

Figure V-4. Plant sociological preferences (Ellenberg et al. 1991; Aeschimann et al. 2004) of the 98 species already present in 1906, the 31 species that arrived later, and of the 126 species present in 2004 (for details and relative values see text).

The growth forms were similarly distributed (Tab. 3), with a large dominance of hemicryptophytes in both groups, although a higher proportion of non-graminoid hemicryptophytes was observed in the original inventory (App. 2 in supplementary archives). The reproduction type showed no difference between inventories, with 74 and 72% of species able to reproduce sexually and clonally in the two groups (Tab. 3). The fertilization type was significantly different because of a higher proportion of ferns among the recently arrived species (24.2% compared to 4.1% among the 1906-species). When only the phanerogames were considered, there was not a significant difference between fertilization types (Tab. 3), with approximately 66% and 68%, respectively, of either obligatory or non-obligatory entomophilous species. Similarly, diaspore weight was significantly different when all the species were considered, with a higher proportion of very light diaspores among colonizing species (Fig. 5) but no significant difference when only phanerogams were considered (Tab. 3). Finally, no difference was found in dispersal vectors, with 83 and 85% of the seeds dispersed by wind or without special device for dispersal and 26-27% of zoochorous dispersal, including unintentional endozoochory by consumption with grass (results not shown). Dispersal distance type showed no significant difference between species present in the 1906-inventory and species that arrived later (Tab. 3; App. 3 in supplementary material).

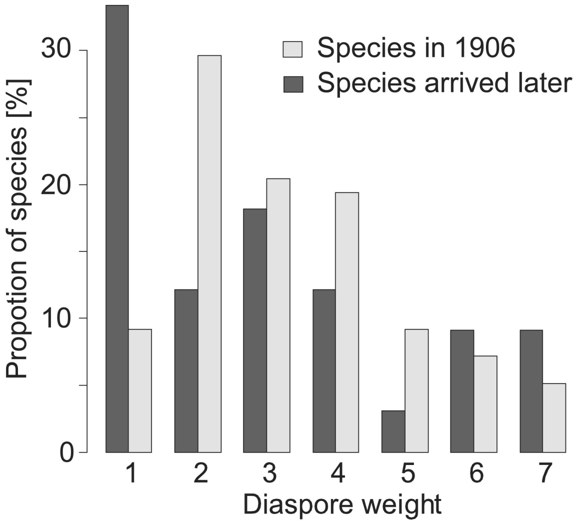

Figure V-5. Distribution of diaspore weight for species present in the 1906-inventory on Isla Persa and the 31 that arrived later (see Methods for the seven types).

F. DISCUSSION

1. Data reliability

The comparison of this type of floristic data in large areas is always confronted with the problem of completeness and reliability. Clearly, the prospecting effort is variable between the different inventories (Tab. 1). For instance, we do not know how much time Rübel spent for the first inventory in 1906, but it was probably less than the 27 day equivalent that Braun-Blanquet invested with his students in 1927 (Flütsch *et al.* 1930). Previous studies have often shown that botanical inventories are rarely exhaustive, even in very small areas (*e.g.* Lepš & Hadincová 1992; Klimeš *et al.* 2001; Kercher *et al.* 2003; Archaux *et al.* 2006; Vittoz & Guisan 2007). Two easy ways to improve data and interpretation exist: working in groups increases the reliability of species lists (Klimeš *et al.* 2001; Vittoz & Guisan 2007) and estimation of cover helps to cautiously interpret the results for new but rare species (Lepš & Hadincová 1992; Kercher *et al.* 2003; Vittoz & Guisan 2007). On Isla Persa, most inventories were completed by teams (Tab. 1) but cover estimates in the earlier inventories would have allowed more detailed analyses of abundance changes (*e.g.*, Vittoz *et al.* 2006).

2. Biodiversity increase and climate change

Climate warming, although less pronounced in this region compared to other Swiss regions (Fig. 2), is probably responsible for the observed species increase on the Isla Persa. This is consistent with newly arrived plant species showing higher temperature requirements (Fig. 3) and observations of particular species at higher altitudes in 2004 than in 1906. The same trend is also observed on many surrounding summits (Braun-Blanquet 1957; Hofer 1992; Grabherr *et al.* 2001; Camenisch 2002; Burga *et al.* 2004; Walther *et al.* 2005a) or in other alpine regions (Grabherr *et al.* 2001; Vittoz *et al.* 2006; Parolo & Rossi 2008). Recent re-observations at an alpine-nival ecotone of the central Alps showed an increase in cover of high-alpine species and a concurrent decline of all subnival to nival species, suggesting a range shift of mountain plants (Pauli *et al.* 2007).

Higher temperatures allow more sensitive plants to colonize the nunatak. These newly arrived species indicate a slow shift of the vegetation from mainly alpine meadows and rocky vegetation to conditions typical of the lower alpine belt, or even the subalpine belt. Although rocky sites and screes are still dominant on the nunatak, most of the new species are indeed associated with grasslands or wooded areas (Fig. 3). The clear increase of *Vaccinium myrtillus*, a typical species of subalpine forests or lower alpine dwarf shrubs heath, indicates a possible belt shift. This development correlates with the results of Wahren *et al.* (2005) in warming experiments on Arctic tundra vegetation showing the increasing size and cover of small shrubs. Similar altitudinal/latitudinal belt shifts were observed in other regions as well, like the expansion of the treeline ecotone (*e.g.* Kullman 1986; Taylor 1995; Peñuelas & Boada 2003; Camarero and Gutiérrez, 2004; Vittoz *et al.* 2008) or the colonization of shrubs in the Arctic tundra (Sturm *et al.* 2001) and in the boreal mountains (Klanderud & Birks 2003). The arrival of *Salix helvetica, Ribes petraeum* and especially the first occurrence of *Larix decidua*, on Isla Persa is perhaps an early indication of the upward expansion of the treeline. This last species is, at present, limited to one individual that colonized the nunatak no earlier than 1994 (based on the annual increments of the shoots).

Another indication of warmer conditions on the nunatak is the observed higher fitness of *Epilobium angustifolium*. Rübel (1912) mentioned its sterile occurrence at the foot of the ‘island’ (2530 m a.s.l). The same species was missing in the inventory of Flütsch *et al.* (1930), whereas De Haas (1973) reported a mainly vegetative spreading species. In 2003, the population was found at the same location in full flower (for the advance of the same species in the Arctic see Kullman 2003). The shift from mainly vegetative to fertile populations of *Epilobium angustifolium* underlines the possibility for species with lower core distribution to colonize and become established at their upper range limit.

Other factors are certainly partially responsible for the observed vegetation changes on Isla Persa: (i) Some new species most likely arrived with a re-colonisation process after the climate change that followed the Little Ice Age (Kammer *et al.* 2007). Species became extinct during this cold period and re-colonised Isla Persa, much like surrounding summits, in warmer conditions. This process was probably slowed by the low dispersal ability of many species and is now being accelerated by anthropogenic warming (Walther *et al.* 2005a). (ii) Another portion of the new species may correspond to the continuous colonization observed on every island (MacArthur & Wilson 1967). With 49 alpine grassland species in 1906, the species pool on Isla Persa was not saturated, since it is estimated that about 100 potential species of acidophilous alpine grasslands exist in the Eastern Swiss Alps (calculated by crossing data from Landolt 1977, Ellenberg *et al.* 1991, Moser *et al.* 2002 and Aeschimann *et al.* 2004). Similarly, the 20 species on rocks, cliffs or screes in 1906 represented less than half of the pool of 54 potential species. Respectively, the 8 and 4 new species associated with these environments (Tab. 2; Fig. 4), some very common in alpine conditions (*e.g.*, *Soldanella alpina* in alpine grasslands and *Cerastium uniflorum* in screes) can be considered as colonizations independent of climate change. (iii) Primary succession in the Rübel area cannot alone be responsible for the increase in species numbers on the nunatak, since it has been ice-free for many thousands of years. It was not covered by ice in 1850 and glaciers in the Alps did not exceed their 1850 extent throughout the Holocene (Maisch *et al.* 1999). Hence, a large part of the local vegetation must have been at the succession climax for a long time. However, a primary succession is possible on some of the rocky areas, with potentially increasing biodiversity, but mostly with already present species. (iv) Interannual fluctuations are sometimes responsible for vegetation changes (van der Maarel 1996). However, the different inventories of the Rübel area showed a continuous increase in species richness and, furthermore, such fluctuations have low amplitudes at these altitudes. Finally, (v) the glacier barrier strongly limits cattle grazing on Isla Persa and a vegetation change after pasture abandonment is very improbable. Only the hikers’ influence seems to have contributed slightly to the enrichment, responsible for the arrival of a few species, like *Poa supina* or *Leontodon* cf. *autumnalis*, which were found on the most trampled spot – all the other newcomer species were recorded well off the track.

3. Biological traits

Apart from temperature and sociology of the species (see above), fertilization type and diaspore weight were the only biological traits considered that showed a significant difference between originally established species (1906) and new species (Tab. 3). For both traits, however, the high proportion of Pteridophytes (26% of the new species but only 4% in the 1906 inventory) is responsible for this difference: they were classified separately for the fertilization type and, with spores, they all have very light diaspores (<0.05 mg category). Similarly, four fern species were classified by Parolo & Rossi (2008) as fast migrants because of their important altitudinal shift between 1959 and 2005. It is very probable that their small spores give them an advantage for long-distance dispersal because of a high efficiency of wind as a dispersal vector. A high proportion of pteridophytes were found as well on a new volcanic island whose situation strongly favored anemochory (Thornton *et al.* 2001). However, pteridophyte establishment in this alpine environment could be more difficult because the small size and dependence of photosynthesis of prothalli (fern gametophytes) which make them little competitive in grasslands (Greer 1993). This may perhaps explain why almost all new pteridophytes are established on mineral soils (stones and/or gravel), even though four species normally grow in forest soils. The number of individuals and species is too low to conclude if the colonization rate of pteridophytes in alpine environments under climate change is generally higher than for other vascular plant species.

The similarity of other biological traits between original species and newly arrived ones show that changes in vegetation structure were not yet important enough to significantly influence the trait pattern. Alpine conditions governed the observed plant traits in both groups: the dominance of hemicryptophytes is typical of alpine vegetation (Illa *et al.* 2006; Körner 2003), as well as a majority of plants with possible clonal reproduction (Stöcklin 1992; Illa *et al.* 2006) and the dominance of insect fertilization (Körner 2003). The seed weight, which shows a comparable majority of seeds <1 mg, as in sub-arctic grasslands (Welling *et al.* 2005), seems not to be related to altitude, with mean weight similar between alpine and lowland grasslands (Körner 1999). Finally, the importance of wind as dispersal vector (including for small seeds without special device; Willson *et al.* 1990) is typical of alpine plant communities, more generally of grasslands and vegetation with an open structure (Willson *et al.* 1990; Stöcklin & Bäumler 1996; Ozinga *et al.* 2004), typical of island colonization (Lloret *et al.* 2005). This similarity strongly limits the opportunities to detect differences in dispersal vectors and distances between established plants in 1906 and newcomers.

4. Importance of the biodiversity increase

Compared to other similar studies, the increase in species richness on Isla Persa is relatively small. The increase of 29% for recorded vascular plant species in the course of one century recorded for the Isla Persa is clearly below the values for most of the surrounding mountain summits. Of the eleven inventoried summits in the Bernina region (Walther *et al.* 2005a; Vittoz unpublished data), eight showed a stronger increase of richness (58–336%, mean = 131%). However, all these mountain summits are at a higher altitude and are dominated by rock surfaces, with very limited areas of alpine grassland. Various reasons may explain this comparatively small change on the nunatak. (i) Physical barriers created by the surrounding glaciers limited the colonization by plants, as was hypothesized for the observed stable richness (since 1937) of the Piz Linard (3411 m) (Pauli *et al.* 2001). Conversely, most of the inventoried summits in the Bernina region have gradually changing conditions, which allows a progressive migration of plants. (ii) The species richness on Isla Persa was about half of the species pool for alpine grasslands and rock areas, limiting the number of potential newcomers. (iii) Subalpine species arriving in well-developed alpine grasslands are not free to colonize all potentially suitable sites because most of them are already occupied, or, at the least, the newcomers need more time to increase their abundance under the still prevailing cold alpine conditions. The increase of *Vaccinium myrtillus* supports this hypothesis as mature plants of this taxon are taller than those of most other alpine species and hence less inhibited by competition. (iv) Surrounding glaciers bring about a colder microclimate than usually exists for other localities at similar altitudes. Unfortunately, comparable floristic data at similar altitudes are lacking, at least assessments covering a time span of a century. Hence, it is impossible to conclude if the Isla Persa species enrichment should have been expected to be higher than observed, as suggested by Grabherr *et al.* (1994) who showed increasing enrichment for decreasing altitudes within upper alpine and nival belts.

The nunatak of Isla Persa in the Eastern Swiss Alps is probably one of the rare available sites at which vegetation changes in the alpine belt can be assessed over the course of 20th century. The observed changes were less pronounced than expected based the results of similar studies for surrounding mountain summits, and while new species colonized the nunatak, most of them are still rare. However, the sum of the evidence presented here indicates a shift towards a vegetation of previously restricted lower altitudinal belts and thus, a trend indicating warmer local growth conditions. The conspicuous increase of *Vaccinium myrtillus* and the new presence of shrub and tree species underline this conclusion. Among the new species, ferns were particularly important, which can be due to a high dispersal potential brought about by their lightweight spores. But altogether, the pool of potential newcomers is still too strongly restricted by the alpine climate to have biological traits distinct from those of the species in the 1906-inventory. Additional data obtained in the future should help to gain a better understanding of processes influencing species composition in alpine grasslands and dwarf shrub heaths in a warmer world.

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G. REFERENCES

Aeschimann D, Lauber K, Moser DM and Theurillat J-P (2004) *Flora alpina*. Belin, 3 vol.

Archaux F, Gosselin F, Bergès L and Chevalier R (2006) Effects of sampling time, species richness and observer on the exhaustiveness of plant censuses. *Journal of Vegetation Science* **17**, 299-306.

Bader S and Bantle H (2004) *Das Schweizer Klima im Trend: Temperatur- und Niederschlagsentwicklung 1864-2001*. Veröffentlichungen 68. MeteoSchweiz, Zürich.

Braun-Blanquet J (1957) Ein Jahrhundert Florenwandel am Piz Linard (3414 m). *Bull. Jardin Bot. Bruxelles, vol. jubil. W. Robyns*: 221-232

Büchi H (1994) Der variskische Magmatismus in der östlichen Bernina (Graubünden, Schweiz). *Schweiz. Mineral. Petrogr. Mitt.* **74**, 359-371.

Burga CA (1999) Vegetation development on the glacier forefield Morteratsch (Switzerland). *Appied Vegetation Science* **2**, 17-24.

Burga CA, Walther G-R and Beissner S (2004) Florenwandel in der alpinen Stufe des Berninagebiets - ein Klimasignal. *Ber. d. Reinh.-Tüxen-Ges.* **16**, 57-66.

Camarero JJ and Gutiérrez E (2004) Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. *Climatic Change* **63**, 181-200.

Camenisch M (2002) Veränderungen der Gipfelflora im Bereich des Schweizerischen Nationalparks: Ein Vergleich über die letzten 80 Jahre. *Jahresber. Naturf. Ges. Graubündens* **111**, 27-37

De Haas JH (1973) *The vegetation of Isla Persa (Bernina, Switzerland) – a standard of climatic changes?* Field reports of the Netherlands centre for alpine biological research, Utrecht, NL.

Dirnböck T, Dullinger S and Grabherr G (2003) A regional impact assessment of climate and land-use change on alpine vegetation. *Journal of Biogeography* **30**, 401-417.

Dobbertin M, Hilker N, Rebetez M, Zimmermann NE, Wohlgemuth T and Rigling A (2005) The upward shift of pine mistletoe (*Viscum album* ssp. *austriacum*) in Switzerland. The result of climate warming? *International Journal of Biometeorology* **50**, 40-47.

Ellenberg H, Weber HE, Düll R, Wirtz V, Werner W and Paulissen D (1991) *Zeigerwerte von Pflanzen in Mitteleuropa.* Scripta Geobotanica 18, Goltze KG, Göttingen.

Flütsch P (1930) Über die Pflanzengesellschaften der alpinen Stufe des Berninagebietes. *Jahresber. Naturf. Ges. Graubündens* **68**, 37-88.

Gottfried M, Pauli H and Grabherr G (1998) Prediction of vegetation patterns at the limits of plant life: a new view of the alpine-nival ecotone. *Arctic and Alpine Research* **30**, 207-221.

Grabherr G, Gottfried M and Pauli H (2001) Long term monitoring of mountain peaks in the Alps. In: Burga, C. & Kratochwil, A. (eds). *Biomonitoring: general and applied aspects on regional and global scales*. Dordrecht, Kluwer.

Grabherr G, Gottfried M and Pauli (1994) Climate effects on mountain plants. *Nature* **369**, 448.

Grabherr G, Gottfried M, Gruber A and Pauli H (1995) Patterns and current changes in alpine plant diversity. In: Chapin III, F.S. & Körner, C. (eds). *Arctic and Alpine Biodiversity*. Ecological Studies 113. Springer, Berlin.

Greer GK (1993) The influence of soil topography and spore-rain density on gender expression in gametophyte populations of the homosporous fern *Aspidotis densa*. *American Fern Journal* **83**, 54-59.

Guisan A and Theurillat J-P (2000) Assessing alpine plant vulnerability to climate change: a modeling perspective. *Integrated Assessment* **1**, 307-320.

Hofer HR (1992) Veränderungen in der Vegetation von 14 Gipfeln des Berninagebietes zwischen 1905 und 1985. *Ber. Geobot. Inst. Eidgenöss. Tech. Hochsch. Stift. Rübel Zür.* **58**, 39-54.

Illa E, Carrillo E and Ninot JM (2006) Patterns of plant traits in Pyrenean alpine vegetation. *Flora* **201**, 528-546.

Kammer PM, Schöb C and Choler P (2007) Increasing species richness on mountain summits: upward migration due to anthropogenic climate change or re-colonisation? *Journal of Vegetation Science* **18**, 301-306.

Kercher SM, Frieswyk CB and Zedler JB (2003) Effects of sampling teams and estimation methods on the assessment of plant cover. *Journal of Vegetation Science* **14**, 899-206.

Klanderud K and Birks HJB (2003) Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *Holocene* **13**, 1-6.

Klimeš L, Dančák M, Hájek M, Jongepierová I and Kučera T (2001) Scale-dependent biases of species counts in a grassland. *Journal of Vegetation Science* **12**, 699-704.

Klotz S, Ingolf K and Durka W (2002) *BIOLFOR – Eine Datenbank mit biologisch-ökologishen Merkmalen zur Flora von Deutschland*. Schriftenreihe für Vegetationskunde 38, Bundesamt für Naturschutz, Bonn.

Körner C (2003) *Alpine plant life*. 2nd ed. Springer, Berlin.

Kudernatsch T (2005) *Auswirkungen der globalen Erwärmung auf die Vegetation alpiner Kalk-Magerrasen im Nationalpark Berchtesgaden*. Doctoral-Thesis, Department of Ecology, Technical University of Munich.

Kullman L (1986) Late Holocen reproductional patterns of *Pinus sylvestris* and *Picea abies* at the forest limit in central Sweden. *Canadian Journal of Botany* **64**, 1682-1690.

Kullmann L (2003) Förändringar i fjällens växtvärld – effekter av varmare klimat. [Changes in alpine plant cover – effects of climate warming.] *Svensk Bot. Tidskr.* **97**, 210-221.

Landolt E (1977) Ökologische Zeigerwerte zur Schweizer Flora. *Veröff. Geobot. Inst. ETH Stiftung Rübel Zürich* **64**, 1-208.

Lechner E (1858) *Piz Languard und die Bernina-Gruppe bei Pontresina*. Wilhelm Engelmann, Leipzig.

Lepš J and Hadincová V (1992) How reliable are our vegetation analyses? *Journal of Vegetation Science* **3**, 119-124.

Lloret F, Medail F, Brundu G, Camarda I, Moragues E, Rita J, Lambdon P and Hulme PE (2005) Species attributes and invasion success by alien plants on Mediterranean islands. *Journal of Ecology* **93**, 512-520.

MacArthur RH and Wilson EO (1967) *The theory of island biogeography*. Princeton University Press, Princeton.

Maisch M, Burga CA and Fitze P (1999) *Lebendiges Gletschervorfeld. Führer und Begleitbuch zum Gletscherlehrpfad Morteratsch.* 2nd Ed. Engadin Press, Samedan.

Moiseev PA and Shiyatov SG (2003) Vegetation dynamics at the treeline ecotone in the Ural highlands, Russia. In: Nagy, L., Grabherr, G., Körner, C. & Thompson, D.B.A. (eds.). *Alpine biodiversity in Europe - A Europe-wide assessment of biological richness and change.* Ecological Studies, Springer, Berlin.

Moser DM, Gygax A, Bäumler B, Wyler N and Palese R (2002) *Liste Rouge des fougères et plantes à fleur menacées de Suisse*. Série OFEFP "L'environnement pratique". Office fédéral de l'environnement, des forêts et du paysage, Berne.

Müller-Schneider P (1986) Verbreitungsbiologie der Blütenpflanzen Graubündens. *Veröff. Geobot. Inst. ETH Stiftung Rübel Zürich* **85**, 1-263.

Ozinga WA, Bekker RM, Schaminée JH and van Groenendael JM (2004) Dispersal potential in plant communities depends on environmental conditions. *Journal of Ecology* **92**, 767-777.

Parolo G, Rossi G (2008) Upward migration of vascular plants following a climate warming trend in the Alps. *Basic and Applied Ecology* **9**, 100-107.

Paul F, Kääb A, Maisch M, Kellenberger T and Haeberli W (2004) Rapid disintegration of Alpine glaciers observed with satellite data. *Geophysical Research Letters* **31**, L21402, doi:10.1029/2004GL020816

Pauli H, Gottfried M, Grabherr G (2001) High summits of the Alps in a changing climate. In: Walther, G.-R., Burga, C.A. & Edwards, P.J. (eds). *‘Fingerprints’ of Climate Change – Adapted behaviour and shifting species ranges*. Kluwer Academic/Plenum Publ., New York.

Pauli H, Gottfried M, Reiter K, Klettner C and Grabherr G (2007) Signals of range expansions and contractions of vascular plants in the high Alps: Observations (1994-2004) at the GLORIA master site Schrankogel, Tyrol, Austria. *Global Change Biology* **13**, 147-156.

Peñuelas J and Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biology* **9**, 131-140.

Pignatti S (2005) Valory di bioindicazione delle piante vascolari della flora d'Italia. *Braun-Blanquetia* **39**, 1-97.

Rebetez M and Reinhard M (2008) Monthly air temperature trends in Switzerland 1901-2000 and 1975-2004. *Theoretical and Applied Climatology*, **91**, 27-34.

Rübel E (1912) *Pflanzengeographische Monographie des Berninagebietes*. Engelmann, Leipzig.

Stöcklin J (1992) Umwelt, Morphology und Wachstumsmuster klonaler Pflanzen - eine Übersicht. *Botanica Helvetica* **102**, 3-21.

Stöcklin J and Bäumler E (1996) Seed rain, seedling establishment and clonal growth strategies on a glacier foreland. *Journal of Vegetation Science* **7**, 45-56.

Sturm M, Racine C and Tape K (2001) Climate change - Increasing shrub abundance in the Arctic. *Nature* **411**, 546-547.

Taylor AH (1995) Forest expansion and climate change in the mountain hemlock (*Tsuga mertensiana*) zone, Lassen Volcanic National Park, California, U.S.A. *Arctic and Alpine Research* **27**, 207-216.

Thornton IWB, Cook S, Edwards JS, Harrison RD, Schipper C, Shanahan M, Singadan R and Yamuna R (2001) Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. VII. Overview and discussion. *Journal of Biogeography* **28**, 1389-1408.

Ungricht S (1995) *Die Flora der Gletscherinsel Isla Persa (Bernina, Graubünden) – Ein Indikator für eine Klimaerwärmung?* Seminar Thesis, ETH Zürich.

van der Maarel E (1996) Pattern and process in the plant community: fifty years after A.S. Watt. *Journal of Vegetation Science* **7**, 19-28.

Vittoz P and Engler R (2007) Seed dispersal distances: a typology based on dispersal modes and plant traits. *Botanica Helvetica* **117**, 109-124

Vittoz P and Guisan A (2007) How reliable is the monitoring of permanent vegetation plots? A test with multiple observers. *Journal of Vegetation Science* **18**, 413-422.

Vittoz P, Jutzeler S and Guisan A (2006) Flore alpine et réchauffement climatique: observation de trois sommets valaisans à travers le 20ème siècle. *Bull. Murithienne* **123/2005**, 49-59.

Vittoz P, Rulence B, Largey T and Freléchoux F (2008) Effects of climate and land-use change on the establishment and growth of cembran pine (*Pinus cembra* L.) over the altitudinal treeline ecotone in the Central Swiss Alps. *Arctic Antarctic and Alpine Research* **40**, 225-232

Wahren C-HA, Walker MD and Bret-Harte MS (2005) Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology* **11**, 537-552.

Walther G-R (2004) Plants in a warmer world. *Perspect. Plant Ecol. Evol. Syst.* **6**, 169-185.

Walther G-R, Beißner S and Burga C-A (2005a) Trends in the upward shift of alpine plants. *Journal of Vegetation Science* **16**, 541-548

Walther G-R, Berger S and Sykes MT (2005b) An ecological „footprint" of climate change. *Proceedings of the Royal Society B: Biological Sciences.* **272**, 1427-1432.

Welling P, Tolvanen A and Laine K (2005) Plant traits: Their role in the regeneration of alpine plant communities in sub-arctic Finland. *Journal of Vegetation Science* **16**, 183-190.

Willson MF, Rice BL and Westoby M (1990) Seed dispersal spectra: a comparison of temperate plant communities. *Journal of Vegetation Science* **1**, 547-562.

H. ANNEX OF THE CHAPTER FIVE

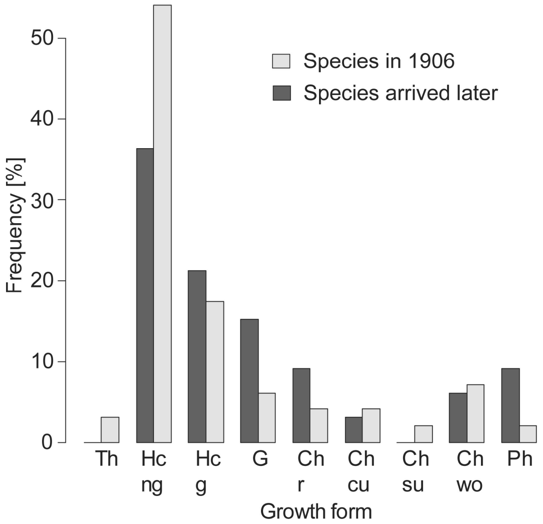
App. 1. Comparative plant inventory on Isla Persa (Swiss Alps). **1** species present without abundance estimation; ***** species probably overlooked because present in a previous and following inventory; **r!** very rare; **r** rare; **s** scattered; **c** common; **d** dominant; precision given if locally different (for example **s-lc** for scattered but locally common).

Species of the Rübel area (= ice-free area in 1906)			**Year**		
Species name	**1906**	**1927**	**1972**	**1995**	**2003/4**
Carex curvula	1	1	1	1	c-ld
Achillea erba-rotta subsp. *moschata*	1	1	1	1	c
Adenostyles leucophylla / A. intermedia	1	1	1	1	c
Agrostis rupestris	1	1	1	1	c
Agrostis schraderiana	1	1	1	1	c
Alchemilla fissa	1	1	1	1	c
Antennaria carpatica	1	1	1	1	c
Anthoxanthum odoratum s.l.	1	1	1	1	c
Cardamine resedifolia	1	1	1	1	c
Carex sempervirens	1	1	1	1	c
Doronicum clusii	1	1	1	1	c
Erigeron uniflorus	1	1	1	1	c
Euphrasia minima	1	1	1	1	c
Festuca violacea aggr.	1	1	1	1	c
Gentiana punctata	1	1	1	1	c
Geum reptans	1	1	1	1	c
Gnaphalium supinum	1	1	1	1	c
Hieracium piliferum aggr.	1	1	1	1	c
Homogyne alpina	1	1	1	1	c
Huperzia selago	1	1	1	1	c
Juncus trifidus	1	1	1	1	c
Juniperus communis subsp. *alpina*	1	1	1	1	c
Leontodon helveticus	1	1	1	1	c
Leucanthemopsis alpina	1	1	1	1	c
Ligusticum mutellina	1	1	1	1	c
Luzula alpinopilosa	1	1	1	1	c
Pedicularis kerneri	1	1	1	1	c
Phyteuma hemisphaericum	1	1	1	1	c
Poa alpina	1	1	1	1	c
Primula latifolia	1	1	1	1	c
Rhododendron ferrugineum	1	1	1	1	c
Salix herbacea	1	1	1	1	c
Saxifraga bryoides	1	1	1	1	c
Senecio incanus subsp. *carniolicus*	1	1	1	1	c
Sibbaldia procumbens	1	1	1	1	c
Solidago virgaurea subsp. *minuta*	1	1	1	1	c
Vaccinium gaultherioides	1	1	1	1	c
Veronica alpina	1	1	1	1	c
Viola biflora	1	1	1	1	c
Astrantia minor	1	1	1	*	c
Silene exscapa	1	1	1	*	c
Cirsium spinosissimum	1	1	1	1	s-lc
Minuartia sedoides	1	1	1	1	s-lc
Phyteuma globulariifolium s.l.	1	1	1	1	s-lc
Poa laxa / P. minor	1	1	1	1	s-lc
Silene acaulis	1	*	1	1	s-lc
Campanula barbata	1	1	1	1	s
Campanula scheuchzeri	1	1	1	1	s
Cystopteris fragilis	1	1	1	1	s
Empetrum nigrum subsp. *hermaphroditum*	1	1	1	1	s
Gentiana acaulis	1	1	1	1	s
Helictotrichon versicolor	1	1	1	1	s
Myosotis alpestris	1	1	1	1	s
Nardus stricta	1	1	1	1	s
Oreochloa disticha	1	1	1	1	s
Oxyria digyna	1	1	1	1	s
Polygonum viviparum	1	1	1	1	s
Potentilla aurea	1	1	1	1	s
Potentilla crantzii	1	1	1	1	s
Primula hirsuta	1	1	1	1	s
Ranunculus montanus	1	1	1	1	s
Saxifraga seguieri	1	1	1	1	s
Sedum alpestre	1	1	1	1	s
Taraxacum alpinum aggr.	1	1	1	1	s
Vaccinium vitis-idaea	1	*	1	1	s
Agrostis alpina	1	1	1	*	s
Selaginella selaginoides	1	*	1	*	s
Adenostyles alliariae	1	1	1	1	r-lc
Bartsia alpina	1	1	1	1	r-lc
Daphne striata	1	1	1	1	r-lc
Epilobium fleischeri	1	1	1	1	r-lc
Lotus alpinus	1	1	1	1	r-lc
Peucedanum ostruthium	1	1	1	1	r-lc

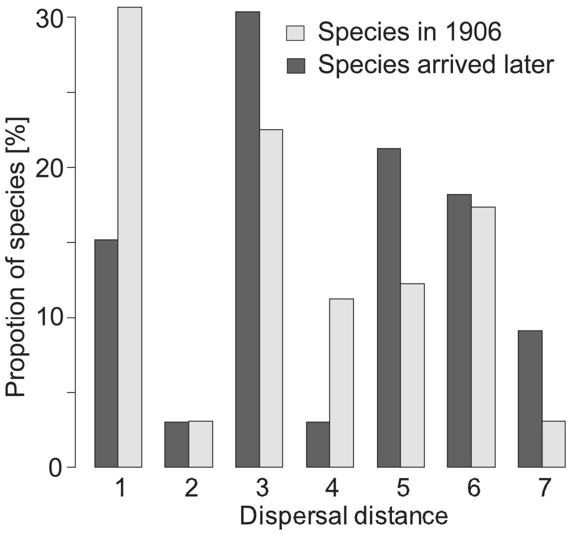
Sempervivum montanum	1	1	1	1	r-lc
Carex frigida / C. ferruginea	1	1	1	*	r-lc
Carex atrata subsp. *aterrima*	1	1	1	1	r-ls
Galium anisophyllon / G. pumilum	1	1	1	1	r-ls
Luzula spicata	1	1	1	1	r-ls
Arenaria biflora	1	1	1	1	r
Botrychium lunaria	1	1	1	1	r
Cerastium pedunculatum	1	1	1	1	r
Gentiana bavarica	1	1	1	1	r
Geum montanum	1	1	1	1	r
Hieracium alpinum	1	1	1	1	r
Lloydia serotina	1	1	1	1	r
Luzula lutea	1	1	1	1	r
Phyteuma hedraianthifolium	1	1	1	1	r
Ranunculus glacialis	1	1	1	1	r
Silene rupestris	1	1	1	1	r
Thesium alpinum	1	1	1	1	r
Cardamine alpina	1	*	1	1	r
Epilobium angustifolium	1	*	1	1	r
Gentiana ramosa	1	*	*	1	r
Achillea nana	1	*	1	*	r
Avenella flexuosa / Deschampsia caespitosa	1	1	1	1	r!
Vaccinium myrtillus		1	1	1	s-lc
Elyna myosuroides		1	1	1	s
Pinguicula leptoceras		1	1	*	s
Soldanella alpina		1	1	*	s
Cerastium uniflorum		1	1	1	r-lc
Primula integrifolia		1	1	*	r-lc
Gentiana brachyphylla		1	1	1	r
Trichophorum cespitosum		1	*	*	r
Antennaria dioica		1	1	*	r!
Cryptogramma crispa			1	1	r
Athyrium distentifolium			1	1	r
Polystichum lonchitis			1	1	r
Trifolium alpinum			1	1	r
Asplenium septentrionale			1	*	r
Coeloglossum viride			1	*	r
Phleum alpinum			1	*	r
Poa supina / P. annua / P. badensis			1	*	r
Sagina saginoides / S. glabra			1	*	r
Salix helvetica			1	1	r!
Diphasiastrum alpinum			1	*	r!
Ribes petraeum			1	*	r!
Gymnocarpium dryopteris				1	r!
Arctostaphylos uva-ursi					r!
cf. *Aster bellidiastrum*					r!
Dryopteris cf dilatata					r!
Dryopteris filix-mas					r!
Festuca rubra aggr.					r!
Gentiana verna					r!
Larix decidua					r!
Leontodon cf. *autumnalis*					r!
Pulsatilla alpina s.l.					r!
Euphrasia rostkoviana	1				
Gentiana campestris	1				
Thymus serpyllum		1			
Festuca halleri			1		
Veronica bellidioides	1	1	1		

Additional species occurring only on the recently deglaciated area			**Year**		
Species name	**1906**	**1927**	**1972**	**1995**	**2003**
Androsace alpina / A. pubescens		1	1	1	1
Saxifraga oppositifolia		1	1	*	1
Saxifraga stellaris		1	1	*	1
Poa nemoralis		1	*	*	1
Arabis caerulea			1	1	1
Artemisia genipi			1	1	1
Salix glaucosericea			1	1	1
Salix hastata			1	1	1
Saxifraga exarata			1	1	1
Veronica fruticans			1	1	1
Arabis alpina			1	*	1
Epilobium anagallidifolium			1	*	1
Hieracium intybaceum			1	*	1
Salix retusa			1	*	1
Salix serpillifolia			1	*	1
Asplenium viride			1	1	
Salix foetida			1	1	
Saxifraga paniculata			1	1	
Tussilago farfara			1		
Linaria alpina				1	1
Erigeron cf. *neglectus*					1
Luzula cf. *sudetica*					1
Phyteuma betonicifolium					1

App. 2. Distribution of the 98 species present in 1906 and the 31 that arrived later on 9 growth-form types (Pignatti 2005; Illa *et al.* 2006): Th, therophytes; Hc ng, non-graminoid hemicryptophytes; Hc g, graminoid hemicryptophytes; G, geophytes; Ch r, creeping chamaephytes; Ch cu, chamaephytes in cushion; Ch su, succulent chamaephytes; Ch wo, woody chamaephytes; Ph, phaneophytes.



App. 3. Distribution of dispersal distance potential for the 98 species present in 1906 and the 31 that arrived later on 7 categories (Vittoz & Engler 2007): 1, 99% of the seeds fall in a distance <1 m; 2, <5 m; 3, <15 m; 4, <150 m; 5, <500 m; 6, <1500 m; 7, <5000 m.



IV. GENERAL DISCUSSION

In the previously presented studies, we observed an upward shift of species or plant communities, at different locations and elevations in the Alps. This was apparently in agreement, at least in terms of direction of change, with the expected response to climate warming. In the first presented study, the species movement was revealed by a significant mean upward shift of modelled distribution optimum of 175 species after 14 years, in the French Mediterranean mountains. However, life traits of those shifting species suggested an influence of forest closure and maturation, confirmed by the insignificant shift for 164 species in only closed forests. In the second presented study, observations and analyses revealed, after 47 years, an upward shift of thermophilous communities along the elevation gradient and the retreat of continental communities from the inner-alpine Maurienne valley, in the French Alps. In the meantime, vegetation also shifted in the same valley toward a more eutrophic state, probably in relation with nitrogen emissions from road traffic. In a third study, among 45 species, 21 showed the upward retreat of their lower limit at the regional scale, whereas 7 only were shifting downward, after one century in Bernina valley, Switzerland, confirming the possible climate control at lower limit of species distribution. In a fourth study, also made in Bernina valley, a peculiar ecological model, the nunatak, an area protected from anthropogenic influences by the important physical barrier of glaciers received 31 new species, mostly from lower elevation belts. All these results point to a response to climate warming, but species and community dynamics also revealed significant responses to other environmental changes.

A. WHAT CONCLUSIONS CAN BE DRAWN BY CONNECTING THE DIFFERENT STUDIES RESULTS?

1. A spatially varied response to climate change

The intensity of the response of species and communities depends on the area and period studied. In the cases of the upward shift of thermophilous communities (Maurienne valley), of the progression of species from lower vegetation belts into the nunatak, or of retreat of species lower limits (Bernina valley), we concluded climate warming was the main factor of vegetation dynamics, but the rate of shift varied among studies (table 1). The mean shift was the highest for plant communities in Maurienne valley forests, +29.0m/decade, a value which is high compared to other studies (table 1) and comparable to results from Lenoir *et al.* (2008) calculated for species optimum over all mountains of France. But, Lenoir *et al*. observed such a high rate between 1971 and 1993 on average, that is to say a period when the climatic trend was steep, of 0.5°C degrees/decade, *i.e.* +89m/decade in elevation equivalent. Thus, there was a strong lag (3 times less), in Lenoir *et al.* study, between the observed species altitudinal shift (+29.4 m/decade) and climate warming (+89 m/decade). In the case of the Maurienne valley, the period studied was 1955-2002. During this period, the increase in average temperature was 0.16°C/decade (28.8m/decade) only, according to the closest long climatic series we could find. The trend have probably been of the same order of magnitude in other parts of Europe for the same period, because it is a general observation that temperature decreased nearly everywhere between the 1950s and the 1970s (see also Sils-Maria meteorological station). Thus, in Maurienne valley, vegetation exactly tracked the change in average temperature.

Shift was only +5.6m/decade at species lower limits in Bernina valley, where the increase in temperature has been steeper. We estimated the latter from nearby station of Sils-Maria (15 km from our sites). Mean temperature of the May to September months, averaged over the 15 preceding years in order to take into account the lagged response of vegetation, has increased by 1.2°, from 8.0°C to 9.2°C between 1910 and 2006. That is equivalent to an altitudinal shift of temperature isolines of 21m/decade, four times larger than the observed shift in lower limits of species.

It was not possible to calculate a shift elevation for nunatak species. Finally, the shift in closed forests of Mediterranean mountains was 6.7 m/decade (13.6 m/decade in opened forests), largely behind the instrumental trend of 0.5°C/decade (89 m/decade) during the study period.

How to interpret these differences? All previous studies published so far have shown an inertia in species response to climate change, with observed mean shifts between 22.3 and 29.4 m/decade for the largest ones (Beckage *et al.* 2008, Dobbertin *et al.* 2005, Kelly & Goulden 2008, Lenoir *et al.* 2008 and table 1). The spatial extent of all the works already done was highly variable, from the study of one summit or a small nunatak, to the study of all mountains of France. On a statistical point of view, the absolute amplitude of the vegetation shifts, whatever their direction, upward or downward, should be the largest when observed on the smallest areas, because the chance for local factors or random effects to play a larger role than global drivers increases when the area under study decreases. However, it is not what we observed in our works. In our largest area of study, the Southern Alps, the elevation shift was the smallest.

Several causes could explain why vegetation did not track the upward movement of temperature isolines, sometimes lagging largely behind. First, plant species could be limited in their dispersal capacities, not being able to colonize new sites at higher elevation. It has been repeatedly shown that ‘true’ forest species have very low colonizing ability (Hermy *et al.* 1999). Typically, geophytes such as *Euphorbia dulcis*, *Lathyrus vernus*, *Mercurialis perennis* or *Polygonatum multiflorum* which were observed as descending species in the south-eastern France are poor colonizers. Species with high dispersal ability were expected to shift higher than other ones, as confirmed by Lenoir *et al.* (2008) or Vittoz *et al.* (2009). Indeed, we detected a larger shift of species with high dispersal ability in the study on upper limits, on the nunatak (Vittoz *et al.* 2008). Even in case of successful dispersion, colonization of new sites could be rendered impossible by competition with other, already installed species. Secondly, at their lower limits, plants could resist for a long time before disappearing because most of forest and mountain species are perennials. Individuals of more than several tens of years old are commonly observed (Schweingruber & Poschlod 2005). In the forest belts, canopy cover moderates climate variability underneath it, and could buffer the temperature increase perceived by understorey species. This could partly explain the weak response of species in Mediterranean closed forests. However, the marked response of communities in Maurienne valley does not confirm this explanation. The case of the nunatak is, of course, particular. Because of its strong isolation, it was more difficult for new species to reach it, crossing the barrier constituted by the glacier. Moreover, its microclimate could be colder than other lands at the same elevation, because glaciers surround it. Indeed, the increase in species richness on Isla Persa was relatively small in comparison to other similar studies on summits of the Bernina region or, more generally, of the Alps.

No differences should be expected in the response of species according to their thermal preference, that is to say their position along the elevational gradient, if climate warming has been homogeneous all along this gradient. It is not yet clear how climate has warmed at different elevations. From a synthesis from a large set of climatic data, we have shown that the rate of warming has been the same at all elevations below 1675m in the French Southern Alps. On the opposite, Beniston (2006) underlined the much higher rate of increase in the Alps in comparison with the northern hemisphere or the surroundings lowlands. Anyway, some authors detected stronger shift in specific thermal ecological groups: upper limit of cryophilous bryophytes shifted higher than intermediate and thermophilous species in Switzerland (Bergamini *et al.* 2009), and montainous rather than ubiquitous species shifted in French mountains (Lenoir *et al.* 2008). We also observed a faster upward movement of thermophilous species in the South-eastern Alps. There are no easy explanations for such a differentiation of responses to climate warming among species according to their thermal requirement.

Studies of vegetation change, in our work and in other already published works, cover a wide range of time spans, from a century to fourteen years only. Depending on how the global change drivers developed over time, the observational time window of vegetation dynamics could play an important role on the results obtained. A long period of observation does not imply that the observed changes will be large, if no environmental changes occurred in the meantime, or if the starting and ending environmental states are the same. As regard climate warming in Western Europe, we know that the general trend was an increase in temperature from the late XIXth century (end of Little Ice Age) to 1950, then a decrease up to the middle of the 1970s, and then a steep increase during the next three decades. Hence, comparisons between 1900 and today should provide the largest responses of vegetation. Comparisons between 1950 and today should give the smallest response, and comparisons made during the last decades should give intermediate responses. We did not observe that. On the opposite, the largest response to temperature was observed in the Maurienne valley, where we compared 1950 and today.

The width of the time window studied also play a role on the statistical power we have to detect changes in vegetation. For a given number of plots, the shortest the time span between two inventories is, the smallest is our capacity to detect a change, because the change will be too small in absolute magnitude due to the short duration of observation. However, in the case of the Mediterranean mountains of the southern Alps where we studied a fourteen-year period only, we had under disposal several ten of thousands of plots, which should have been enough to detect the expected 125 m shift (0.5°C/decade, *i.e.* 89 m/decade, *i.e.* 125 m in fourteen years).

Last, the duration of the interval could also play a role on data quality. The accuracy of the data probably worsens a bit with time the further we go in the past. Because the exact delineation of the plots, the exact duration of the plant censuses, the date in the year of the observations, the way vertical layers were taken into account, the number of observers were not well recorded or controlled in the past, we have some difficulties today to accurately reproduce ancient protocols.

2. Responses to land-use change and other anthropogenic pressures

From a careful examination of the ecology of shifting species, we could identify some other important phenomena responsible for vegetation changes apart from the sole temperature increase. Most shifting species in east-southern France had life traits associated to forest successional dynamics and not climate change. Moreover, the mean shift was not anymore significant when running the analysis in closed forests only, confirming an effect of forest closure and maturation. The areal decrease of open forest at lower elevations could have induced changes in the frequency of species only at one side of their distribution, leading to a change in their calculated optimum. In Maurienne valley, the response of species to climate warming was accompanied by an eutrophication, *i.e.* an enrichment in nitrogen demanding species. On the nunatak, a few species arrived probably thanks to hikers' influence.

It was rather unexpected to observe so large effects of land abandonment, in southeastern France, and nitrogen deposition, in Maurienne valley, whereas our sampling design was mainly planned to detect the impact of climate change. It implies that more specific sampling designs than ours, more adapted to the sole detection of effects of nitrogen deposition or the effects of old-field succession could be much more efficient and should be applied, in the future, to the same region we studied.

For example, one could stratify the sample according to the distance from main nitrogen emitters and the background regional levels of deposition in order to better assess the specific effects of nitrogen deposition. Deletraz (2002) measured and modelled total nitrogen deposition along a highway in the Pyrenees mountains varying between 100 kg.ha^{-1}.yr^{-1} close to the traffic and 3 kg.ha^{-1}.yr^{-1} at distance. Interestingly and logically, she observed that, for a given amount of nitrogen emitted, the deposition was higher along surrounding slopes when they are steep than when the landscape is more opened. Thus, there exist a strong gradient of decreasing deposition with increasing distance from the highway, and which intensity depends on the slope angle. It would be interesting, in the Maurienne valley, to better study this important cause of plant communities' dynamics, at least by launching a synchronic study.

It could be interesting to test if the eutrophication observed in Maurienne valley has also occurred in Mediterranean mountains of the Southern Alps. Unfortunately, because Ellenberg and Landolt type indicator values have not yet been established for Mediterranean vegetation, values were missing for too many species, even among the most frequent, preventing to test the importance of this phenomenon in this region. Such indicator values have been proposed for species of Italy and Greece. But they are not publicly available, and they cover only a part of the French list of species. We think there is an urgent need for the establishment of a complete set of indicator values for nitrogen availability in the Mediterranean region. However, the regional component of nitrogen deposition is probably lower in the south-eastern part of the Alps than in the Maurienne valley. The Renecofor Level II network indicated 4.4 kg.ha^{-1}.yr^{-1} in the Southern Alps, close to out study based on National Forest Inventory data and 7.4 kg.ha^{-1}.yr^{-1} in the vicinity of the Maurienne valley.

Nitrogen demanding species are more ubiquitous than oligotrophic species. Thus, the shift toward more nitrophilous states of forests in the Maurienne valley is probably accompanied by a decrease in beta-diversity. As regard the elevational shift, it has also been shown by Jurasinski & Kreyling (2007) that the arrival of new species from lower elevation upon the summits of Bernina decreased beta-diversity among summits.

In the south-eastern alps, one of the conclusion is that it would have been profitable to introduce in our analyses and models a direct information about the old-field succession stage of the forest, or the ancientness of the forest status. Ancient maps such as the Military Survey Map, or the Napoleonian cadastre, from the first half of the XIXth century provide this information for the whole of France (Dupouey *et al.* 2007). However, these documents are not yet digitized. In view of the prime importance of the land-use change driver in our landscapes, we think it would be valuable to digitize and make available all these maps for a general audience.

Another, but indirect, way to characterise the dynamic status of a plot is to collect detailed dendrometric and cover variables, as we did in south-eastern France. In the absence of direct information about the historical land use on each plot, the detection of climate change impact would be pertinent only when associated to the analysis of changes in forest stands characteristics. Whereas it is assumed that species distribution on broad scales is controlled by climate (Woodward 1987), local factors such as forest structure play an increasing role as the surface of the area under study decreases. Even in rather large mountainous zones, forest structure can play a larger role in vegetation variability than the elevational climatic gradient (Bacaro *et al.* 2008, Moning *et al.* 2009).

In the Maurienne valley, effects of ancient land use were largely limited, even made nil, because, at the second inventory, we selected only plots that were already forested at the date of the first inventory. Because we selected our 2002 plots only within forested units of the 1955 map, they were probably forest since a long time ago. However, we do not have information about the history of silvopastoralism in these forests, which could have also impacted vegetation.

Tourist pressure has highly increased over one century in all the Alps. It could have two opposite effects in the frame of the present work. On the nunatak, it could have favoured the colonization by new species because of seed transportation from lower elevation by hikers and opening of ground spaces by trampling. At the lower limits of species, it could have promoted habitat loss through infrastructure development (skiing resorts, buildings), accelerating the effect of climate change.

3. Advantages and drawbacks of different methods: sampling bias, spatial scale and sampling intensity

The reinventory of an existing area often lead to an increase in the species richness, sometimes at the level of the entire area under study (gamma-diversity), but more surely, in nearly every cases, at the level of the plot (alpha-diversity). Extreme care should be taken when analysing this increase in species number, as it can often be the effect of sampling bias. Increase in exhaustiveness can be explained by a better observers' carefulness during plant censuses, or by a larger inventoried area since no detailed plot area was specified in any historical study (Archaux *et al.* 2006). National forest inventories should be able to provide a high level of homogeneity between successive inventories, because they usually have to describe and record precisely the methodology used. Unfortunately, in our work, the sampling method for collection of NFI data in Mediterranean mountains had changed between the two inventories. Plot area had increased from a 6 m radius circle to a 15 m radius circle, increasing the plot species richness. It had constrained us to work only with species optima that are not influenced by a homogeneous increase of species frequency, and had precluded the study of range limits or changes in average elevation that are sensitive to this increase. In this study, the total species number recorded in the entire area under study (gamma-diversity) was approximately the same at each inventory, but the mean number of species per plot increased dramatically. The intense and systematic sampling scheme of National Forest Inventory (30985 plots) could explain why even rare species were observed at the first inventory and, thus, why an increase of plot area at the second inventory did not lead to the detection of new species. In Maurienne valley, the number of species per plot had also increased a lot, probably because of a larger effective plot area. We got rid of this bias thanks to the use of indicator values, which provide a global ecological value for the plant community. Few papers have addressed the question of the independence of global community ecological indicators (Ellenberg indicator values, position along ordination axes…) from the species exhaustiveness bias. The exact question to be addressed in the future should be: are there any observe bias toward the overlooking or, conversely, over-representation of species carrying specific ecological information, *i.e.* thermophilous or nitrogen demanding species? In the absence of true answers to this important question, we assume that such biases are minimal. In the Maurienne valley, the total species number recorded at each inventory increased from 396 to 630. The less frequent species, not observed at the first inventory, were detected at the second one probably because of larger sampling plots and better exhaustiveness.

On the nunatak Isla Persa, study directly dealt with changes in species number per plot. However, the delimitation of the area was clear, and attention was paid, in the interpretation of the results, to the time spent and number of observers at each inventory. Moreover, conclusions about new but rare species were cautious because of possible previous overlooking.

But, there is a strong and well known gradient of decreasing species richness (both alpha- and gamma-diversity) with increasing elevation (Grabherr *et al.* 1994). Based on this gradient, the observed increase in species number per plots at the upper limits of species ranges has been often interpreted as an upward shift of climatic belts. This is true at the absolute condition that plant census exhaustiveness has not changed between inventories, a condition which is very difficult to verify and probably false in most cases.

At upper limits of species distribution range, the potential bias results mostly from species overlooking in previous inventories or exhaustiveness increase in today inventories, due for example to a larger area of sampling surfaces, creating an apparent upward shift of species. At lower limits, the bias problem is different and depends on the type of site under study. If the detection of species lower limit is done in small, localized, areas, as it has been done for the detection of upper limits on alpine summits, an increase in exhaustiveness will lead to an apparent (and false) downward movement of the species. But, usually, the search for lower limits can be undergone in large areas, because low elevations represent much larger land areas than summits. In the case of the search for lower limits in Bernina, we did not resampled small plots, but looked for a limited set of species along large slopes of the valleys. Thus, the bias is the reverse as for small plots: the probability of overlooking is probably higher today than before. To find more species today than in the past in a small plot or quadrat is easy. One just needs to increase the pressure of observation. But on the opposite, to find back the lowest locality of a species in a large area is difficult. Lower limit of species in Bernina valley showed an upward shift, but we do not have a precise estimate of our overlooking rate (leading to false absences) in the search for species at their ancient localities. Such false absences could have artificially inflated the upward observed shift.

Finally, we summarize in table 2 the requirements, advantages and drawbacks of the different cases. A large number of plots is needed to seize the distribution of a single species in an adequate model. Studying a large number of species helps testing the homogeneity of the directional shift among species. Moreover, having a large set of studied species makes possible inferences on the causes of the observed shift from an analysis of species life traits, as we did here in several occasions.

Table VI-1: Comparison of average altitudinal species shift observed in various studies. Treeline studies are excluded. (n.p.pl.: non-permanent plots; p.pl.: permanent plots).

Method	Study area and vegetation type	Calculation method for the shift	Period studied (time span in years)	Additional information	Number of sample plots or localities	Number of species used for calculations	Mean (median) shift over the total time span	Mean (median) shift in m per decade	Main causes attributed to the species shift
Modelled species optimum	**Forest vegetation of Southern Alps and Mediterranean piedmont, France (Bodin *et al.* submitted, chapter two)**	Mean of species optimum shift	**1985-1999 (14.1)**	**All forests type** ***Closed forests only***	**30985 n.p.pl.** ***24368***	**175 sp.** ***64 sp.***	+17.9* (+19.2) -3.0(+9.5)	+12.6* (+13.6) -2.1(+6.7)	**Changes in forest dynamics**
	French mountain forests (Lenoir *et al.* 2008)		1971-1993 (22)		7982 n.p.pl.	171 sp.	+64.8***	+29.4***	Climate change
Species mean elevation	Briançonnais, Southern French Alps (Dupouey *et al.* 1998)	Mean shift of the species mean elevation	~1970-1993 (22)	Subalpine forests	73 p.pl	316 sp.	+16***	+7.3***	Climarte change
	Forests to desert scrub in Southern California's Santa Rosa mountains (Kelly & Goulden 2008)	Mean shift of the cover-weighted mean elevation	1977-2007 (30)		20 p.plots for 1 transect	10 sp.	+65±34	+21.7±11.3	Climate change
Species community	**Forest understorey vegetation of inner Alps, Maurienne valley, France (This thesis, chapter three)**	**Elevation equivalent shift issued from the Landolt indicator value for temperature shift**	**1956-2003 (47)**		**475 n.p.pl** ***Calc.: 240*** ***Non-calc.: 235***	516	+139.2*** +176.7*** +97.0***	+29.0*** +36.9*** +20.2***	**Climate change and probably land-use change; eutrophictaion**
	Vegetation composition of the nunatak Isla Persa (Vittoz *et al.* 2008, chapter five)	**Species number**	**1906-2004 (100)**	**Local scale**	**1 p.pl.**		**31 new arrived species**		**Climate change**
Lower limit of species	**Subalpine and alpine belt in Swiss Alps (Walther *et al.* submitted, chapter four)**	**Mean shift of the species lower limit**	**1906-2006 (100)**	**Local scale**	46 sp.*localities	**35 sp.**	**-2.4 (+1.0)**	**-0.2 (+0.1)**	**Climate change**
				Regional scale		**45 sp.**	+55.8* (+15.0)	+5.6* (+1.5)	**Climate change**
Upper limit of species	Summit vegetation in the Swiss Alps (Walther *et al.* 2005)	Mean shift of the species upper limit newly recorded at summits	1906-2003 (97)	Species reaching a summit for the first time		18 sp.	+269.7	+27.8 (calculated on upward shifting species only)	Climate change
				All species (1)		105 sp.	+62.6***(+5.0)	+6.4***(+0.5)	
	Summit vegetation in the Swiss Alps (Walther *et al.* submitted)		1906-2005 (99)	All species	1 summit	172 sp.	+145.3***	+14.7***	Climate change
				All species except Languard		119 sp.	+138.4***	+14.0***	
				Languard last 300m		53 sp.	+161***	+16.3***	
	Pine mistletoe in Swiss mountain forests (Dobbertin *et al.* 2005)		1910-1995 (85)			1 sp.	+190	+22.3	Climate change
	Alpine nival plant species in Austria and Switzerland (Grabherr *et al.* 1994)		1900's-1992 (70-90)	Alpine-nival summits	26 summits	9 sp.		+1 to +4 (calculated on upward shifting species only)	Climate change
	Grisons summits, Switzerland (Holzinger *et al.* 2008)		1885/1958-2004 (46-120)	Alpine-nival summits	12 summits	140 sp.		+2.2	Climate change
	Rhaetian Alps, Italy (Parolo & Rossi 2008)	Shift of the species upper limit recorded along an altitudinal transect	1958-2005 (47)	Alpine-nival vegetation	1 transect	93 species		(+23.9) (calculated on upward shifting species only)	Climate change
	Sub-antartic Marion Island (le Roux & McGeoch 2008)		1966-2006 (40)		Several transects	21 sp.	69.6*	+17.4*	Climate change
Biome limit	Vermont, USA (Beckage *et al.* 2008)	Shift of limit between hardwood and boreal forests	1962-2005 (43)		Aerial photographs	/	91-119	+21.2-+27.7	Climate change

(1): Mean shift calculated based on the upper limit given by Walther *et al*. 2005 and historical upper limit in the valley (Rübel 1912).

B. GENERAL CONCLUSIONS

We analyzed long-term vegetation changes in different regions of the Alps, on different time windows. We developed methods adapted to the analysis of vegetation changes in non-permanent sampling designs. Thousands of ancient relevés are becoming available in Western Europe thanks to the progresses in the computerization of vegetation data. They were most often not precisely localized at the first sampling date. Our methods open large perspectives for the valuation of these ancient data.

Our main conclusion is that climate warming during the XXth century did not have a homogeneous impact on vegetation all over the Alps. In some areas, vegetation exactly tracked the observed increase in temperature, in some others not. We have no real good explanation for such regional differences. It must be pointed out that spatial variations in the XXth century trends of temperature have not yet been mapped in Europe.

A second important conclusion is that vegetation is always lagging behind the upward movement of temperature isolines. Whereas we worked in mountains, where the steep adiabatic lapse rate should have allowed species to stay more easily in balance with their climatic niche, they did not migrate fast enough. It probably implies that, in the lowlands, where the latitudinal rate of change in temperature is one thousand times less steep than along slopes of mountains, the lag between climate warming and plant species migration will exacerbate.

In the case of the two main forest studies undergone in France, we had chosen to work in forested areas because we wanted to avoid the problem of confusion between the effects of climate change and abandonment of pastoralism which often darkened the interpretation of long-term studies above the treeline. But, so doing, we revealed, in the Mediterranean mountains, other potential confusion factors operating within forest belts, mainly changes in forest successional dynamics linked to ancient land-use and forest management changes. Because such drivers currently operate over all Europe, together with climate change, they should be controlled for in long-term resampling or monitoring studies. In this perspective, maps of ancient land-use are urgently needed.

Although not specifically planned for such a purpose, we also detected another strong signal, namely eutrophication of vegetation in the Maurienne valley. As for climate, we do not have a mapped history of nitrogen deposition in Europe. What is worse, we still do not have precise maps of today spatial variations in nitrogen deposition. Hence, although we have some clues regarding the causes of this eutrophication (increase in local road traffic), we still cannot insure that it is not a general phenomenon occurring all over the Alps.

On the conservation point of view, our results imply that, if we have to act against the effects of climate change on vegetation, it is not really because of already observed effects that are still unclear, but more because of the strong planned responses of plant biota to the coming warming. The focus should be perhaps given more to direct effects of anthropogenic actions such as habitat loss, isolation or transformations and to some pollution effects today under-evaluated.

Our work has some practical conclusions as regard monitoring of vegetation in current observational networks. A measure of observers' exhaustiveness should be included in the quality control program of these networks. If the objective is the long-term and repeatability of methods, the minimal area method should not be selected to delineate the plant census area. Number of observers, their identity, the exact duration of the plant census should be all recorded. Above all, initial methods selected for plant census (and usually any other target parameter…) should not be changed between two successive inventories. If such a change in methods appears necessary, the ancient method, used at the previous inventory, should be applied at the next one, together with the new method, a costly but mandatory constraint. For example, the very simple ‘duration of observation’ or ‘number of observers” are not even recorded in European databases, whatever the vegetation network. Indeed, only a few countries decided to control for these parameters in their field manuals.

Finally, our results are calling into question the currently dominant interpretation of vegetation changes in mountains. Many broadly distributed phenomena are occurring in parallel with climate warming and are also able to induce vegetation changes. They should be more carefully considered in long-term studies of vegetation dynamics, before incriminating the sole climate change.

Table VI-2: Comparison of some advantages, drawbacks and adapted analytical approaches, depending on the type of long-term study.

		Permanent plots	**Non-permanent plots**
		. Abiotic factors are inherently kept constant in permanent plots . Bias due to stand ageing	. Need for a stratification of abiotic factors, homogenously through successive inventories
Large set of plots	. costly . more significant results	. Direct comparison of positional parameters of the species distribution (mean, amplitude, limits) between inventories . Changes in species frequencies of occurrence (if no exhaustiveness bias) . Changes in communities indicators values	. Changes in model (position of optimum, amplitude, limits) of species distribution according to abiotic factors . Changes in average level of probability of presence (if no exhaustiveness bias) . Changes in model of plant communities indicators according to abiotic factors
Medium size sample of plots		. Changes in communities indicators values	. Changes in model of plant communities indicators according to abiotic factors

C. REFERENCES

Archaux F, Gosselin F, Bergès L, Chevalier R (2006) Effects of sampling time, species richness and observer on the exhaustiveness of plant censuses. *Journal of Vegetation Science*, **17**, 299-306.

Bacaro G, Rocchini D, Bonini I, Marignani M, Maccherini S, Chiarucci A (2008) The role of regional and local scale predictors for plant species richness in Mediterranean forests. *Plant Biosystems*, **142**, 630-642.

Beckage B, Osborne B, Gavin DG, Pucko C, Siccama T, Perkins T (2008) A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 4197-4202.

Beniston M (2006) Mountain weather and climate: A general overview and a focus on climatic change in the Alps. *Hydrobiologia*, **562**, 3–16.

Bergamini A, Ungricht S, Hofmann H (2009) An elevational shift of cryophilous bryophytes in the last century – an effect of climate warming? *Diversity and Distributions*, **15**, 871-879.

Deletraz G (2002) *Géographie des risques environnementaux lies aux transports routiers en montagne; Incidences des émissions d'oxydes d'azote en vallées d'Aspe et de Biriatou (Pyrénées)*. Unpublished PhD thesis, Université de Pau et des Pays de l'Adour, .

Dobbertin M, Hilker N, Rebetez M, Zimmermann NE, Wohlgemuth T, Rigling A (2005) The upward shift in altitude of pine mistletoe (*Viscum album* ssp. *austriacum*) in Switzerland—the result of climate warming?. *International Journal Biometeorology*, **50**, 40-47.

Dupouey J, Becker M, Bert D, Cadel G, Lefèvre Y, Picard J, Thimonier A (1998) Évolution récente des sols, de la végétation et de la productivité des forêts de montagne françaises. *Écologie*, **29**, 341-349.

Dupouey J, Bachacou J, Cosserat R, Aberdam S, Vallauri D, Chappart G, Corvisier de Villèle M (2007) Vers la réalisation d'une carte géoréférencée des forêts anciennes de France. *Le Monde des Cartes*, **191**, 85-98.

Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. *Nature*, **369**, 448.

Hermy M, Honnay O, Firbank L, Grashof-Bokdam C, Lawesson J (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation*, **91**, 9-22.

Holzinger B, Hulber K, Camenisch M, Grabherr G (2008) Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates. *Plant Ecology*, **195**, 179-196.

Jurasinski G, Kreyling J (2007) Upward shift of alpine plants increases floristic similarity of mountain summits. *Journal of Vegetation Science*, **18**, 711-718.

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11823-11826.

Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768-1771.

Moning C, Werth S, Dziock F, Bassler C, Bradtka J, Hothorn T, Muller J (2009) Lichen diversity in temperate montane forests is influenced by forest structure more than climate. *Forest Ecology and Management*, **258**, 745-751.

Parolo G, Rossi G (2008) Upward migration of vascular plants following a climate warming trend in the Alps. *Basic And Applied Ecology*, **9**, 100-107.

Schweingruber FH, Poschlod P (2005) Growth rings in herbs and shrubs: life span, age determination and stem anatomy. *Forest Snow and Landscape Research*, **79**, 195-415.

Vittoz P, Bodin J, Ungricht S, Burga C, Walther GR (2008) One century of vegetation change on Isla Persa, a nunatak in the Bernina massif in the Swiss Alps. *Journal of Vegetation Science*, **19**, 671-680.

Vittoz P, Dussex N, Wassef J, Guisan A (2009) Diaspore traits discriminate good from weak colonisers on high-elevation summits. *Basic and Applied Ecology*, **10**, 508-515.

Walther G, Beißner S, Burga CA (2005) Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, **16**, 541-548.

Woodward FI (1987) *Climate and plant distribution*. Cambridge University Press.

le Roux PC, McGeoch MA (2008) Rapid range expansion and community reorganization in response to warming. *Global Change Biology*, **14**, 2950-2962.

ANNEXES

PEER REVIEWED ARTICLES

One century of vegetation change on Isla Persa, a nunatak in the Bernina massif in the Swiss Alps. 2008. *Journal of Vegetation Science* **19**: 671-680. VITTOZ P.; BODIN J.; UNGRICHT S.; BURGA C.; WALTHER G.-R.

NOT PEER REVIEWED ARTICLES

Déplacements déjà observés des espèces végétales : quelques cas emblématiques mais pas de migrations massives. 2007. *RDV techniques hors-série* **3**, 34-39 - *ONF*. DUPOUEY J.-L.; BODIN J.

CONFERENCES

Changements observés de la végétation de montagne au XXe siècle : quel impact du réchauffement climatique ? *Actes du colloque Géoflore*, 10-12 May 2007, Velaine en Haye (France) 59-64. BODIN, J.; DUPOUEY, J.-L.; BADEAU, V.; CLUZEAU, C.; DRAPIER, J.; BRUNO, É. (Oral presentation)

Remontée de l'optimum des espèces forestières sur les reliefs du sud-est de la France, réchauffement climatique ou changement d'utilisation du sol ? BODIN J.; BADEAU V.; DUPOUEY J.-L.; BRUNO É.; CLUZEAU C. *Colloque de Phytosociologie*, 12-14 November 2008, Velaine en Haye (France). (Poster)

Impact of climate warming on species' distribution in mountain areas, which processes limit lower range margins? BODIN J.; WALTHER G.-R. *Jahrestagung der Reinhold-Tüxen-Gesellschaft* 12-14 May 2006, Rinteln (Germany). (Poster)

Évolutions passée et future des aires de répartition des espèces forestières en France ; *Académie d'Agriculture de France – Forêts et Changements Climatiques* ; 2007. Séance du 30 mai 2007. DUPOUEY J.-L.; BODIN J.; BADEAU, V.

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One century of vegetation change on Isla Persa, a nunatak in the Bernina massif in the Swiss Alps

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Abstract

Question: How did the vascular plant species composition of a nunatak in the alpine vegetation belt change over a time span of 100 years?
Location: A 5.6-ha nunatak, Isla Persa in the Swiss Alps, that remained ice-free during the last maximum glacier advance in the 1850s and is today partly covered with climactic alpine grassland and dwarf heath shrubs.
Methods: Floristic inventories in 1906, 1927, 1972, 1995, 2003 and 2004 and a comparative analysis of the species composition over the period 1906-2004.
Results: 31 species that were not recorded in the first inventory were found in the following surveys. However, among them only six were common by 2004. Generally, the new species prefer warmer conditions than those previously present and most newcomers are associated with montane or sub-alpine grasslands and woodlands. In particular, the observed increase of *Vaccinium myrtillus* and the arrival of shrub and tree species further substantiate a trend towards vegetation composition of the lower altitudinal belt. Ferns represented 26% of the newcomers, probably due to the high dispersal ability of their lightweight spores. The observed species enrichment was globally small compared to previously inventoried summits.
Conclusion: Floristic change strongly suggests warmer climatic conditions as the main factor contributing to species compositional change. The relative stability of species richness may be explained by several factors: the isolation of the nunatak and the difficulties for plants to reach the site, the colder local climate, a limited available species pool and interactions of established alpine plants with newly immigrating taxa. Supplementary data collected at a similar altitude would be necessary to better understand the influence of climate change on alpine grasslands.

Keywords: Alpine vegetation; Global warming; Long-term monitoring; Plant trait; Species diversity; Switzerland.

Nomenclature: Aeschimann et al. (2004).

Introduction

Climate warming induces upward range shifts of plant species in mountain areas. This trend was predicted by many studies (e.g. Gottfried et al. 1998; Guisan & Theurillat 2000; Dirnböck et al. 2003) and it has also been substantiated by observations on many high alpine, rocky summits (Braun-Blanquet 1957; Hofer 1992; Grabherr et al. 1994, 1995; Burga et al. 2004; Walther et al. 2005a; Vittoz et al. 2006; Parolo & Rossi 2008), by single species re-surveys (Dobbertin et al. 2005; Walther et al. 2005b) and by altitudinal shifts of the treeline ecotone (Kullman 1986; Taylor 1995; Moiseev & Shiyatov 2003; Camarero & Gutiérrez 2004; Vittoz et al. 2008; for a review see Walther 2004). However, data for long-term vegetation changes in subalpine or alpine grasslands are lacking (for shorter time scales see Kudernatsch 2005). Long-term series of permanent plots are few or unavailable for studying upward range shifts of mountain plants due to anthropogenic disturbances.

In the Alps, the glaciers reached their last maximum extent in the 1850s (see references in Burga 1999) and have been shrinking since then. The rate of glacier retreat has increased further in the last few decades (Paul et al. 2004). In previous centuries, throughout the Holocene period, the extent of the glaciers of the Alps is assumed to have reached the 1850 maximum but never substantially exceeded this level (Maisch et al. 1999). Hence, isolated rocks surrounded by glaciers in 1850, called nunataks, may at least be partly covered with ancient soils and with vegetation in climax states.

Isla Persa (literally the 'lost island' in Rhaeto-Romanic) in the eastern Swiss Alps is such a nunatak in the alpine belt. It remained ice-free during the last maximum of the local glaciers (Fig. 1; Lechner 1858) and is covered with large patches of climactic alpine grasslands. The nunatak

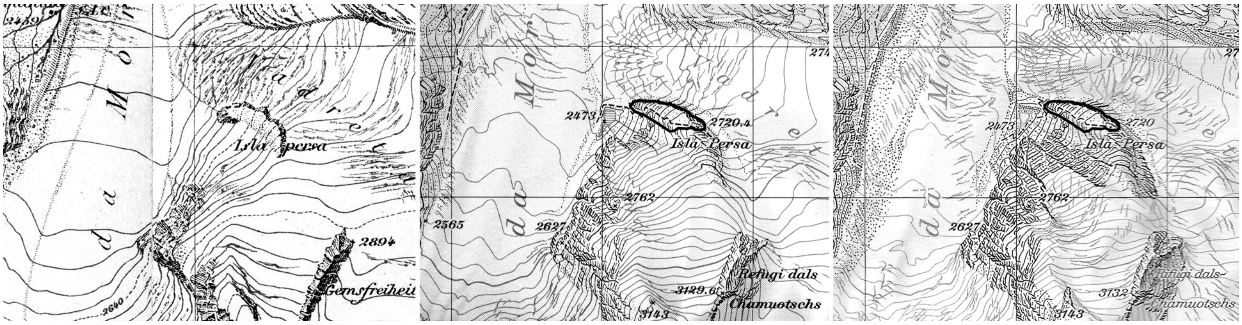

Fig. 1. Glacier retreat around Isla Persa between 1876 (left), 1965 (centre) and 1991 (right). The Rübel area is delimited by the Morteratsch glacier to the west, the Pers glacier to the north and east, and the Fortezza glacier to the South in 1876 and by the black line in 1965 and 1991. Swisstopo, Siegfried map no. 521 at 1:50000 in 1896, Landeskarte no. 268 in 1965 and 1991 at 1:50000 with a grid size of 1 km. Reproduced by permission of Swisstopo (BA071283). Isla Persa extends now on the whole rocky area (grey part in the south of the Rübel area).

is an interesting area for vegetation studies due to its isolation from intensive anthropogenic disturbance and has, therefore, attracted the interest of botanists since the early 20th century.

The first floristic inventory of this nunatak was published in Rübel's monograph (1912) on the vegetation of the Bernina region, named after the highest mountain peak (Piz Bernina 4049 m a.s.l.) of the eastern Alps. The nunatak was revisited three times in the 20th century but the inventories remained partly unpublished (Flütsch et al. 1930; De Haas 1973; Ungricht 1995). With the present article, we wish to compile all these historic data and integrate two recent inventories. Altogether, these inventories provide a rare opportunity for the analysis of vegetation change in alpine grasslands during the course of one century. Specifically, we address the following questions: (1) how much has the floristic species richness changed through time, (2) is climate change likely to be responsible for the observed development and (3) which are the biological traits linked to the observed colonization process?

Study area

The investigation area, a nunatak named Isla Persa (46°24' N, 9°56' E), is delimited to the west by the Morteratsch glacier, to the north and east by the Pers glacier and to the south by the Fortezza glacier (Fig. 1). At present, the altitudinal range of the Isla Persa is between 2450 m and 2850 m a.s.l., which is within the alpine belt (2300-3000 m a.s.l. in the region). Isla Persa is isolated from the surrounding ice-free areas by 500 m to the north and 900 m to the west. It is very unlikely that it was ever permanently inhabited or grazed by domestic cattle or sheep. However, the nunatak is now frequently visited by hikers crossing the ice-free area between the two adjoining glaciers.

The nunatak belongs to the lower eastern-Alpine Bernina nappe. The rocks consist mainly of granites, granodiorites, diorites and gabbros (Büchi 1994). A large part of the Isla Persa represents a granitic rock outcrop partly covered with screes. The vegetation consists of scattered alpine grasslands and some heath dwarf shrubs on well developed alpine regosols and leptosols, especially on the southern part of the nunatak.

At the time when it was first investigated in 1906 by Rübel (1912), the Isla Persa covered ca. 5.6 ha and comprised altitudes between 2510 m a.s.l. and 2720 m a.s.l. Since then, the ice-free surface has increased to ca. 68 ha as a consequence of rapid glacier retreat (Fig. 1). However, since the 1940s, the total area of the nunatak can no longer be clearly delimited because another ice-free rocky area merged at its southwestern corner, extending to 3143 m a.s.l.

The closest meteorological station is located in Sils-Maria, at 1802 m a.s.l., 15 km to the west of Isla Persa. Both sites are located in the Inner Alps, which have low precipitation and air humidity. Mean annual temperature (± 1 SD) for the 1961-1990 period was 1.6 °C ± 0.5 °C (– 7.2 °C ± 1.9 °C in January and 10.4 °C ± 1.2 °C in July) and the mean annual precipitation was 978 mm ± 168 mm, with drier winters (mean of the sum for December to February 143 mm ± 61 mm) than summers (June to August 335 mm ± 98 mm). During the 20th century, a general temperature increase during the growth season (May-September) occurred between 1918 and 1951, a decrease was observed till 1974 and since then an increase has again been observed (Fig. 2) in accordance with other regions in Switzerland (Bader & Bantle 2004). However, the temperature increase was altogether lower in Sils-Maria than in other Swiss regions: +0.4 °C/100 years in summer for the period 1864-2001 compared with +0.6 °C – 0.9 °C/100 years for the lowland and northern Alps (Bader & Bantle 2004). In common with all other regions, most of this increase took place in the most recent decades and the mean annual increase was similar to records for the northern hemisphere (Rebetez & Reinhard 2008).

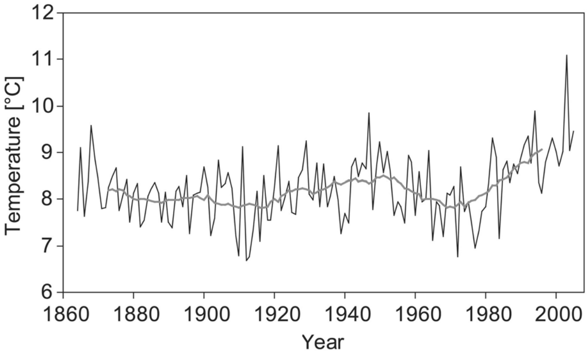

Fig. 2. Mean growth season (May-September) temperature in Sils-Maria (1802 m a.s.l., 15 km from Isla Persa; data MeteoSwiss). The grey line is the 20-year mobile mean.

Methods

Field plant inventories

A set of six consecutive plant species inventories of the Isla Persa area was available, spanning the period of one century (Table 1). Two inventories were made in the first half of the 20th century by Rübel (1912) in 1906 and Braun-Blanquet in 1927 (Flütsch 1930), followed by two inventories in the second half of the 20th century (De Haas 1973; Ungricht 1995). In 2003 the full ice-free area was again inventoried by two of the authors (Walther, Burga and collaborators). In 2004, a further inventory took place by another author (Vittoz), which was restricted to the original ice-free core area of the nunatak, i.e. the same area as originally inventoried by Rübel (designated as Rübel area, Table 1). The different inventories were accomplished by varying numbers of observers over varying numbers of days, hence with different levels of assessment effort. However, all included the most favourable period as judged by the phenology of alpine plants. At all inventories only the presence of the species was recorded, with occasional indications for rare species, except the last inventory (2004) in which abundance estimates to classes were provided (Table 2; cf. Grabherr et al. 2001) and data about plant location and substrate was recorded for most of the rarest species.

By comparing the two last inventories and previous indications of species location, we established a comparative species list for the Rübel area and a list of additional species from the newly deglaciated area (App. 1). For each inventory it was possible to obtain a comprehensive species list for the Rübel area, but the data were inadequate to get species lists for the newly ice-free area. Therefore, we limited our study to the Rübel area.

From the different species lists, the following species were merged because of suspected misidentifications: *Avenella flexuosa-Deschampsia caespitosa*; *Adenostyles leucophylla-A. intermedia*; *Carex frigida-C. ferruginea*; *Galium anisophyllon-G. pumilum*; *Poa supina-P. annua-P. badensis*; *Poa laxa-P. minor* and *Sagina saginoides-S. glabra*.

Analyses

It is likely that some rare and/or inconspicuous species were overlooked in all inventories (Vittoz & Guisan 2007). Hence, species present in an earlier inventory that lacked confirmation in an intermediate inventory, but were 'rediscovered' in a later survey were considered present throughout the entire interval. It is more likely for a missed species to have been overlooked in the intermediate inventory than for it to have disappeared and re-colonized the area in the given time interval. For the same reason, we assumed that no species disappeared or appeared between 2003 and 2004 and we merged these last two inventories (Table 1).

We used biological traits to assess if newcomer species (i.e. species that were found for the first time after 1906) differed from the original species (already present in 1906). Five of the recorded traits were indicative of the ecological conditions under which the species occur. The

Table 1. Authors, dates, assessment areas, number of observers, assessment time and recorded species numbers of the six inventories on Isla Persa (Swiss Alps). All but the last author inventoried the complete ice-free area, which increased through time. The area inventoried by Rübel in 1906 is here defined as the 'Rübel area' and used for the analyses in this paper. The corrected number of species incorporates the potentially overlooked species observed by a previous and the following inventory. The two last inventories were merged as they were separated by only one year.

Author	Date of publication	Date of inventory	Inventoried area	Number of observers	Time used	Number of recorded species		
						inventoried area	Rübel area	corrected for Rübel area
Rübel	1912	1906	Ice-free area = Rübel area	1 ?	?	98	98	98
Flütsch	1930	1927	Ice-free area	27	1 day	103	99	106
De Haas	1973	1971-72	Ice-free area	several	44 days	134	116	118
Ungricht	1995	1994-95	Ice-free area	1-4	40 hours	110	99	117
Walther & Burga		2003	Ice-free area	3-4	7 days	136	115	126
Vittoz		2004	Rübel area	2	3 days	122	122	

ecological indicator values (Landolt 1977) vary between 1 and 5 and are available for each Swiss species following its ecological preferences. The soil texture (1 = stony – 5 = clayey); soil humus content (1 = no humus – 5 = peaty); soil nutrients content (1 = oligotrophic – 5 = eutrophic); and temperature (1 = alpine-nival belt – 5 = collinean belt) were used. The sociological classification of species simplified from Ellenberg et al. (1991) – or Aeschimann et al. (2004) in cases the species is not listed in the former – completed the ecological indicator values with a more integrative view of the species ecological preferences. The nomenclature for plant sociological units follows Ellenberg et al. (1991). The growth forms were simplified from Pignatti (2005) (therophytes, non-graminoid hemicryptophytes, graminoid hemicryptophytes, geophytes, creeping chamaephytes, chamaephytes in cushions, succulent chamaephytes, woody chamaephytes, phanerophytes). Four traits were related to reproduction. The respective importance of sexual and clonal reproduction was assessed following the BIOLFLOR databank (Klotz et al. 2002) in three categories: sexual reproduction only, sexual and clonal reproduction possible and mainly clonal reproduction. The same reference was used for the fertilization type in five categories: only self-fertilization, wind as vector, insects, mainly insects but possible self-fertilization and fern gametophyte fertilization. Data on seeds or weight of other diaspores were taken from Klotz et al. (2002) and Müller-Schneider (1986). Since values were still missing for 29% of the species, we used seven categories for which diaspore weight of unknown species were attributed on the basis of the closest related species:

1 = < 0.05 mg; 2 = 0.06-0.2 mg; 3 = 0.21-0.5 mg; 4 =

Table 2. Species that have disappeared or were newly recorded on Isla Persa between 1906 and 2004. **1** = species present without abundance estimation; ***** = species probably overlooked because present in the previous and following inventory; **r!** = very rare; **r** = rare; **s** scattered; **r-lc** = rare but locally common; **s-lc** = scattered but locally common (for a complete species list see App. 1). The highest altitudes are the recorded altitudinal limit for the whole Bernina regions in 1906 (Rübel 1912) and for the Isla Persa in 2004. Species sociology is simplified from Ellenberg et al. (1991) or Aeschimann et al. (2004) and the occupied substrate refers to the conditions where the individuals were recorded in 2004.

Plant species	1906	1927	1972	1995	2004	Highest altitude [m]		Sociology	Occupied substrate
						1906	2004		
Disappeared species									
Veronica bellidioides	1	1	1			3260		Alpine grasslands	
Euphrasia rostkoviana	1					2600		Lowland meadows	
Gentiana campestris	1					2700		Lowland meadows	
Thymus serpyllum		1				2700		Others	
Festuca halleri			1			3400		Alpine grasslands	
New species									
Vaccinium myrtillus		1	1	1	s-lc	2750	2520	Scrubs and forests	Grassland and heathland
Elyna myosuroides		1	1	1	s	3090	2520	Alpine grasslands	
Soldanella alpina		1	1	*	s	2700	2510	Alpine grasslands	Grassland
Pinguicula leptoceras		1	1	*	s	2260	2520	Others	Grassland
Primula integrifolia		1	1	*	r-lc	3010	2510	Alpine grasslands	
Cerastium uniflorum		1	1	1	r-lc	3400	2660	Rocks, cliffs, screes	Stones and/or gravel
Gentiana brachyphylla		1	1	1	r	3260	2560	Lowland meadows	Grassland
Trichophorum cespitosum		1	*	*	r	2450	2510	Others	Grassland
Antennaria dioica		1	1	*	r!	3010	2560	Lowland meadows	Grassland
Phleum alpinum			1	*	r	2830		Alpine grasslands	
Sagina saginoides / S. glabra			1	*	r	2550	2540	Alpine grasslands	Stones and/or gravel
Asplenium septentrionale			1	*	r	2470	2530	Rocks, cliffs, screes	Cliff
Cryptogramma crispa			1	1	r	2730	2560	Rocks, cliffs, screes	Stones and/or gravel
Polystichum lonchitis			1	1	r	2550	2540	Rocks, cliffs, screes	Stones and/or gravel
Coeloglossum viride			1	*	r	2650	2520	Lowland meadows	Grassland
Trifolium alpinum			1	1	r	2730		Lowland meadows	
Athyrium distentifolium			1	1	r	2230	2700	Scrubs and forests	Stones and/or gravel
Poa supina / P. annua / P. badensis			1	*	r	2600	2720	Others	Track
Diphasiastrum alpinum			1	*	r!	2630	2700	Lowland meadows	Grassland
Ribes petraeum			1	*	r!	2450	2530	Shrubs and forests	Heathland
Salix helvetica			1	1	r!	2500	2510	Shrubs and forests	Stones and/or gravel
Gymnocarpium dryopteris				1	r!	2570	2540	Shrubs and forests	Stones and/or gravel
cf. *Aster bellidiastrum*					r!	2600	2540	Alpine grasslands	
Gentiana verna					r!	2900	2560	Alpine grasslands	Grassland
Leontodon cf. *autumnalis*					r!	2320	2720	Lowland meadows	Track
Pulsatilla alpina s.l.					r!	2730	2710	Lowland meadows	Grassland
Arctostaphylos uva-ursi					r!	2550	2500	Scrubs and forests	Stones and/or gravel
Dryopteris filix-mas					r!	2540	2540	Scrubs and forests	Stones and/or gravel
Larix decidua					r!	2660	2510	Scrubs and forests	Stones and/or gravel
Dryopteris cf. *dilatata*					r!	2260	2520	Scrubs and forests	Stones and/or gravel
Festuca rubra agg.					r!	2650	2540	Others	Grassland

0.51-1 mg; 5 = 1.01-2 mg; 6 = 2.01-10 mg; 7 = > 10 mg. Dispersal vector of the seeds followed Müller-Schneider (1986) and dispersal distance of the diaspores was simplified in seven types following Vittoz & Engler (2007), which takes into account the main dispersal vector and important species traits influencing dispersal. The types chosen were:

1 when 99% of the seeds fall < 1 m; 2, < 5 m; 3, < 15 m; 4, <150 m; 5, < 500 m; 6, < 1500 m; 7, < 5000 m. χ^2-tests were used in statistical analyses of trait differences.

Results

During the assessment window of nearly 100 years, the number of species increased almost continuously in the Rübel area from 98 in 1906 (Rübel 1912) to 126 in 2004 (Table 1). However, most of the newly recorded species were rare in 2004 and only some species, which arrived between 1906 and 1927, were locally common in 2004 (Table 2). The abundance of *Vaccinium myrtillus*, *Elyna myosuroides* and *Cerastium uniflorum* was relatively high at the last inventory and these species have never been overlooked since their first record (in 1927) making it likely that they immigrated after 1906. *Pinguicula leptoceras*, *Soldanella alpina* and *Primula integrifolia* were present in a particular sector of the nunatak only. These species were also recorded for the first time in 1927. We assumed that, although present, they may have been overlooked in the 1906 inventory but nonetheless they are considered to have colonized the nunatak when observed for the first time in 1927.

Among the 31 new species, ten species were found at a higher altitude in 2004 (Table 2) than reported for the whole Bernina region at the beginning of the 20th century (Rübel 1912). These altitudinal shifts were particularly pronounced for *Athyrium distentifolium* (+470 m), *Diphasiastrum alpinum* (+340 m), *Pinguicula leptoceras* (+260 m) and *Poa supina* (+120 m) (identification was uncertain for two poorly developed, supplementary species: *Dryopteris dilatata* and *Leontodon autumnalis*).

Some species disappeared or were not found after the first observation (Table 2). Misidentifications cannot be discounted, but they were rather unlikely. Three of these species (*Euphrasia rostkoviana, Gentiana campestris, Thymus serpyllum*) occurred close to their highest altitudinal range in the region (Rübel 1912).

None of the ecological indicator values (Landolt 1977) for soil conditions showed differences between species that had recently colonized Isla Persa compared to those present in 1906 (Table 3). The mean values (± 1 SD) for 1906 species and colonizing species, respectively, were 3.31 ± 0.91 and 3.42 ± 1.15 for soil texture, 3.27 ± 0.71 and 3.42 ± 0.87 for soil humus content and 2.19 ± 0.71 and 2.39 ± 0.79 for soil nutrient content. In contrast, the temperature indicator value showed a highly significant difference between inventories, with means 1.53 ± 0.58 for the 1906 inventory compared to 2.09 ± 0.53 for the new species (Table 3, Fig. 3). This corresponded with a continuously decreasing proportion of alpine and nival species (value 1, representing only 9.1% of the new species) in the inventories and a corresponding increase in subalpine species (value 2, 72.7% of the new species) and montane or indifferent species (value 3, 21.2% of the new species).

The sociology of original and recent plant species differed significantly (Table 3). The newly arrived species were associated in similar proportions with forests (*Vaccinio-Piceetea, Erico-Pinetea, Querco-Fagetea*), alpine grasslands (*Salicetea herbaceae, Juncetea trifidi, Seslerietea albicantis, Carici rupestri-Kobresietea, Loiseleurio-Vaccinietalia, Poion alpinae*) or montane and/or sub-alpine grasslands (*Nardo-Callunetea, Molinio-Arrhenatheretea*) (Table 2; Fig. 4). Altogether, forests and montane-sub-alpine grassland species represented 23% of the 1906 floristic composition but 45% of the new species. By contrast, alpine grassland and rock/scree species (*Asplenietea trichomanis, Thlaspietea rotundifolii, Sedo-Scleranthetea*) comprised only 36% of the new species, while they comprised 70% of the 1906 composition (Fig. 4).

The growth forms were similarly distributed (Table 3), with a large dominance of hemicryptophytes in both groups, although a higher proportion of non-graminoid hemicryptophytes was observed in the original inventory (App. 2). The reproduction type showed no difference between inventories, with 74% and 72% of species able to reproduce sexually and clonally in the two groups (Table 3). The fertilization type was significantly different because of a higher proportion of ferns among the recently arrived species (25.8% compared to 4.1% among the 1906 species). When only the phanerogams were considered, there was no significant difference between fertilization types (Table 3), with ca. 66% and 68%, respectively, of either obligatory or non-obligatory entomophilous species. Similarly, diaspore weight was significantly different when all the species were considered, with a higher proportion of very light diaspores among colonizing species (Fig. 5) but no significant difference when only phanerogams were considered (Table 3). Finally, no difference was found in dispersal vectors, with 83% and 85% of the seeds dispersed by wind or without special device for dispersal and 26%-27% of zoochorous dispersal, including unintentional endozoochory by consumption with grass (results not shown). Dispersal distance type showed no significant difference between species present in the 1906 inventory and species that arrived later (Table 3; App. 3).

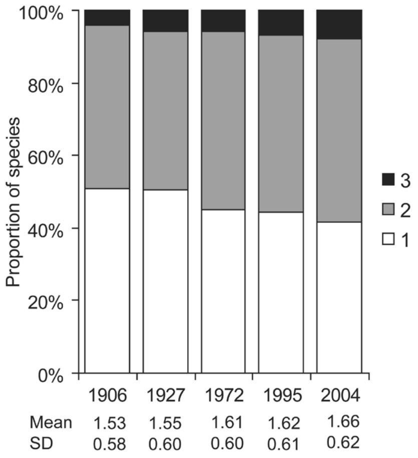

Fig. 3. Proportion of species corresponding to the different temperature indicator values following Landolt (1977) in the floristic inventories on Isla Persa: **1** = species typically distributed in alpine and nival belts, **2** = subalpine species, **3** = montane or indifferent species. Mean and SD for the complete inventories are given for the individual years.

Discussion

Data reliability

The comparison of this type of floristic data in large areas is always confronted with the problem of completeness and reliability. Clearly, the prospecting effort is variable between the different inventories (Table 1). For instance, we do not know how much time Rübel spent for the first inventory in 1906, but it was probably less than the 27 day equivalent that Braun-Blanquet invested with his students in 1927 (Flütsch 1930). Previous studies have often shown that botanical inventories are rarely exhaustive, even in very small areas (e.g. Lepš & Hadincová 1992; Klimeš et al. 2001; Kercher et al. 2003; Archaux et al. 2006; Vittoz & Guisan 2007). Two easy ways to improve data and interpretation exist: working in groups increases the reliability of species lists (Klimeš et al. 2001; Vittoz & Guisan 2007) and estimation of cover helps to cautiously interpret the results for new but rare species (Lepš & Hadincová 1992; Kercher et al. 2003; Vittoz & Guisan 2007). On Isla Persa, most inventories were completed by teams (Table 1) but cover estimates in the earlier inventories would have allowed more detailed analyses of abundance changes (e.g. Vittoz et al. 2006).

Biodiversity increase and climate change

Climate warming, although less pronounced in this region compared to other Swiss regions (Fig. 2), is probably responsible for the observed species increase on the Isla Persa. This is consistent with newly arrived plant species with higher temperature requirements (Fig. 3) and observations of particular species at higher altitudes in 2004 than in 1906. The same trend is also observed on many surrounding summits (Braun-Blanquet 1957; Hofer 1992; Grabherr et al. 2001; Camenisch 2002; Burga et al. 2004; Walther et al. 2005a) or in other alpine regions (Grabherr et al. 2001; Vittoz et al. 2006; Parolo & Rossi 2008). Recent re-observations at an alpine-nival ecotone of the central Alps showed an increase in cover of high alpine species and a concurrent decline of all subnival to nival species, suggesting a range shift of mountain plants (Pauli et al. 2007).

Higher temperatures allow more sensitive plants to colonize the nunatak. These newly arrived species indicate a slow shift of the vegetation from mainly alpine meadows and rocky vegetation to conditions typical of the lower alpine belt, or even the sub-alpine belt. Although rocky sites and screes are still dominant on the nunatak, most of the new species are associated with grasslands or wooded areas (Fig. 3). The clear increase of *Vaccinium myrtillus*, a typical species of sub-alpine forests

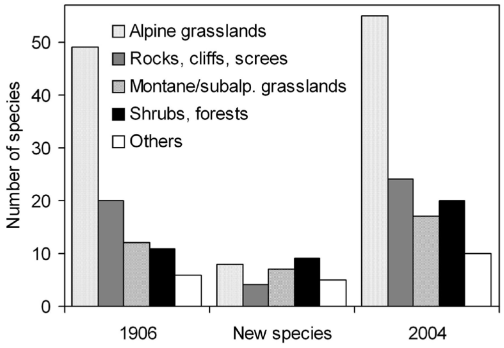

Fig. 4. Plant sociological preferences (Ellenberg et al. 1991; Aeschimann et al. 2004) of the 98 species already present in 1906, the 31 species that arrived later and of the 126 species present in 2004 (for details and relative values see text).

Table 3. *p*-values for the comparisons of biological traits between the species present in the 1906-inventory on Isla Persa and those that arrived later are obtained by χ^2-tests (see Methods for the description of traits).

Biological trait	*p*-value
Soil texture	0.134
Soil humus content	0.130
Soil nutrients content	0.257
Temperature	< 0.0001
Sociology	0.009
Growth form	0.243
Reproduction type	0.288
Fertilization type	0.006
Fertilization type (without ferns)	0.351
Diaspore weight	0.017
Diaspore weight (without ferns)	0.497
Dispersal distance	0.240

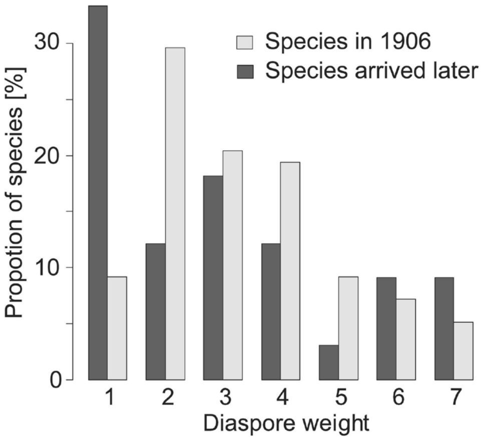

Fig. 5. Distribution of diaspore weight for species present in the 1906-inventory on Isla Persa and the 31 that arrived later (see Methods for the seven types).

or lower alpine dwarf shrubs heath, indicates a possible belt shift. This development correlates with the results of Wahren et al. (2005) in warming experiments on Arctic tundra vegetation showing the increasing size and cover of small shrubs. Similar altitudinal/latitudinal belt shifts were also observed in other regions, such as the expansion of the treeline ecotone (e.g. Kullman 1986; Taylor 1995; Peñuelas & Boada 2003; Camarero & Gutiérrez 2004; Vittoz et al. 2008) or the colonization of shrubs in the Arctic tundra (Sturm et al. 2001) and in the boreal mountains (Klanderud & Birks 2003). The arrival of *Salix helvetica, Ribes petraeum* and, especially the first occurrence of *Larix decidua* on Isla Persa is perhaps an early indication of the upward expansion of the treeline. This last species is, at present, limited to one individual that colonized the nunatak no earlier than 1994 (based on the annual increments of the shoots).

Another indication of warmer conditions on the nunatak is the observed higher fitness of *Epilobium angustifolium*. Rübel (1912) mentioned its sterile occurrence at the foot of the 'island' (2530 m a.s.l). The same species was missing in the inventory of Flütsch (1930), whereas de Haas (1973) reported a mainly vegetative spreading species. In 2003, the population was found at the same location in full flower (for the advance of the same species in the Arctic see Kullman 2003). The shift from mainly vegetative to fertile populations of *Epilobium angustifolium* underlines the possibility for species with lower core distribution to colonize and become established at their upper range limit.

Other factors are certainly partially responsible for the observed vegetation changes on Isla Persa: (1) Some new species probably arrived with a recolonization process after the climate change that followed the Little Ice Age (Kammer et al. 2007). Species became extinct during this cold period and recolonized Isla Persa, much like surrounding summits, in warmer conditions. This process was probably slowed by the low dispersal ability of many species and is now being accelerated by anthropogenic warming (Walther et al. 2005a). (2) Another portion of the new species may correspond to the continuous colonization observed on every island (MacArthur & Wilson 1967). With 49 alpine grassland species in 1906, the species pool on Isla Persa was not saturated, since it is estimated that about 100 potential species of acidophilous alpine grasslands exist in the eastern Swiss Alps (calculated by crossing data from Landolt 1977; Ellenberg et al. 1991; Moser et al. 2002; Aeschimann et al. 2004). Similarly, the 20 species on rocks, cliffs or screes in 1906 represented less than half of the pool of 54 potential species. Respectively, the eight and four new species associated with these environments (Table 2; Fig. 4), some very common in alpine conditions (e.g., *Soldanella alpina* in alpine grasslands and *Cerastium uniflorum* in screes) can be considered as colonizations independent of climate change. (3) Primary succession in the Rübel area alone cannot be responsible for the increase in species numbers on the nunatak, since it has been ice-free for many thousands of years. It was not covered by ice in 1850 and glaciers in the Alps did not exceed their 1850 extent throughout the Holocene (Maisch et al. 1999). Hence, a large part of the local vegetation must have been in the climax phase for a long time. However, a primary succession is possible on some of the rocky areas, with potentially increasing biodiversity, but mostly with already present species. (4) Interannual fluctuations are sometimes responsible for vegetation changes (van der Maarel 1996). However, the different inventories of the Rübel area showed a continuous increase in species richness and, furthermore, such fluctuations have low amplitudes at these altitudes. Finally, (5) the glacier barrier strongly limits cattle grazing on Isla Persa and a vegetation change after pasture abandonment is very improbable. Only influence of hikers seems to have contributed slightly to the enrichment, being responsible for the arrival of a few species, such as *Poa supina* and *Leontodon* cf. *autumnalis,* which were found on the most trampled spot – all the other newcomer species were recorded well off the track.

Biological traits

Apart from temperature and sociology of the species (see above), fertilization type and diaspore weight were the only biological traits considered that showed a significant difference between originally established species (1906) and new species (Table 3). For both traits, however, the high proportion of pteridophytes (26% of the new species but only 4% in the 1906 inventory) is responsible for this difference: they were classified separately for the fertilization type and, with spores, they all have very light diaspores (< 0.05 mg category). Similarly, four fern species were classified by Parolo & Rossi (2008) as fast migrants because of their important altitudinal shift between 1959 and 2005. It is very probable that their small spores give them an advantage for long-distance dispersal because of a high efficiency of wind as a dispersal vector. A large proportion of pteridophytes was also found on a new volcanic island whose situation strongly favoured anemochory (Thornton et al. 2001). However, pteridophyte establishment in this alpine environment could be more difficult because of the small size and dependence on photosynthesis of prothalli (fern gametophytes) which make them poor competitors in grasslands (Greer 1993). This may perhaps explain why almost all new pteridophytes are established on mineral soils (stones and/or gravel), even though four species normally grow in forest soils. The number of individuals and species is too low to conclude if the colonization rate of pteridophytes in alpine environments under climate change is generally higher than for other vascular plant species.

The similarity of other biological traits between original species and newly arrived ones show that changes in vegetation structure were not yet important enough to significantly influence the trait pattern. Alpine conditions governed the observed plant traits in both groups: the dominance of hemicryptophytes is typical of alpine vegetation (Illa et al. 2006; Körner 2003), as well as a majority of plants with possible clonal reproduction (Stöcklin 1992; Illa et al. 2006) and the dominance of insect fertilization (Körner 2003). The seed weight, which shows a comparable majority of seeds < 1 mg, as in sub-arctic grasslands (Welling et al. 2005), seems not to be related to altitude, with mean weight similar between alpine and lowland grasslands (Körner 2003). Finally, the importance of wind as a dispersal vector (including for small seeds without special device; Willson et al. 1990) is typical of alpine plant communities, more generally of grasslands and vegetation with an open structure (Willson et al. 1990; Stöcklin & Bäumler 1996; Ozinga et al. 2004), typical of island colonization (Lloret et al. 2005). This similarity strongly limits the opportunities to detect differences in dispersal vectors and distances between established plants in 1906 and newcomers.

Importance of the biodiversity increase

Compared to other similar studies, the increase in species richness on Isla Persa is relatively small. The increase of 29% for recorded vascular plant species in the course of one century recorded for the Isla Persa is clearly below the values for most of the surrounding mountain summits. Of the 11 inventoried summits in the Bernina region (Walther et al. 2005a; Vittoz unpubl. data), eight had a larger increase in richness (58% - 336%, mean = 131%). However, all these mountain summits are at a higher altitude and are dominated by rock surfaces, with very limited areas of alpine grassland. Various reasons may explain this comparatively small change on the nunatak. (1) Physical barriers created by the surrounding glaciers limited the colonization by plants, as was hypothesized for the observed stable richness (since 1937) of the Piz Linard (3411 m a.s.l.) (Pauli et al. 2001). Conversely, most of the inventoried summits in the Bernina region have gradually changing conditions, which allows a progressive migration of plants. (2) The species richness on Isla Persa was about half of the species pool for alpine grasslands and rock areas, limiting the number of potential newcomers. (3) Sub-alpine species arriving in well developed alpine grasslands are not free to colonize all potentially suitable sites because most of them are already occupied or, at least, the newcomers need more time to increase their abundance under the still prevailing cold alpine conditions. The increase of *Vaccinium myrtillus* supports this hypothesis as mature plants of this taxon are taller than those of most other alpine species and hence less inhibited by competition. (4) Surrounding glaciers bring about a colder microclimate than usually exists for other localities at similar altitudes. Unfortunately, comparable floristic data at similar altitudes are lacking, certainly assessments covering a time span of a century. Hence, it is impossible to conclude if the Isla Persa species enrichment should have been expected to be higher than observed, as suggested by Grabherr et al. (1994) who showed increasing enrichment for decreasing altitudes within upper alpine and nival belts.

The nunatak of Isla Persa in the eastern Swiss Alps is probably one of the rare available sites at which vegetation changes in the alpine belt can be assessed over the course of the 20th century. The observed changes were less pronounced than expected based on the results of similar studies for surrounding mountain summits, and while new species colonized the nunatak, most of them are still rare. However, the sum of the evidence presented here indicates a shift towards a vegetation of previously restricted lower altitudinal belts and, thus, a trend indicating warmer local growth conditions. The conspicuous increase of *Vaccinium myrtillus* and the new presence of shrub and tree species underline this conclusion. Among the new species, ferns were particularly important, which can be due to a high dispersal potential brought about by their lightweight spores. But altogether, the pool of potential newcomers is still too strongly restricted by the alpine climate to have biological traits distinct from those of the species in the 1906 inventory. Additional data obtained in the future should help to gain a better understanding of processes influencing species composition in alpine grasslands and dwarf shrub heaths in a warmer world.

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References

Aeschimann, D., Lauber, K., Moser, D.M. & Theurillat, J.-P. 2004. *Flora alpina*. 3 Vols. Belin, Paris, FR.

Archaux, F., Gosselin, F., Bergès, L. & Chevalier, R. 2006. Effects of sampling time, species richness and observer on the exhaustiveness of plant censuses. *Journal of Vegetation Science* 17: 299-306.

Bader, S. & Bantle, H. 2004. *Das Schweizer Klima im Trend: Temperatur- und Niederschlagsentwicklung 1864-2001*. Veröffentlichungen 68. MeteoSchweiz, Zürich, CH.

Braun-Blanquet, J. 1957. Ein Jahrhundert Florenwandel am Piz Linard (3414 m). *Bulletin du Jardin Botanique de Bruxelles, Vol. W. Robyns*, pp. 221-232.

Büchi, H. 1994. Der variskische Magmatismus in der östlichen Bernina (Graubünden, Schweiz). *Schweizerische Mineralogische und Petrographische Mitteilungen* 74: 359-371.

Burga, C.A. 1999. Vegetation development on the glacier forefield Morteratsch (Switzerland). *Applied Vegetation Science* 2: 17-24.

Burga, C.A., Walther, G.R. & Beissner, S. 2004. Florenwandel in der alpinen Stufe des Berninagebiets - ein Klimasignal. *Berichte der Reinhold-Tüxen-Gesellschaft* 16: 57-66.

Camarero, J.J. & Gutiérrez, E. 2004. Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. *Climatic Change* 63: 181-200.

Camenisch, M. 2002. Veränderungen der Gipfelflora im Bereich des Schweizerischen Nationalparks: Ein Vergleich über die letzten 80 Jahre. *Jahresbericht der Naturforschende Gesellschaft Graubündens* 111: 27-37

de Haas, J.H. 1973. *The vegetation of Isla Persa (Bernina, Switzerland) – a standard of climatic changes?* Field reports of the Netherlands Centre for Alpine Biological Research, Utrecht, NL.

Dirnböck, T., Dullinger, S. & Grabherr, G. 2003. A regional impact assessment of climate and land-use change on alpine vegetation. *Journal of Biogeography* 30: 401-417.

Dobbertin, M., Hilker, N., Rebetez, M., Zimmermann, N.E., Wohlgemuth, T. & Rigling, A. 2005. The upward shift of pine mistletoe (*Viscum album* ssp. *austriacum*) in Switzerland. The result of climate warming? *International Journal of Biometeorology* 50: 40-47.

Ellenberg, H., Weber, H.E., Düll, R., Wirtz, V., Werner, W. & Paulissen, D. 1991. *Zeigerwerte von Pflanzen in Mitteleuropa*. Scripta Geobotanica 18, Goltze KG, Göttingen, DE.

Flütsch, P. 1930. Über die Pflanzengesellschaften der alpinen Stufe des Berninagebietes. *Jahresbericht der Naturforschende Gesellschaft Graubündens* 68: 37-88.

Gottfried, M., Pauli, H. & Grabherr, G. 1998. Prediction of vegetation patterns at the limits of plant life: a new view of the alpine-nival ecotone. *Arctic and Alpine Research* 30: 207-221.

Grabherr, G., Gottfried, M. & Pauli, H. 1994. Climate effects on mountain plants. *Nature* 369: 448.

Grabherr, G., Gottfried, M., Gruber, A. & Pauli, H. 1995. Patterns and current changes in alpine plant diversity. In: Chapin III, F.S. & Körner, C. (eds.) *Arctic and alpine Biodiversity*. Ecological Studies 113. Springer, Berlin, DE.

Grabherr, G., Gottfried, M. & Pauli, H. 2001. Long term monitoring of mountain peaks in the Alps. In: Burga, C. & Kratochwil, A. (eds.) *Biomonitoring: general and applied aspects on regional and global scales*. Kluwer, Dordrecht, NL.

Greer, G.K. 1993. The influence of soil topography and spore-rain density on gender expression in gametophyte populations of the homosporous fern *Aspidotis densa*. *American Fern Journal* 83: 54-59.

Guisan, A. & Theurillat, J.-P. 2000. Assessing alpine plant vulnerability to climate change: a modeling perspective. *Integrated Assessment* 1: 307-320.

Hofer, H.R. 1992. Veränderungen in der Vegetation von 14 Gipfeln des Berninagebietes zwischen 1905 und 1985. *Berichte des Geobotanische Instituts der ETH Stiftung Rübel Zürich* 58: 39-54.

Illa, E., Carrillo, E. & Ninot, J.M. 2006. Patterns of plant traits in Pyrenean alpine vegetation. *Flora* 201: 528-546.

Kammer, P.M., Schöb, C. & Choler, P. 2007. Increasing species richness on mountain summits: upward migration due to anthropogenic climate change or re-colonisation? *Journal of Vegetation Science* 18: 301-306.

Kercher, S.M., Frieswyk, C.B. & Zedler, J.B. 2003. Effects of sampling teams and estimation methods on the assessment of plant cover. *Journal of Vegetation Science* 14: 899-906.

Klanderud, K. & Birks, H.J.B. 2003. Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *Holocene* 13: 1-6.

Klimeš, L., Dančák, M., Hájek, M., Jongepierová, I. & Kučera, T. 2001. Scale-dependent biases of species counts in a grassland. *Journal of Vegetation Science* 12: 699-704.

Klotz, S., Ingolf, K. & Durka, W. 2002. *BIOLFOR – Eine Datenbank mit biologisch-ökologishen Merkmalen zur Flora von Deutschland*. Schriftenreihe für Vegetationskunde 38, Bundesamt für Naturschutz, Bonn, DE.

Körner, C. 2003. *Alpine plant life*. 2nd. ed. Springer, Berlin, DE.

Kudernatsch, T. 2005. *Auswirkungen der globalen Erwärmung auf die Vegetation alpiner Kalk-Magerrasen im Nationalpark Berchtesgaden*. Doctoral Thesis Technical University of Munich, DE.

Kullman, L. 1986. Late Holocene reproductional patterns of *Pinus sylvestris* and *Picea abies* at the forest limit in central Sweden. *Canadian Journal of Botany* 64: 1682-1690.

Kullmann, L. 2003. Förändringar i fjällens växtvärld – effekter av varmare klimat. [Changes in alpine plant cover – effects of climate warming.] *Svensk Botanisk Tidskrift* 97: 210-221.

Landolt, E. 1977. Ökologische Zeigerwerte zur Schweizer Flora. *Veröffentlichungen des Geobotanischen Instituts der ETH Stiftung Rübel Zürich* 64: 1-208.

Lechner, E. 1858. *Piz Languard und die Bernina-Gruppe bei Pontresina*. Wilhelm Engelmann, Leipzig, DE.

Lepš, J. & Hadincová, V. 1992. How reliable are our vegetation analyses? *Journal of Vegetation Science* 3: 119-124.

Lloret, F., Medail, F., Brundu, G., Camarda, I., Moragues, E., Rita, J., Lambdon, P. & Hulme, P. E. 2005. Species attributes and invasion success by alien plants on Mediterranean islands. *Journal of Ecology* 93: 512-520.

MacArthur, R.H. & Wilson, E.O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ, US.

Maisch, M., Burga, C.A. & Fitze, P. 1999. *Lebendiges Gletschervorfeld. Führer und Begleitbuch zum Gletscherlehrpfad Morteratsch*. 2nd. ed. Engadin Press, Samedan, CH.

Moiseev, P.A. & Shiyatov, S.G. 2003. Vegetation dynamics at the treeline ecotone in the Ural highlands, Russia. In: Nagy, L., Grabherr, G., Körner, C. & Thompson, D.B.A. (eds.) *Alpine biodiversity in Europe – A Europe-wide assessment of biological richness and change*. Ecological Studies, Springer, Berlin, DE.

Moser, D.M., Gygax, A., Bäumler, B., Wyler, N. & Palese, R. 2002. *Liste Rouge des fougères et plantes à fleur menacées de Suisse*. Série OFEFP 'L'environnement pratique'. Office fédéral de l'environnement, des forêts et du paysage, Berne, CH.

Müller-Schneider, P. 1986. Verbreitungsbiologie der Blütenpflanzen Graubündens. *Veröffentlichungen des Geobotanischen Instituts der ETH Stiftung Rübel Zürich* 85: 1-263.

Ozinga, W.A., Bekker, R.M., Schaminée, J.H. & van Groenendael, J.M. 2004. Dispersal potential in plant communities depends on environmental conditions. *Journal of Ecology* 92: 767-777.

Parolo, G. & Rossi, G. 2008. Upward migration of vascular plants following a climate warming trend in the Alps. *Basic and Applied Eco*logy 4: 100-107.

Paul, F., Kääb, A., Maisch, M., Kellenberger, T. & Haeberli, W. 2004. Rapid disintegration of Alpine glaciers observed with satellite data. *Geophysical Research Lett*ers 31. L21402, doi:10.1029/2004GL020816

Pauli, H., Gottfried, M., Grabherr, G. 2001. High summits of the Alps in a changing climate. In: Walther, G.-R., Burga, C.A. & Edwards, P.J. (eds) *Fingerprints of Climate Change – Adapted behaviour and shifting species ranges*. Kluwer/ Plenum, New York, NY, US.

Pauli, H., Gottfried, M., Reiter, K., Klettner, C., & Grabherr, G. 2007. Signals of range expansions and contractions of vascular plants in the high Alps: Observations (1994-2004) at the GLORIA master site Schrankogel, Tyrol, Austria. *Global Change Biology* 13: 147-156.

Peñuelas, J. & Boada, M. 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biology* 9: 131-140.

Pignatti, S. 2005. Valory di bioindicazione delle piante vascolari della flora d'Italia. *Braun-Blanquetia* 39: 1-97.

Rebetez, M. & Reinhard, M. 2008. Monthly air temperature trends in Switzerland 1901-2000 and 1975-2004. *Theoretical and Applied Climatology* 91: 27-34.

Rübel, E. 1912. *Pflanzengeographische Monographie des Berninagebietes*. Engelmann, Leipzig, DE.

Stöcklin, J. 1992. Umwelt, Morphology und Wachstumsmuster klonaler Pflanzen – eine Übersicht. *Botanica Helvetica* 102: 3-21.

Stöcklin, J. & Bäumler, E. 1996. Seed rain, seedling establishment and clonal growth strategies on a glacier foreland. *Journal of Vegetation Science* 7: 45-56.

Sturm, M., Racine, C. & Tape, K. 2001. Climate change – Increasing shrub abundance in the Arctic. *Nature* 411: 546-547.

Taylor, A.H. 1995. Forest expansion and climate change in the mountain hemlock (*Tsuga mertensiana*) zone, Lassen Volcanic National Park, California, U.S.A. *Arctic and Alpine Research* 27: 207-216.

Thornton, I.W.B., Cook, S., Edwards, J.S., Harrison, R.D., Schipper, C., Shanahan, M., Singadan, R. & Yamuna, R. 2001. Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. VII. Overview and discussion. *Journal of Biogeography* 28: 1389-1408.

Ungricht, S. 1995. *Die Flora der Gletscherinsel Isla Persa (Bernina, Graubünden) – Ein Indikator für eine Klimaerwärmung?* Seminar Thesis, ETH Zürich, CH.

van der Maarel, E. 1996. Pattern and process in the plant community: fifty years after A.S. Watt. *Journal of Vegetation Science* 7: 19-28.

Vittoz, P. & Engler, R. 2007. Seed dispersal distances: a typology based on dispersal modes and plant traits. *Botanica Helvetica* 117: 109-124.

Vittoz, P. & Guisan, A. 2007. How reliable is the monitoring of permanent vegetation plots? A test with multiple observers. *Journal of Vegetation Science*18: 413-422.

Vittoz, P., Jutzeler, S. & Guisan, A. 2006. Flore alpine et réchauffement climatique: observation de trois sommets valaisans à travers le 20ème siècle. *Bulletin Murithienne* 123/2005: 49-59.

Vittoz, P., Rulence, B., Largey, T. & Freléchoux, F. 2008. Effects of climate and land-use change on the establishment and growth of cembran pine (*Pinus cembra* L.) over the altitudinal treeline ecotone in the Central Swiss Alps. *Arctic, Antarctic and Alpine Research* 40: 225-232.

Wahren, C.-H.A., Walker, M.D. & Bret-Harte, M.S. 2005. Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology* 11: 537-552.

Walther, G.-R. 2004. Plants in a warmer world. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 169-185.

Walther, G.-R. Beißner, S. & Burga, C.-A. 2005a. Trends in the upward shift of alpine plants. *Journal of Vegetation Science* 16: 541-548.

Walther, G.-R., Berger, S. & Sykes, M.T. 2005b. An ecological 'footprint' of climate change. *Proceedings of the Royal Society of London, Series B-Biological Science* 272: 1427-1432.

Welling, P., Tolvanen, A. & Laine, K. 2005. Plant traits: Their role in the regeneration of alpine plant communities in sub-arctic Finland. *Journal of Vegetation Science* 16: 183-190.

Willson, M.F., Rice, B.L. & Westoby, M. 1990. Seed dispersal spectra: a comparison of temperate plant communities. *Journal of Vegetation Science* 1: 547-562.

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For App. 1-3, see below (online version)
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App. 1. Comparative plant inventory on Isla Persa (Swiss Alps). **1** = species present without abundance estimation; ***** = species probably overlooked because present in a previous and following inventory; **r!** = very rare; **r** rare; **s** = scattered; **c** = common; **d** = dominant; precision given if locally different (for example **s-lc** for scattered but locally common).

Species of the Rübel area (= ice-free area in 1906)			**Year**		
Species name	**1906**	**1927**	**1972**	**1995**	**2003/4**
Carex curvula	1	1	1	1	c-ld
Achillea erba-rotta ssp. *moschata*	1	1	1	1	c
Adenostyles leucophylla / A. intermedia	1	1	1	1	c
Agrostis rupestris	1	1	1	1	c
Agrostis schraderiana	1	1	1	1	c
Alchemilla fissa	1	1	1	1	c
Antennaria carpatica	1	1	1	1	c
Anthoxanthum odoratum s.l.	1	1	1	1	c
Cardamine resedifolia	1	1	1	1	c
Carex sempervirens	1	1	1	1	c
Doronicum clusii	1	1	1	1	c
Erigeron uniflorus	1	1	1	1	c
Euphrasia minima	1	1	1	1	c
Festuca violacea agg.	1	1	1	1	c
Gentiana punctata	1	1	1	1	c
Geum reptans	1	1	1	1	c
Gnaphalium supinum	1	1	1	1	c
Hieracium piliferum agg.	1	1	1	1	c
Homogyne alpina	1	1	1	1	c
Huperzia selago	1	1	1	1	c
Juncus trifidus	1	1	1	1	c
Juniperus communis ssp. *alpina*	1	1	1	1	c
Leontodon helveticus	1	1	1	1	c
Leucanthemopsis alpina	1	1	1	1	c
Ligusticum mutellina	1	1	1	1	c
Luzula alpinopilosa	1	1	1	1	c
Pedicularis kerneri	1	1	1	1	c
Phyteuma hemisphaericum	1	1	1	1	c
Poa alpina	1	1	1	1	c
Primula latifolia	1	1	1	1	c
Rhododendron ferrugineum	1	1	1	1	c
Salix herbacea	1	1	1	1	c
Saxifraga bryoides	1	1	1	1	c
Senecio incanus ssp. *carniolicus*	1	1	1	1	c
Sibbaldia procumbens	1	1	1	1	c
Solidago virgaurea ssp. *minuta*	1	1	1	1	c
Vaccinium gaultherioides	1	1	1	1	c
Veronica alpina	1	1	1	1	c
Viola biflora	1	1	1	1	c
Astrantia minor	1	1	1	*	c
Silene exscapa	1	1	1	*	c
Cirsium spinosissimum	1	1	1	1	s-lc
Minuartia sedoides	1	1	1	1	s-lc
Phyteuma globulariifolium s.l.	1	1	1	1	s-lc
Poa laxa / P. minor	1	1	1	1	s-lc
Silene acaulis	1	*	1	1	s-lc
Campanula barbata	1	1	1	1	s
Campanula scheuchzeri	1	1	1	1	s
Cystopteris fragilis	1	1	1	1	s
Empetrum nigrum ssp. *hermaphroditum*	1	1	1	1	s
Gentiana acaulis	1	1	1	1	s
Helictotrichon versicolor	1	1	1	1	s
Myosotis alpestris	1	1	1	1	s
Nardus stricta	1	1	1	1	s
Oreochloa disticha	1	1	1	1	s
Oxyria digyna	1	1	1	1	s
Polygonum viviparum	1	1	1	1	s
Potentilla aurea	1	1	1	1	s
Potentilla crantzii	1	1	1	1	s
Primula hirsuta	1	1	1	1	s
Ranunculus montanus	1	1	1	1	s
Saxifraga seguieri	1	1	1	1	s
Sedum alpestre	1	1	1	1	s
Taraxacum alpinum agg.	1	1	1	1	s

App. 1-3. Internet supplement to: Vittoz, P. et al. 2008.
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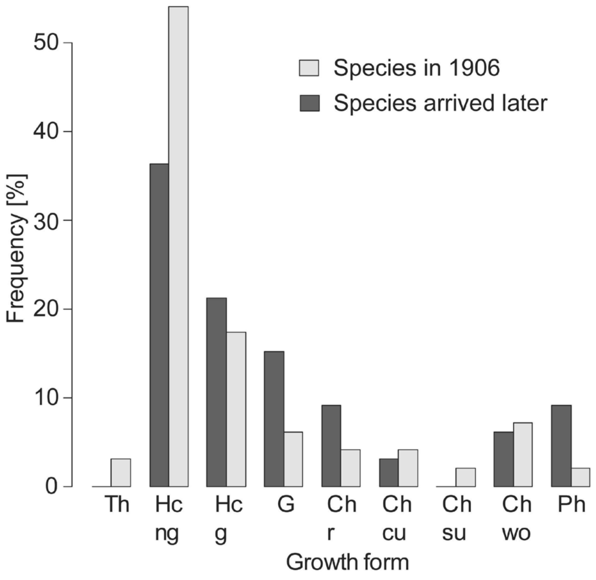
App. 1, cont.

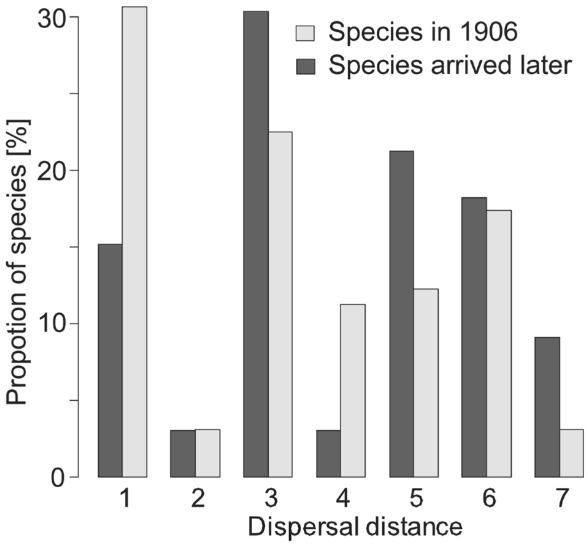
Species of the Rübel area (= ice-free area in 1906)			**Year**		
Species name	**1906**	**1927**	**1972**	**1995**	**2003/4**
Vaccinium vitis-idaea	1	*	1	1	s
Agrostis alpina	1	1	1	*	s
Selaginella selaginoides	1	*	1	*	s
Adenostyles alliariae	1	1	1	1	r-lc
Bartsia alpina	1	1	1	1	r-lc
Daphne striata	1	1	1	1	r-lc
Epilobium fleischeri	1	1	1	1	r-lc
Lotus alpinus	1	1	1	1	r-lc
Peucedanum ostruthium	1	1	1	1	r-lc
Sempervivum montanum	1	1	1	1	r-lc
Carex frigida / C. ferruginea	1	1	1	*	r-lc
Carex atrata ssp. *aterrima*	1	1	1	1	r-ls
Galium anisophyllon / G. pumilum	1	1	1	1	r-ls
Luzula spicata	1	1	1	1	r-ls
Arenaria biflora	1	1	1	1	r
Botrychium lunaria	1	1	1	1	r
Cerastium pedunculatum	1	1	1	1	r
Gentiana bavarica	1	1	1	1	r
Geum montanum	1	1	1	1	r
Hieracium alpinum	1	1	1	1	r
Lloydia serotina	1	1	1	1	r
Luzula lutea	1	1	1	1	r
Phyteuma hedrianthifolium	1	1	1	1	r
Ranunculus glacialis	1	1	1	1	r
Silene rupestris	1	1	1	1	r
Thesium alpinum	1	1	1	1	r
Cardamine alpina	1	*	1	1	r
Epilobium angustifolium	1	*	1	1	r
Gentiana ramosa	1	*	*	1	r
Achillea nana	1	*	1	*	r
Avenella flexuosa / Deschampsia caespitosa	1	1	1	1	r!
Vaccinium myrtillus		1	1	1	s-lc
Elyna myosuroides		1	1	1	s
Pinguicula leptoceras		1	1	*	s
Soldanella alpina		1	1	*	s
Cerastium uniflorum		1	1	1	r-lc
Primula integrifolia		1	1	*	r-lc
Gentiana brachyphylla		1	1	1	r
Trichophorum cespitosum		1	*	*	r
Antennaria dioica		1	1	*	r!
Cryptogramma crispa			1	1	r
Athyrium distentifolium			1	1	r
Polystichum lonchitis			1	1	r
Trifolium alpinum			1	1	r
Asplenium septentrionale			1	*	r
Coeloglossum viride			1	*	r
Phleum alpinum			1	*	r
Poa supina / P. annua / P. badensis			1	*	r
Sagina saginoides / S. glabra			1	*	r
Salix helvetica			1	1	r!
Diphasiastrum alpinum			1	*	r!
Ribes petraeum			1	*	r!
Gymnocarpium dryopteris				1	r!
Arctostaphylos uva-ursi					r!
cf. *Aster bellidiastrum*					r!
Dryopteris cf. *dilatata*					r!
Dryopteris filix-mas					r!
Festuca rubra agg.					r!
Gentiana verna					r!
Larix decidua					r!
Leontodon cf. *autumnalis*					r!
Pulsatilla alpina s.l.					r!
Euphrasia rostkoviana	1				
Gentiana campestris	1				
Thymus serpyllum		1			
Festuca halleri			1		
Veronica bellidioides	1	1	1		

App. 1, cont.

Additional species occurring only on the recently deglaciated area Species name	1906	1927	Year 1972	1995	2003
Androsace alpina / *A. pubescens*		1	1	1	1
Saxifraga oppositifolia		1	1	*	1
Saxifraga stellaris		1	1	*	1
Poa nemoralis		1	*	*	1
Arabis caerulea			1	1	1
Artemisia genipi			1	1	1
Salix glaucosericea			1	1	1
Salix hastata			1	1	1
Saxifraga exarata			1	1	1
Veronica fruticans			1	1	1
Arabis alpina			1	*	1
Epilobium anagallidifolium			1	*	1
Hieracium intybaceum			1	*	1
Salix retusa			1	*	1
Salix serpyllifolia			1	*	1
Asplenium viride			1	1	
Salix foetida			1	1	
Saxifraga paniculata			1	1	
Tussilago farfara			1		
Linaria alpina				1	1
Erigeron cf. *neglectus*					1
Luzula cf. *sudetica*					1
Phyteuma betonicifolium					1



App. 2. Distribution of the 98 species present in 1906 and the 31 that arrived later of 9 growth-form types (Pignatti 2005; Illa et al. 2006): Th = therophytes; Hc ng = non-graminoid hemicryptophytes; Hc g = graminoid hemicryptophytes; G = geophytes; Ch r = creeping chamaephytes; Ch cu = chamaephytes in cushions; Ch su = succulent chamaephytes; Ch wo = woody chamaephytes; Ph = phanerophytes.



App. 3. Distribution of dispersal distance potential in seven categories for the 98 species present in 1906 and the 31 that arrived later (Vittoz & Engler 2007): 1, 99% of the seeds fall in a distance < 1 m; 2, < 5 m; 3, < 15 m; 4, < 150 m; 5, < 500 m; 6, < 1500 m; 7, < 5000 m.

Déplacements déjà observés des espèces végétales : quelques cas emblématiques mais pas de migrations massives

La seconde moitié du 20^e siècle a connu une évolution significative du climat, accompagnée de changements observables dans le fonctionnement des couverts végétaux, notamment de leur phénologie. Mais observe-t-on des évolutions de la composition de la végétation ? Quels milieux, quelles espèces sont affectés ? Faisons le point, très concrètement, sur cette question faussement simple, qui introduit la problématique du suivi des effets du changement climatique.

Intérêt de l'étude de la végétation dans l'observation des effets du changement climatique

Les végétaux présentent un double intérêt dans l'étude de l'impact du changement climatique. D'une part, ce sont des indicateurs précieux des modifications de l'environnement, telles qu'elles sont perçues par la forêt. Ce rôle bio-indicateur de la végétation est utilisé depuis longtemps pour la typologie des stations forestières par exemple. Il est surtout joué par les espèces du sous-bois, plus nombreuses et moins soumises à la sylviculture que les espèces de la strate arborescente, sous fort contrôle de la gestion forestière. Mais surtout, les végétaux constituent une composante majeure de la biodiversité forestière et, à ce titre, ont une valeur écologique intrinsèque, fournissant services écologiques et réservoir de diversité. C'est évident dans le cas des arbres, espèces « clef de voûte » de l'écosystème forestier, mais c'est aussi le cas des espèces du sous-bois. Ces dernières constituent en effet la majeure partie de la diversité des gènes d'origine végétale présents dans l'écosystème : dans le réseau Renecofor par exemple, on compte 17 espèces (appartenant à 10 familles) au maximum dans la strate arborescente de la placette la plus riche, contre 130 espèces (appartenant à 68 familles) dans les strates basses. De plus, les espèces du sous-bois peuvent constituer, dans les peuplements ouverts, une part importante des flux d'eau, d'énergie et de nutriments de l'écosystème. La modification de la composition en espèces peut donc affecter de façon importante le fonctionnement et la valeur des écosystèmes forestiers. À ces divers titres, il est nécessaire de connaître le devenir des communautés végétales sous l'impact du réchauffement climatique.

Les modèles d'impact du changement climatique sur l'aire de répartition des espèces forestières prévoient d'importants déplacements des aires potentielles des espèces au cours du 21^e siècle (Badeau *et al.*, ce volume). La paléoécologie, quant à elle, nous enseigne que les espèces ont vu leur aire de répartition modifiée à l'échelle de l'ensemble de l'Europe dans des périodes de temps de quelques milliers d'années. Au cours des 10 000 dernières années par exemple, les actuelles forêts collinéennes du nord de la France ont connu successivement des phases de pelouses puis landes subarctiques, de forêts où ont dominé le bouleau, le noisetier, puis les chênes et l'orme et, enfin, le hêtre. Mais que s'est-il passé au cours du 20^e siècle ? Observe-t-on déjà des effets du réchauffement climatique sur l'aire de répartition des végétaux ? Comment les mettre en évidence ? C'est à ces questions d'écologie historique que nous apportons quelques éléments de réponse dans cet article.

Quelles sont les caractéristiques de l'oscillation climatique du 20^e siècle ? On observe un réchauffement global de la planète de 0,7 °C depuis 1850. Mais le réchauffement observé en France est plus élevé, de 0,9 °C au cours du 20^e siècle (Moisselin *et al.* 2002). Il est plus important pour les températures minimales (+1,2 °C) que pour les maximales (+0,6 °C). Il est moins marqué en hiver que durant le reste de l'année. Mais surtout, ce réchauffement est intervenu en deux phases bien différenciées, au cours de la première moitié du 20^e siècle d'une part et depuis le milieu des années 1970 d'autre part. La tendance des 30 dernières années est ainsi beaucoup plus élevée que sur le siècle entier, de +0,5 °C par décennie. Les pluies montrent une tendance globalement non significative à l'augmentation, plutôt en hiver. On observe enfin une tendance à l'augmentation de l'aridité du climat dans les régions les plus méridionales.

Comment mettre en évidence les effets du changement climatique sur la répartition des végétaux ?

Pour évaluer l'impact de ce réchauffement sur l'aire de répartition des espèces forestières, il faut pouvoir disposer de données anciennes, relevés de végétation ou herbiers, avec lesquelles on pourra comparer la végétation actuelle. Paradoxalement, alors que la paléoécologie, qui s'intéresse à des périodes plus anciennes, peut s'appuyer sur de nombreuses références palynologiques (pollens) et anthracologiques (charbons de bois) trouvées dans les tourbières ou les sites archéologiques, l'étude de l'évolution de la végétation au cours du dernier siècle se heurte au manque de données de référence. Il existe bien sûr de très nombreux relevés de végétation anciens, faits à l'occasion des typologies de station forestière par exemple. Mais, pour la plupart, ils n'ont pas été réalisés dans l'optique d'un échantillonnage ultérieur. En particulier, ils n'ont pas été localisés avec précision et la végétation n'a pas été relevée de façon exhaustive. Nos prédécesseurs n'avaient malheureusement pas de GPS pour géoréférencer leurs observations ! Les réseaux d'observation *ad hoc* sont de création récente, et la détection des mouvements de végétation y est donc encore très délicate. Les premières observations floristiques systématiques de l'Inventaire forestier national, du réseau de surveillance de l'état de santé des forêts et du réseau Renecofor datent de 1985, 1993 et 1995 respectivement.

En limite d'aire de répartition, la progression ou la régression des arbres peuvent aussi être étudiées par dendrochronologie, en caractérisant les structures d'âge des populations.

Premières observations : en montagne et dans les régions boréales

Les observations de déplacement d'espèces végétales dans les plaines et collines de la zone tempérée attribuables au changement climatique sont encore très rares. Dès 1993, Mandin constatait en Ardèche la progression vers le Nord de plusieurs espèces thermophiles méditerranéennes dont la férule commune. Mais l'impact du réchauffement climatique a surtout été recherché dans les montagnes. Non pas que le réchauffement y soit plus fort qu'ailleurs, mais parce que le gradient de température est très fort, en moyenne de 0,6 °C pour 100 m d'altitude, comparé aux plaines françaises où il est environ 1 000 fois plus faible, de l'ordre de 0,5 °C pour 100 km de latitude. L'augmentation de température observée au 20^e siècle en France correspond donc à une montée des isothermes de 15 m/décennie environ en montagne. En plaine, ce réchauffement correspond, en moyenne sur la France, à un déplacement vers le nord de 36 km, 9 km et 18 km par décennie des isothermes de température minimale, maximale et moyenne, respectivement. Il est donc probable que les espèces puissent suivre de façon plus rapide et refléter de façon plus étroite les changements climatiques en montagne. En plaine, où les forêts sont en outre beaucoup plus morcelées qu'en montagne, de nombreuses espèces ne peuvent se déplacer à cette vitesse.

En 2003, Camille Parmesan et Gary Yohe publiaient dans la revue Nature la première synthèse scientifique annonçant l'observation d'effets globaux, généralisés et significatifs du réchauffement climatique en cours sur l'aire de répartition des espèces. L'analyse des déplacements de près de 1 000 espèces animales et végétales montrait un déplacement significatif des limites de leur aire de répartition, évalué à 6,1 km vers le nord, soit 6,1 m en altitude par décennie. Mais qu'en était-il des seuls végétaux ?


J.L. Dupouey, INRA

Progression en altitude du pin à crochets dans les Pyrénées : déprise pastorale ou réchauffement climatique ? On observe des bouquets d'arbres d'âges décroissants en remontant dans les rhodoraies situées au contact des massifs forestiers.

En fait, les études analysées dans cette synthèse concernaient principalement les végétaux des régions arctique et antarctique. Dans les régions européennes, un seul travail était pris en compte (Grabherr *et al.*, 1994). Il s'agit du rééchantillonnage à long terme d'une trentaine de sommets alpins, presque tous dépassant 3 000 m d'altitude. Ces rééchantillonnages ont montré dans la majorité des cas (70 %) une augmentation au cours du 20^e siècle du nombre d'espèces présentes sur ces sommets : on observe une pénétration des espèces de l'étage subalpin dans cet étage nival, qui est attribuée par les auteurs de cette étude au réchauffement climatique. Mais les études méthodologiques menées dans le réseau Renecofor (Camaret *et al*. 2004) nous ont aussi montré à quel point le nombre d'espèces observées en un site est un paramètre entaché d'une très forte erreur, car fortement variable d'un observateur à l'autre. Dans une même bande de 100 m², les écarts peuvent aller de 70 à 105 espèces pour des observateurs pourtant expérimentés et en condition de test. L'interprétation des variations de la richesse en espèces au cours du temps doit donc rester très prudente.

Plus bas en altitude, au contact des zones forestières, on observe dans de nombreuses régions du monde une forte progression vers le haut de la limite de la forêt. La dendrochronologie, qui permet de caractériser la dynamique de ces populations d'altitude et de dater avec précision l'âge d'installation de chaque arbre, montre que ces recolonisations sont le plus souvent récentes. Mais leur attribution de façon univoque au changement climatique est quasiment impossible, puisque la déprise pastorale dans les montagnes européennes et le réchauffement du 20e siècle sont concomitants, et les deux causes sont donc très difficiles à distinguer. Il est d'ailleurs très probable que la diminution de la pression de pâturage ait joué un rôle bien supérieur au changement climatique dans cette fluctuation du niveau supérieur de la forêt. De nombreux indices, phytosociologiques, dendrométriques, historiques ou anthracologiques indiquent que la forêt européenne est actuellement plusieurs centaines de mètres plus bas que sa limite climatique, pour des causes anthropiques. Finalement, peu de sites supra-forestiers permettent l'étude de l'impact du changement climatique seul. Dans les montagnes de l'Oural, on a pu mettre en évidence une progression de 20 à 40 m entre 1910 et 2000 du mélèze de Sibérie à sa limite altitudinale, alors que l'herbivorie y est supposée sans effet (Shiyatov, 2003). Dans le même temps, l'isotherme de juin-juillet a monté de 120-130 m.

La progression des espèces laurifoliées

Les études en milieu forestier échappent, pour partie, au problème de l'évolution de la pression de pâturage. La première observation a été faite par Gian-Reto Walther dans les chênaies du piedmont Suisse (2002). Sur le versant sud des Alpes, il a observé par échantillonnage à 30 ans d'intervalle (années 1960 puis années 1990) une forte progression des espèces à feuilles larges et pérennes. Parmi celles-ci, on trouve quelques espèces indigènes, telles que le houx, le lierre, le petit houx ou le daphné lauréole. Mais surtout, on observe l'apparition dans ces forêts d'un cortège important d'espèces introduites : palmier de Chine, laurier-cerise, laurier-sauce, camphrier du Népal (*Cinnamonum glanduliferum*)… L'aspect des forêts en est fortement affecté (photo ci-dessous) ! Ces espèces ont été introduites pour la plupart depuis plus d'un siècle dans les jardins de la région. Mais elles ne se sont répandues dans les forêts que récemment. Walther relie cette expansion des espèces « laurifoliées » à la diminution drastique du nombre de jours de gel observée dans la même région en un siècle : de 75 à 30 jours en moyenne entre la première moitié du 20e siècle et les 3 dernières décennies. Il faut souligner l'intérêt de ces observations : le changement climatique ne favorisera pas que les espèces autochtones et son interaction avec les introductions d'espèces pourra amener à l'apparition de combinaisons d'espèces très imprévisibles dans nos forêts.


V. Badeau, INRA

Les espèces laurifoliées (ici, palmier de Chine) envahissent les chênaies du piedmont alpin, en Suisse

Cette première observation a été confirmée pour le houx dans d'autres sites, et en particulier dans les zones de plaine. Un rééchantillonnage à 50 ans d'intervalle montre que l'espèce progresse rapidement vers le nord le long des côtes sud de la Suède, à la limite de son aire de répartition actuelle. En France, nous avons pu étudier son évolution dans les quelques départements où l'Inventaire forestier national (IFN) a déjà effectué deux cycles complets d'inventaire (Cluzeau *et al*., 2001). Ainsi, dans les Ardennes, l'espèce progresse très fortement entre 1987 et 1998, passant de 10 à 21 % de présence dans les relevés floristiques de l'IFN (figure 1). La limite climatique de cette espèce se situe sur l'isotherme -0,5 °C de température moyenne du mois le plus froid de l'année. Dans les Ardennes, cette température du mois le plus froid a progressé de plus de 2 °C entre les deux inventaires, entre les décennies 1978-1987 et 1989-1998, alors qu'elle se situait justement à peine au-dessus de la limite de -0,5 °C lors de la première de ces deux périodes. Roland Carbiener avait déjà observé il y a plusieurs décennies que la dynamique du houx dans les Vosges était fortement liée à l'évolution des gelées. On ne peut exclure aussi le rôle de la sylviculture dans cette progression du

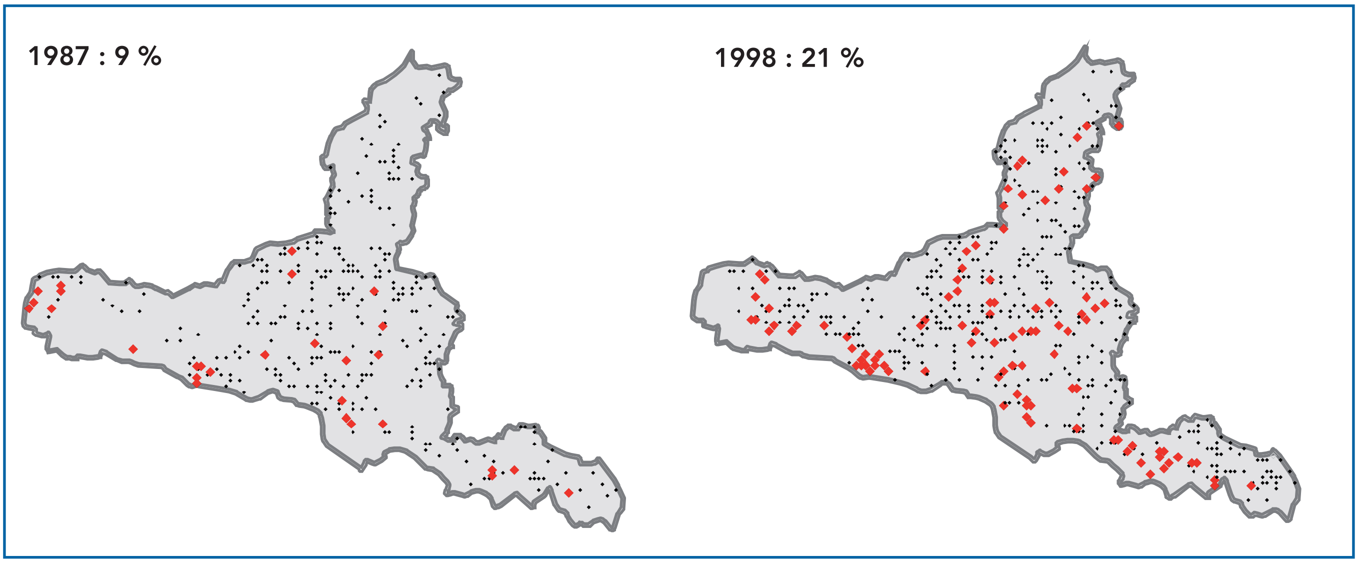


Fig. 1 : progression du houx dans l'Ardenne Primaire entre 1987 et 1998 dans les relevés de l'IFN

Les points noirs indiquent les relevés IFN et les points rouges ceux où le houx est présent.

houx, puisque, en France du moins, cette espèce naguère considérée comme gênante pour le forestier est aujourd'hui nettement favorisée afin d'introduire une certaine diversité dans des peuplements par ailleurs très pauvres en essences.

Le gui, une autre espèce à feuilles pérennes, montre aussi des déplacements d'aire de répartition significatifs. Dans le Valais suisse, Matthias Dobbertin (2005) a montré que cette espèce a progressé sur pin sylvestre de 200 m en altitude, de 1050 à 1250 m, entre 1910 et la fin du 20e siècle. Conformément à l'hypothèse d'une mise en équilibre avec le climat, cette progression est parfaitement cohérente avec les modèles connus de limitation du gui par la température du mois le plus froid et par les changements observés de cette température dans le Valais. Le gui, lorsqu'il est présent, entraîne un surcroît de mortalité du pin sylvestre de 10 % environ. Le changement climatique entraîne donc aussi des modifications de l'aire de répartition des parasites des plantes. Là encore, cela conduira à terme à un fort remaniement des combinaisons d'espèces.

Dans les zones plus méridionales de France et d'Europe, les espèces à feuilles caduques de la zone tempérée entrent en contact avec les espèces sclérophylles des forêts méditerranéennes qui pourraient, elles aussi, progresser sous l'effet du réchauffement climatique. Peñuelas et Boada (2003) ont ainsi observé une régression significative des surfaces de hêtraie entre 1945 et 1994 sur le flanc sud du massif de Montseny, en Catalogne, entre 800 et 1 200 m, au profit du chêne vert. Cette disparition s'accompagne de divers symptômes de régression dans les hêtraies encore en place : morcellement des peuplements, faiblesse de la régénération, niveau élevé de défoliation.

Un changement global dans lequel il est difficile de faire la part des différentes modifications de l'environnement

Dans les étages sylvatiques des Alpes françaises, nous avons mené trois études afin de rechercher d'éventuels impacts des changements climatiques. Dans le Briançonnais, nous avons rééchantillonné un ensemble de 73 placettes à 23 ans d'intervalle, entre 1969 et 1992, stratifié selon les conditions de substrat, altitude et exposition. L'évolution de la végétation montre une progression significative des espèces vers de plus hautes altitudes (Dupouey *et al.*, 1998). Cette évolution est en fait nulle dans l'étage montagnard et très significative dans l'étage subalpin et en particulier sur les versants nord, où elle correspond, ramenée au gradient de température, à une augmentation de 0,09 °C/décennie (figure 2). Il faut noter que ces peuplements subalpins de versant nord sont aussi ceux qui ont subi les changements de pression anthropique les plus faibles au cours de la période étudiée. Dans la vallée de la Maurienne, nous avons refait en 2002 et 2003 un échantillonnage identique à celui mis en place par Charles Bartoli à partir des années 1950 pour l'étude des types de station de cette vallée. La comparaison des deux échantillons montre la progression des espèces nitrophiles et à caractère océanique. Ces deux facteurs sont intimement corrélés et nous ne pouvons pas encore identifier sans ambiguïté le facteur responsable de cette évolution (pollution azotée d'origine autoroutière ou réelle océanisation du climat).

Enfin, nous étudions actuellement l'évolution en 14 ans (1984 à 1998 en moyenne) de la végétation dans les Alpes du Sud au travers des relevés de l'Inventaire forestier national. Sur un total de près de 2000 taxons inventoriés dans 31 000 relevés, 341 espèces présentent une fréquence d'observation supérieure à 50 placettes aux deux dates d'échantillonnage, 227 parmi celles-ci ont une réponse de type « courbe en cloche » à l'altitude, montrant donc une altitude optimale qu'il est possible d'estimer aux deux dates d'échantillonnage. Parmi ces 227 espèces, 177 sont considérées comme identifiées de façon fiable par l'IFN aux deux dates. Sur ces 177 espèces, le déplacement médian en 14 ans est de +21 m, correspondant à un réchauffement de +0,08 °C / décennie (figure 3). Contrairement à ce que nous avons observé en Briançonnais, ce déplacement est surtout visible pour les espèces des étages inférieurs (supra-méditerranéen et montagnard).

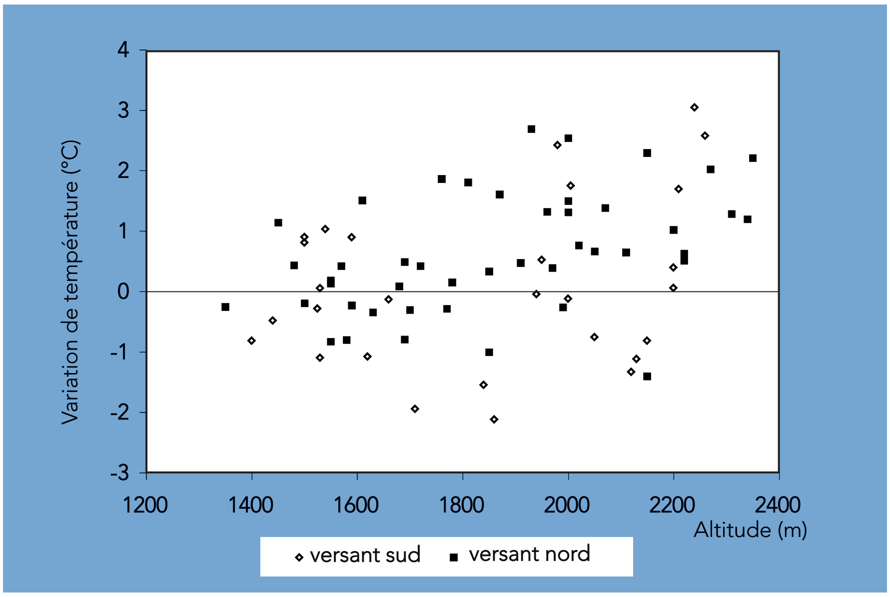


Fig. 2 : estimation des modifications de température indiquées par les changements de végétation entre 1969 et 1992 dans les forêts du Briançonnais

En abscisse, altitude mesurée des 73 relevés de végétation échantillonnés. En ordonnée, déplacement altitudinal de la végétation en 23 ans, calibré en équivalent température (°C/siècle), à partir du gradient vertical de 0,6 °C/100 m.

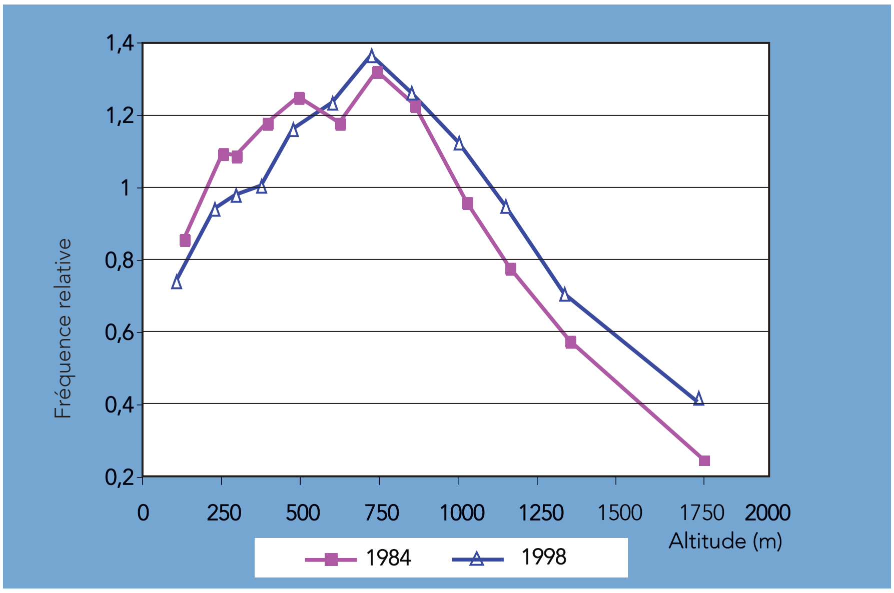


Fig. 3 : déplacement altitudinal de la germandrée petit chêne, une espèce forestière commune, dans la région PACA entre 1984 et 1998, d'après les données de l'IFN

En ordonnée : fréquence relative de l'espèce par rapport à sa fréquence moyenne d'observation à chaque date (28 % en 1984 et 40 % en 1998).

De la nécessité de réseaux d'observation cohérents, fiables et pérennes

En conclusion, nous n'assistons pas encore aujourd'hui à un déplacement massif des espèces végétales forestières sous l'effet du changement climatique en cours. La situation est différente de celle constatée pour la phénologie des plantes, avec un accroissement bien documenté de plus de 10 jours de la durée de saison de végétation au cours des dernières décennies (Seguin *et al.*, ce volume). Certains indices, souvent encore ambigus, vont bien dans le sens d'une pression accrue des variations du climat sur la dynamique des communautés végétales. Mais les déplacements observés sont souvent inférieurs à ce qu'on pourrait attendre à partir de simples calculs de rééquilibrage avec les variations du climat. Ce fait est à relier au constat que les espèces herbacées forestières ont, du moins pour celles de forêts anciennes, des capacités de dispersion très faibles (Dupouey *et al.*, 2002). Il faut donc s'attendre logiquement à ce que la dynamique des communautés végétales, même en montagne, ne suive celle du climat qu'avec un temps de latence plus ou moins long. Les espèces semblent ne pas toutes avoir réagi de la même façon. En accord avec leurs traits d'histoire de vie, les espèces lauriphylles en particulier seraient favorisées par le réchauffement climatique, puisque la pérennité des feuilles leur permet d'assimiler le carbone dès que la chaleur est suffisante.

L'écologie historique est là face à deux difficultés majeures : disposer de données anciennes fiables et adéquates d'une part et séparer le signal climatique des autres facteurs de changement dans les évolutions observées. Le changement climatique intervient en effet en même temps que d'autres évolutions drastiques de l'environnement forestier : évolution de l'acidité des pluies, des niveaux de dépôts azotés (Dupouey *et al.*, 1999), accroissement du volume sur pied des peuplements forestiers, progression des forêts sur abandons culturaux en plaine et zones de déprise pastorale en montagne, intensification de la sylviculture (tassement du sol lié à la mécanisation croissante, augmentation de la densité du réseau de routes forestières…), introduction d'espèces. Il ne faut pas s'y tromper, ces facteurs réunis ont très certainement joué, jusqu'à maintenant, un plus grand rôle que le changement climatique dans la dynamique de la végétation.

Seule la maintenance dans le long terme de réseaux de suivi de la végétation de plus en plus cohérents et fiables (Renecofor, réseau 16 km x 16 km, IFN, réseau du Département de la Santé des Forêts) permettra de mesurer et comprendre les effets réels du changement climatique sur la dynamique de la végétation forestière. À ce dispositif déjà existant, il faudrait idéalement pouvoir ajouter le suivi spécifique des populations ou espèces en limite de leur aire de répartition, en plaine et en montagne.

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Bibliographie

CAMARET S., BOURJOT L., DOBREMEZ J.F., BRÊTHES A., COQUILLARD P., CORRIOL G., DUMÉ G., DUPOUEY J.L., FORGEARD F., LEBRET M., GUEUGNOT J., PICARD J.F., SCHMITT A., TIMBAL J., ULRICH E., 2004. RENECOFOR - Suivi de la composition floristique des placettes du réseau (1994/95-2000) et élaboration d'un programme d'assurance qualité intensif. Fontainebleau : ONF Direction technique. 86 p.

CLUZEAU C., DRAPIER J., VIRION R., DUPOUEY J.L., 2001. Changements à long terme de la végétation forestière : apport des données de l'IFN. Rapport Projet GIP-ECOFOR « Forêt et Modifications de l'Environnement ». Paris : GIP-ECOFOR. 36 p. + ann.

DOBBERTIN M., HILKER N., REBETEZ M., ZIMMERMANN N.E., WOHLGEMUTH T., RIGLING A., 2005, The upward shift in altitude of pine mistletoe (*Viscum album ssp. austriacum*) in Switzerland - the result of climate warming? International Journal of Biometeorology, vol. 50, n° 1, pp. 40–47

DUPOUEY J.L., BECKER M., BERT D., CADEL G., LEFÈVRE Y., PICARD J.F., THIMONIER A., 1998. Évolution récente des sols, de la végétation et de la productivité des forêts de montagne françaises. Écologie, vol. 29, n° 1-2, pp. 341-349

DUPOUEY J.L., THIMONIER A., LEBOURGEOIS F., BECKER M., PICARD J.F., TIMBAL J., 1999. Changements de la végétation dans les forêts du Nord-Est de la France entre 1970 et 1990. Revue Forestière Française, vol. 51, n° 2, pp.219-230

DUPOUEY J.L., SCIAMA D., KOERNER W., DAMBRINE E., RAMEAU J.C., 2002. La végétation des forêts anciennes. Revue Forestière Française, vol. 54, n° 6, pp. 521-532

GRABHERR G., GOTTFRIED M., PAULI H., 1994. Climate effects on mountain plants. Nature, vol. 369, n° 6480, p. 448

MANDIN J.P., 1993. Progression actuelle d'espèces méditerranéennes vers le nord : le cas de *Ferula communis* L. *subsp. glauca* (L.) Rouy et Camus en Ardèche (France). Acta Botanica Gallica, vol. 140, pp. 81-90

MOISSELIN J.M., SCHNEIDER M., CANELLAS C., MESTRE O., 2002. Les changements climatiques en France au XXe siècle : étude des longues séries homogénéisées de données de température et de précipitations. La Météorologie, n° 38, pp. 45-56. <en ligne : http://www.smf.asso.fr/Ressources/Moisselin38.pdf>

PEÑUELAS J., BOADA M., 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). Global Change Biology, vol. 9, n° 2, pp. 131-140

PARMESAN C., YOHE G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature, vol. 421, n° 6918, pp. 37-42

SHIYATOV S.G., 2003. Rates of change in the upper treeline ecotone in the Polar Ural mountains, 2002. Past Global Changes News, vol. 11, n° 1, pp. 8-10. <en ligne : http://www.pages.unibe.ch/cgi-bin/WebObjects/products.woa/wa/product?id=3>

WALTHER G.R., 2002. Weakening of climatic constraints with global warming and its consequences for evergreen broad-leaved species. Folia Geobotanica, vol. 37, n° 1, pp. 129-139

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Cartographie de la flore, de la végétation et des milieux

Changements observés de la végétation dans les montagnes du Sud-Est de la France entre 1984 et 1998

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Résumé

La végétation du sous-bois forestier est un excellent bio-indicateur de l'environnement, climatique en particulier. En montagne, où les gradients verticaux de température et donc de végétation sont forts, on peut espérer pouvoir suivre les effets des changements climatiques en cours grâce à un rééquilibrage rapide de la végétation avec cet environnement climatique.

Nous présentons ici les résultats d'une étude de rééchantillonnage de la végétation dans 11 départements du Sud-Est de la France entre 1984 et 1998, sans relocalisation des placettes anciennes. Nous étudions les modifications de l'optimum d'altitude des espèces. Sur 1949 taxons échantillonnés, 123 sont suffisamment fréquents, bien reconnus et présentent une réponse à l'altitude en forme de courbe « en cloche » aux deux dates d'échantillonnage. Pour ces 123 taxons, le déplacement moyen en 14 ans est de 20 m vers le haut. Ce résultat suggère un effet du réchauffement climatique en cours, mais d'autres interprétations possibles sont discutées.

Mots-clés : dynamique de la végétation ; forêt ; montagne ; altitude ; changement climatique ; Inventaire forestier national ; rééchantillonnage

Abstract

Forest floor vegetation is a reliable bioindicator of the environment, including of climatic conditions. In the mountains, where vertical gradients of temperature and, hence, vegetation, are strong, one can expect monitoring early impacts of climate warming because species should be able to rapidly track their climatic niche.

Here we present first results from a resampling study of vegetation in southeastern part of France, between 1984 and 1998. The sampling scheme was not based on permanent plots and the two samples from each date were independent. The number of plots observed by National forest inventory teams was high: over 15000 at each date. Consequently, we modelled species presence as a function of elevation at each of the two sampling dates and analyzed shifts of the estimated optimum of presence within 14 years. Over 1949 observed taxa, 123 only were frequent enough, reliably identified and presented a bell-shaped curve at the two sampling dates. The average elevation shift of the optimum over these 123 taxa was of 20 metres towards highest elevation. This result suggests an impact of climatic warming in the Alps on forest vegetation. However, other potential causes of this shift are discussed.

Keywords : vegetation dynamics ; forest ; mountain ; elevation ; climatic change ; national forest inventory ; resampling.

Contexte et objectifs

La température moyenne annuelle de la planète a augmenté de 0,6°C au cours du XX^e siècle. En France, ce réchauffement a été plus élevé, de 0,9°C pour la température moyenne et de 1,2°C pour la température minimale (Moisselin *et al.* 2002). Ce réchauffement s'est accéléré à la fin du XX^e siècle, atteignant 0,5°C/décennie entre 1970 et 2000. Peut-on déjà observer des effets de cette augmentation de la température sur l'aire de répartition des espèces ? Nous avons, pour répondre à cette question, étudié les changements de la végétation forestière dans les montagnes du Sud-Est de la France, observés au travers des données de l'Inventaire forestier national (Ifn).

En montagne, la diminution de température est en moyenne de 1°C pour une élévation en altitude de 150 mètres, alors que, en plaine, ce même écart de température correspond à un déplacement de 150 kilomètres vers le Nord. On considère donc qu'en réponse au réchauffement du climat, puisque la distance à parcourir est beaucoup plus faible, les espèces peuvent plus facilement retrouver l'optimum de leur niche climatique en montagne qu'en plaine. De plus, les obstacles à la migration dus à l'urbanisation et aux surfaces agricoles y sont moindres.

Ainsi, Grabherr *et al.* (1994) et Walther *et al.* (2005) ont observé une augmentation de la richesse en espèces des sommets alpins, liée à une immigration d'espèces des étages inférieurs qu'ils interprètent comme un effet du réchauffement climatique. D'autre part, une remontée de la limite supérieure de la forêt est observée dans de nombreuses régions du monde. Ces observations faites dans les milieux supra-forestiers sont délicates à interpréter en raison des récentes et fortes variations de la pression de pâturage dans les mêmes zones (Didier & Brun 1998).

Les forêts de montagne présentent, par rapport aux milieux supra-forestiers, l'avantage d'avoir été moins influencées par ces variations des pratiques de pâturage, ou du moins cette influence est-elle un peu moins récente. D'autre part, la sylviculture y est en moyenne moins intensive qu'en plaine.

La majorité des études réalisées sur les changements de végétation à moyen ou long terme l'ont été par rééchantillonage de placettes permanentes. Cette méthode présente l'inconvénient de confondre les effets du vieillissement des peuplements avec ceux des changements environnementaux. Nous utilisons ici une nouvelle méthode, basée sur le rééchantillonnage de placettes non permanentes. Au lieu d'étudier l'apparition ou la disparition d'espèces dans des placettes permanentes, nous bâtissons des modèles de présence de chaque espèce en fonction de l'altitude et nous testons le décalage éventuel de ces courbes de réponse au cours du temps.

Echantillonnage

L'Ifn a réalisé deux cycles complets de relevés phytoécologiques en 1984 et 1998 dans le Sud-Est de la France. Il s'agit de l'année moyenne de chacun des deux cycles d'inventaire, qui se sont étalés en fait de 1981 à 1989 pour le premier et de 1992 à 2004 pour le second. Les relevés sont répartis dans 11 départements (Alpes de Haute Provence, Hautes Alpes, Alpes maritimes, Ardèche, Bouches du Rhône, Drôme, Gard, Hérault, Var, Vaucluse et Corse du Nord). Ils sont distribués de 0 à 2500 mètres d'altitude. L'échantillonnage est stratifié, par département, en fonction du type de peuplement (essence dominante et structure) et de la classe de propriété foncière. Il est reconstruit de façon indépendante à chacun des deux inventaires.

Les relevés contiennent des observations topographiques (pente, altitude, exposition…), pédologiques et floristiques. La végétation est inventoriée dans un cercle de 6 m de rayon lors du premier inventaire et de 15 m de rayon lors du second. La liste des espèces ligneuses et herbacées (bryophytes terricoles et ptéridophytes comprises) présentes dans la placette est dressée, chaque taxon étant affecté d'une note de dominance dérivée du coefficient de Braun-Blanquet (Cluzeau & Virion, ce volume).

Nous disposons au total de 15754 relevés pour le premier inventaire floristique et de 15231 pour le second. Le nombre moyen d'espèces par relevé est de 16,6 en 1984, pour 25,3 en 1998. On comptabilise au total 1949 taxons sur les deux cycles, dont 1139 taxons communs aux deux cycles. Nous disposons enfin d'une note de fiabilité de la détermination du taxon estimée par les observateurs de l'IFN.

Analyse des données

La présence des espèces est modélisée par régression logistique, en introduisant comme variables explicatives l'altitude et son carré :

$$\text{logit}(p) = \log[p/(1-p)] = a*\text{altitude}^2 + b*\text{altitude} + c + \varepsilon \qquad (1)$$

avec p : probabilité de présence de l'espèce,
a, b et c : paramètres du modèle,
ε : erreur.

La position altitudinale de l'optimum de l'espèce est estimée à partir des paramètres du modèle :

$$\text{optimum} = -b/2a \qquad (2)$$

Le modèle (1) est ajusté indépendamment pour chaque espèce et pour chacun des deux cycles d'inventaire. Seules les espèces présentant un nombre d'occurrences supérieur à 50 à chaque date ont été retenues dans cette analyse. Celles pour lesquelles le paramètre *a* du modèle (1) est positif et significativement différent de zéro présentent une réponse de type « courbe en cloche » à l'altitude. Parmi ces espèces, nous ne conservons que celles pour lesquelles l'optimum d'altitude estimé par le modèle se situe dans la gamme des altitudes échantillonnées (0 à 2200 m). Lorsque c'est le cas aux deux dates, on peut alors calculer le déplacement de leur optimum entre les deux cycles d'inventaire. Nous avons finalement testé, par un test t apparié de comparaison de moyenne, si le déplacement moyen de l'ensemble de ces espèces était significativement différent de zéro, indiquant alors un mouvement altitudinal global de la végétation. Nous n'avons retenu, pour ce test, que les espèces reconnues avec une fiabilité maximale par les équipes de l'Ifn.

Résultats

Le tableau I synthétise les résultats obtenus :

- Sur les 1949 taxons observés aux deux échantillonnages, seuls 386 présentent une fréquence de présence supérieure à 50 à chacune des deux dates d'inventaire.
- Parmi ceux-ci, 243 montrent une distribution « en cloche » en fonction de l'altitude, mais seuls 157 présentent un optimum situé entre 0 et 2200 m.
- On ne conserve enfin que les 123 taxons ayant une très bonne fiabilité de reconnaissance par les équipes de terrain.

Sur ces 123 taxons retenus, 79 présentent un décalage positif de leur optimum, c'est-à-dire une montée en altitude (fig. 1a), contre 44 seulement présentant un décalage négatif (fig. 1b). La valeur moyenne des déplacements de ces 123 taxons est de +20,0 mètres (+17,8 mètres en valeur médiane). Cette valeur est significativement différente de 0 selon un test t apparié. En considérant que le gradient de température moyenne est de -0,56°C/100 m, une remontée de 17,8 mètres en 14 ans équivaut, dans le cadre hypothétique d'un rééquilibrage parfait de l'optimum de la niche des espèces avec leur climat, à un changement de température de +0,07°C par décennie.

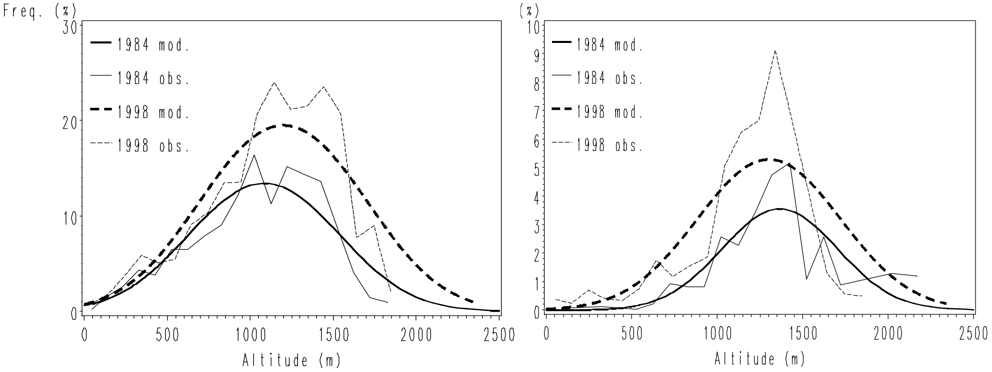

Figure 1 : Distribution observée de la fréquence de deux espèces par classes d'altitudes (vert : 1984 ; bleu : 1998), et ajustement d'un modèle de régression logistique (noir : 1984 ; rouge : 1998). a) exemple de déplacement vers le haut : *Corylus avellana*. b) exemple de déplacement vers le bas : *Mercurialis perennis*.

Discussion

Méthodes

Le mode de rééchantillonnage sur placettes non permanentes a produit des résultats utilisables pour l'étude des modifications de la végétation sur 14 ans. La très forte intensité d'échantillonnage (plus de 15000 relevés à chaque cycle, soit environ un relevé pour 130 ha de forêt à chaque date) permet d'estimer la courbe de réponse des espèces à l'altitude, et en particulier la position de son optimum, avec une bonne précision. On peut ainsi détecter des changements de faible amplitude et mettre en évidence des évolutions de la végétation malgré la courte période de temps séparant les deux échantillonnages.

Nombre total	1949 taxons
Occurrence > 50 à chaque date	**386 taxons**
Courbe « en cloche » et optimum entre 0 et 2200 m	**157 taxons**
Forte fiabilité de reconnaissance	**123 taxons**
Augmentation / diminution d'altitude	**79 / 44 taxons**
Valeur médiane des déplacements	**+ 17,8 m**
Déplacement en équivalent température	**0,08°C / décennie**

Tableau I : Résultats de l'analyse par régression logistique du déplacement altitudinal des taxons dans le Sud-Est de la France entre 1984 et 1998.

Il faut noter que le nombre moyen d'espèces par relevé a fortement augmenté entre les deux inventaires en raison d'une surface d'observation plus importante et d'une meilleure exhaustivité du relevé au deuxième cycle d'échantillonnage. Or, ce nombre moyen d'espèces a augmenté plus fortement dans les altitudes élevées qu'en plaine et collines : au-dessus de 1000 m d'altitude, il passe de 16,7 à 27,3 espèces par relevé entre les deux dates d'échantillonnage, alors qu'il passe de 16,6 à 24,7 espèces par relevé en dessous de cette altitude. Les augmentations d'altitude que nous avons observées sont donc en partie liées à cet accroissement différentiel de la richesse spécifique entre haute et basse altitude. Le rôle exact de ce possible biais reste à quantifier.

Résultats

Un nombre significatif d'espèces, soit plus de deux tiers des espèces retenues dans l'analyse, montre une augmentation de leur optimum. La valeur médiane de la remontée est de 18 mètres, correspondant à un réchauffement de 0,07°C par décennie. Cette valeur est légèrement en deçà du réchauffement moyen mesuré en France au cours de l'ensemble du XX^{ème} siècle qui est de presque 0,1°C par décennie. Elle est largement inférieure aux valeurs observées depuis 1970, qui atteignent 0,5°C par décennie. Plusieurs facteurs peuvent expliquer ce retard entre le réchauffement réellement mesuré et les déplacements observés de la végétation. De nombreuses espèces forestières sont connues pour leur très faible pouvoir de dispersion (Dupouey *et al.* 2002). En montagne, la remontée en altitude des graines pourrait être plus difficile que leur descente. Pour de nombreuses espèces, les milieux forestiers fermés sont peu favorables à la colonisation et seule l'ouverture du couvert suite à une perturbation peut permettre leur installation.

Notre modèle n'intègre que l'altitude. Or, d'autres facteurs environnementaux pourraient venir modifier la relation que nous avons observée entre la présence des espèces et l'altitude, au premier rang desquels l'exposition. Il faut donc soit s'assurer que ces facteurs n'ont pas varié dans l'ensemble de l'échantillon entre les deux cycles d'inventaire, soit les intégrer dans notre modèle de présence des espèces. Une analyse de la distribution aux deux dates des expositions mesurées sur le terrain n'indique pas de variation nette. Mais d'autres modifications de l'environnement forestier sont intervenues au cours de la seconde moitié du XX^{ème} siècle. Ainsi, les surfaces libérées par l'abandon du pâturage et la déprise agricole en montagne ont permis la progression de la forêt, en particulier dans le Sud de la France (Saïd *et al.* 2003). Le second cycle d'inventaire contient donc probablement plus de forêts récentes que le premier. D'autre part, on constate une eutrophisation des sols forestiers entraînée par les dépôts d'azote atmosphériques, menant également à une modification des communautés végétales par l'augmentation de la fréquence de présence des espèces nitrophiles (Thimonier 1994). L'analyse des caractéristiques écologiques et fonctionnelles des espèces pour lesquelles nous avons observé une variation d'altitude devrait permettre de mieux interpréter les causes des changements observés.

En conclusion, si nous observons bien une remontée globale de la végétation, celle-ci ne peut pas être reliée de façon non ambiguë au réchauffement climatique. En effet, les échantillons que nous avons étudiés présentent des variations entre les deux dates, soit en raison des méthodes d'échantillonnage, soit en raison d'autres changements de l'environnement que le seul réchauffement climatique, qui pourraient venir interagir avec l'effet de l'altitude.

Références

Cluzeau C., Virion R., 2007 ; L'Inventaire forestier national : un outil pour l'inventaire et la cartographie de la végétation. Actes du Colloque Géoflore, Nancy, 10-12/5/07, ce volume.

Didier L., Brun J.-J., 1998 ; Limite supraforestière et changements environnementaux : pour une approche pluriscalaire et spatialisée des écosystèmes d'altitudes. Géographie physique et quaternaire, 52, 1-9.

Dupouey JL., Sciama D., Koerner W., Dambrine E. et Rameau JC., 2002 ; La végétation des forêts anciennes, Revue Forestière Française, 54 (6), p. 521-531.

Grabherr G., Gottfried M., Pauli H., 1994 ; Climate effects on mountain plants. Nature, 369, 448.

Moisselin J.-M., Schneider M., Canellas C., Mestre O., 2002 ; Les changements climatiques en France au XX^{ème} siècle. Étude des longues séries homogénéisées de données de température et de précipitations. La météorologie, 38, 45-56.

Said S., Rameau J., Brun J.-J., 2003 ; Evolution et diversité végétales en Corse suite à la déprise agricole. Revue Forestière Française, 55 (4), 309-322.

Thimonier A., 1994 ; Changements de la végétation et des sols en forêt tempérée européenne au cours de la période 1970-1990. Rôle possible des apports atmosphériques. Thèse de Doctorat, Paris XI-Orsay.

Walther, G.-R., Beissner S. & Burga C., 2005 ; Trends in the upward shift of alpine plants. Journal of Vegetation Science, 16, 541-548.

Remontée de l'optimum des espèces forestières sur les reliefs du sud-est de la France,
réchauffement climatique ou changement d'utilisation du sol ?

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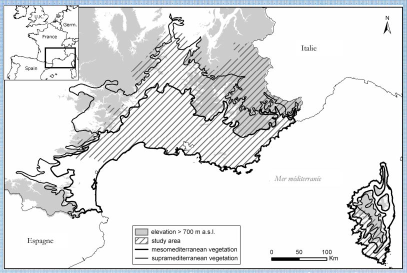
INTRODUCTION

De nombreux travaux ont mis en évidence la remontée des espèces en altitude au cours des dernières décennies - le plus souvent au niveau de leur limite supérieure - mettant en cause le réchauffement climatique. Cependant, d'autres changements d'origine anthropique ont eu lieu au cours du siècle dernier et peuvent aussi influencer les mouvements de végétation.

Nous étudions ici les déplacements altitudinaux des espèces au travers des données de l'Inventaire forestier national. Ces données, basées sur un échantillonnage rigoureux, permettent de mieux quantifier ces déplacements et d'en approcher les causes.

ZONE D'ETUDE



Carte : E. Bienaimé et E. Granier

Alpes du sud, région méditerranéenne

- 2 millions d'hectares de forêts inventoriées dans les années 80 puis 90,
- plus de 15 000 relevés à chaque date,
- écart moyen : 14 ans,
- altitude de 0 à 2300 mètres.

DONNEES DE VEGETATION

Nombre d'espèces moyen par relevé :

- *premier cycle :* *16,8*
- *deuxième cycle :* *25,2*

On sélectionne les espèces suffisamment fréquentes et sans erreur de détermination :

- Nombre d'espèces total : **1949**
  - *premier cycle :* *1536*
  - *deuxième cycle :* *1546*
- Nombre d'espèces en commun : **1137**
- dont occurrence supérieure à 50 : **386**
- dont forte fiabilité de reconnaissance : **252**

MODELE DE DISTRIBUTION

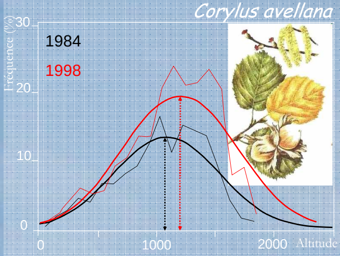
Pour chaque espèce, on ajuste une régression logistique d'ordre 2 sur sa distribution en altitude et en exposition :

- $\text{logit}(p) = a*\text{altitude}^2 + b*\text{altitude} + c*\text{exposition}^2 + d*\text{exposition} + e + f*\text{cycle} + g*\text{altitude}*\text{cycle} + \varepsilon$

On calcule alors son optimum d'altitude à chaque date :

- $\text{optimum}(\text{altitude}) = -(b + g*\text{cycle}) / 2a$

Corylus avellana



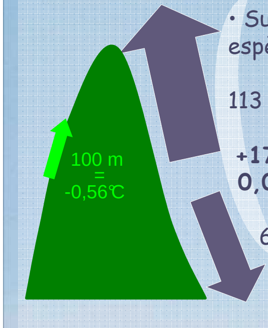
On sélectionne ensuite les espèces selon les résultats du modèle :

Effet global p<0,05 :	**251**
Courbe 'en cloche' (a≠0):	**232**
Maximum borné (a<0) :	**217**
Optimum dans la gamme d'altitude 0-2200 m :	**175**

L'interaction altitude*cycle indique si le déplacement altitudinal est significatif.

DES REMONTEES DE L'OPTIMUM SIGNIFICATIVES, ...

déplacement = opt2 – opt1



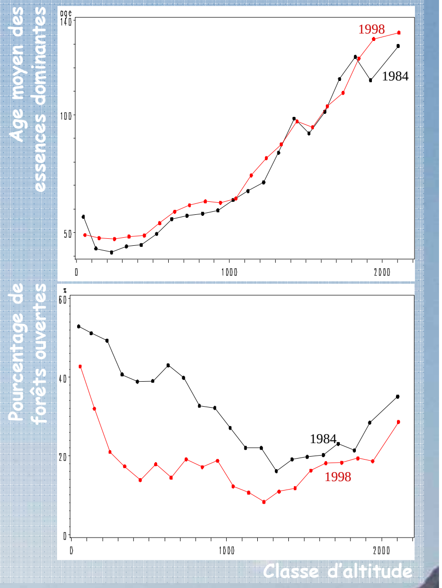
• Sur les 175 espèces :	**• 74 ont un déplacement significatif :**
113 montantes	**56 montantes**
+17,9m **0,07°C/10 ans**	+47,3m 0,19°C/10 ans
62 descendantes	**18 descendantes**

Augmentation constatée de la température :
- 0,9°C au cours du siècle dernier,
- soit 0,09°C par décennie

MAIS les espèces montantes ne sont pas celles attendues, et la structure de la forêt a évolué différemment selon l'altitude.

Espèces montantes :
- phanérophytes caduques, nanophanérophytes caduques et sempervirents
- ligneux
- ligneux bas
- caduques
- héliophiles
- pionnières
- appartenant à stade jeune

Espèces descendantes :
- Géophytes, phanérophytes sempervirentes, chaméphytes herbacées, hémicryptophytes
- herbacées
- ligneux hauts
- sempervirents
- sciaphiles
- non pionnières
- appartenant à stade vieux



CONCLUSION

Nous confirmons, à la suite d'autres auteurs (Lenoir *et al.*, 2008), la remontée en altitude d'un certain nombre d'espèces forestières. Mais, les causes de cette remontée restent encore à préciser. Le réchauffement climatique peut bien sûr être mis en cause, mais d'autres facteurs entrent en compte. L'analyse des traits de vie des espèces qui se déplacent suggère un fort effet de la maturation des forêts observée à basse altitude. L'impact anthropique, qu'il soit direct ou indirect, reste prépondérant.

Cette étude souligne l'importance, pour les suivis de végétation, d'une méthodologie rigoureuse et homogène et l'intérêt des réseaux d'observation à long terme, qui permettent en particulier de mieux contrôler la nature des échantillonnages réalisés à chaque date.

Bibliographie :

-Lenoir, J.; Gégout, J. C.; Marquet, P. A.; de Ruffray, P. & Brisse, H. - A significant upward shift in plant species optimum elevation during the 20th century - *SCIENCE*, **2008**, *320*, 1768-1771

Photo : J. Jonck

Impact of climate warming on species' distribution in mountain areas, which processes limit lower range margins?

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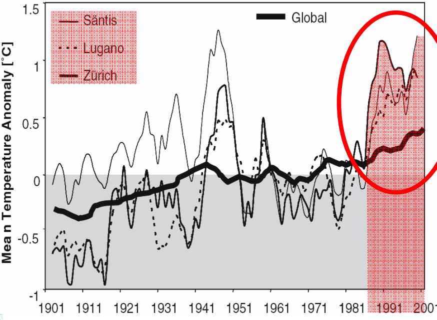


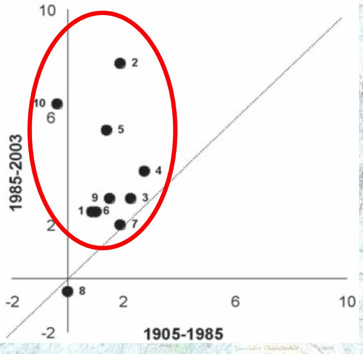
Temperature departures from the 1961-1990 climatological mean in the Swiss Alps compared to global temperature anomalies (Beniston 2006).

During the last decade, **climate warming was more pronounced in the Swiss Alps** than on the global scale (Beniston 2006), inducing ecological response of species.

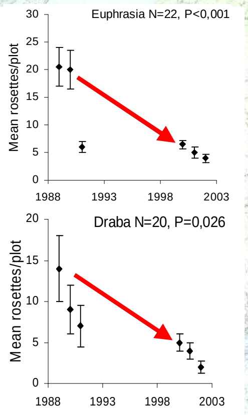
How mountain plant distribution is responding to global warming is now well known at the upper limit. First results, at the beginning of this warm period, showed an **increase of species richness** on mountain summits in western Austria and eastern Switzerland (Hofer 1992, Grabherr *et al.* 1994), as **a consequence of the upward migration of species from lower areas**.

In the Bernina area, Grisons, Switzerland, the dataset of 10 summits with two old records were extended by a third survey and the current species composition was compared with the past records (Walther *et al.* 2005).

Compared to the period 1905-1985, **the upward shift of alpine plants has accelerated in accordance with the warmer climatic conditions of the recent past.**



Decadal rate of change. Matched pairs of investigated mountain summits with the per decade rates of change in species numbers for the two intervals 1905-1985 and 1985-2003 respectively. 1-10: different summits in the Bernina area (Walther *et al.* 2005).



Density of rosettes (±SE), (Lesica & McCune 2004)

But what happens at the lower limit of species' distribution?

Modeling studies expect a **retreat of the alpine species** at their lower limit as a **direct impact of global warming** (e.g. Thuiller *et al.* 2005)

However **"rear edge" populations** (Hampe & Petit 2005) are growing in areas strongly influenced by **humans** and with **higher species richness.**

In order **to distinguish climatic effects from other factors** such as **habitat fragmentation** or **biotic interactions**, more knowledge is needed to understand which processes limit the lower range margins.

In the Rocky Mountains, four out of seven selected species **showed a declining trend at their lower limit** (Lesica & McCune 2004). However, the authors could not rigorously infer that **climate warming caused the observed decline**.

A century old dataset is available for the Bernina area in Switzerland

From a total of 977 taxa (Rübel 1912), those species were selected **with information on the lower limit**. For **173 species** the information is detailed enough to serve as **sample species** for investigating **potential range shifts at lower altitudes**, among others: *Androsace alpina, Euphrasia minima, Eritrichium nanum, Ranunculus glacialis, Salix herbacea*…

The according field work is scheduled for this summer to verify the **response of a selection of species at the lower limit**, and to try to **identify responsible drivers.**

Androsace alpina (Flora Helvetica) *Euphrasia minima, Eritrichium nanum, Ranunculus glacialis, Salix herbacea* (sophy.u-3mrs.fr)

References:
Beniston 2006, Mountain weather and climate: A general overview and a focus on climatic change in the Alps. *Hydrobiologia* 562: 3-16; **Grabherr G., Gottfried H.P. & Pauli H., 1994**, Climate effects on mountain plants. *Nature* 369: 448; **Hampe A. & Petit R.J., 2005**, Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters* 8: 461-467; **Lauber K. & Wagner G. 1996,** Flora Helvetica. *Verlag Paul Haupt, Bern-Stuttgart-Wien*. 1616 p. **Lesica P. & McCune B. 2004**, Decline of arctic-alpine plants at the southern margin of their range following a decade of climatic warming. *Journal of Vegetation Science* 15: 679-690; **Rübel E. 1912,** *Pflanzengeographische Monographie des Berninagebietes*. Engelman, Leipzig, DE; **Thuiller W., Lavorel S., Araujo M.B. *et al.* 2005**, Climate change threat to plants diversity in Europe *PNAS* 102(23): 8245-8250; **Walther G.-R., Beißner S. & Burga C.A. 2005**, Trends in the upward shift of alpine plants. *Journal of Vegetation Science* 16: 541-548.

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ÉVOLUTIONS PASSÉE ET FUTURE DES AIRES DE RÉPARTITION DES ESPÈCES FORESTIÈRES EN FRANCE

par Jean-Luc **Dupouey**[1], Jeanne **Bodin**[2] et Vincent **Badeau**[2]

L'impact des changements climatiques sur la forêt se manifeste dans un premier temps par des modifications du fonctionnement physiologique des plantes, qui peuvent à terme déboucher sur des changements de leur aire de répartition. On assiste ainsi en Europe à une modification progressive de la phénologie des arbres et à une augmentation de leur productivité.

La palynologie nous enseigne que les arbres se sont en effet déplacés sur de grandes distances au cours des cycles glaciaires, en particulier à l'Holocène.

Au cours du XX$^{\text{ème}}$siècle, le climat de la France s'est réchauffé d'un degré Celsius. Les impacts de ce réchauffement sont-ils déjà visibles dans l'aire de répartition des espèces ? Assiste-t-on à un déplacement global des cortèges biogéographiques ? Nous faisons le point, au cours de cette présentation, sur nos travaux concernant les déplacements en cours de la végétation forestière, ainsi que sur les modèles de distribution future de l'aire climatique potentielle des principales espèces forestières françaises.

Les observations de déplacement d'espèces forestières sont encore très ténues. Ces déplacements ont été principalement recherchés en montagne, où le fort gradient de température permet de faire l'hypothèse d'un rééquilibrage plus rapide qu'en plaine de la végétation avec le climat. Dans tous les cas, on s'est basé sur le ré échantillonnage d'anciennes études. Dans le Briançonnais, nous avons observé une progression en altitude des espèces de l'étage subalpin de versant Nord seulement. En Maurienne, les espèces à caractère atlantique et nitrophile progressent de façon conjointe. Dans les Alpes du Sud enfin, on observe bien une progression globale des espèces vers le haut. Mais la dynamique forte d'abandon des terrains agricoles et de baisse des niveaux de prélèvement de bois vient perturber l'interprétation de ces signaux. La difficulté de la mise en évidence de ces changements d'aire de répartition souligne l'importance des réseaux de monitoring actuels de la biodiversité : RENECOFOR, Vigie-Plante, réseau DSF, IFN…

Pour le XXI$^{\text{ème}}$ siècle, le modèle de Météo-France ARPEGE B2, pourtant relativement modéré, indique un déplacement fort des aires bioclimatiques potentielles des espèces. L'étage supra-méditerranéen se retrouve en 2100 nettement au Nord de la Loire. Les aires des espèces d'affinités continentale et montagnarde (sapin, hêtre) régressent fortement.

Les espèces seront-elles capables de migrer à la vitesse de ces changements et de suivre leur niche potentielle ? De nombreuses observations obtenues lors des études de changements d'utilisation des sols montrent au contraire que les espèces herbacées forestières ont des vitesses de colonisation très faibles, entraînant un risque pour la biodiversité. Il existe donc finalement un hiatus entre des observations de déplacements encore modérés au XX$^{\text{ème}}$ siècle et des prévisions plutôt pessimistes pour le XXI$^{\text{ème}}$ siècle.

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Zusammenfassung

Krautige Pflanzen sind gute Zeiger für Änderungen von Umweltfaktoren. Deshalb wurden sie häufig benutzt, um Umweltveränderungen zu detektieren, insbesondere jene anthropogenen Ursprungs wie Überdüngung, Acidifizierung der Atmosphäre, Einfluss durch Landnutzungsänderungen oder Herbivoren-Befall.

Seit kurzem werden vor allem auch die Auswirkungen des Klimawandels auf Ökosysteme im Allgemeinen und der Vegetation im speziellen diskutiert. Bergregionen werden für diese Studien bevorzugt, da der Temperaturgradient ausgelöst durch die Reliefstruktur tausendmal höher ist (-0,56 °C/100 Höhenmeter) als in ebenen Regionen. Zusätzlich werden Bergregionen weniger stark besiedelt und wirtschaftlich genutzt, weshalb die Einschränkung der Artverbreitung geringer ausfällt. All diese Faktoren tragen dazu bei, dass Bergregionen als gute Forschungsgebiete dienen, um die Auswirkung des Klimawandels auf die Artverbreitung zu studieren.

Bis jetzt fokussierten diesbezügliche Studien auf einige wenige Pflanzenarten, kleine Versuchsgebiete oder Versuchsflächen mit geringem Potential der Datenübertragung auf größere Skalen. Für einen ersten Teil der vorgestellten Arbeit diente als Versuchsgebiet ein Bergwald mit geringer Beweidung. In einem weiteren Teil der Arbeit wurde eine Modellierungsmethode entwickelt, die die verändernde Vegetationszusammensetzung bezogen auf den Höhengradienten errechnet. Dies hilft, die Abhängigkeit von wiederholten Probenahmen auf derselben Parzelle zu verringern und somit auch ältere Daten mit in die Analyse einfließen zu lassen, bei denen exakte Ortsangaben fehlen. Mit Hilfe der entwickelten Methode konnten zwei wichtige Faktoren der Vegetationsanalyse herausgearbeitet werden: einmal die optimale Höhe in der Verbreitung der die einzelnen Pflanzenarten und die Veränderung des Zeigerwerts von Vegetationseinheiten. Zusätzlich wurden im Langzeitvergleich tiefstgelegene Vorkommen einzelner Pflanzenarten untersucht, um zu überprüfen, ob Arealuntergrenzen sich in ähnlicher Weise verändert haben, wie dies für Arealobergrenzen festgestellt wurde. Als letztes wurde die Flora an einem weitgehend von menschlichen Einflüssen geschützten Standort untersucht, dessen Lage aufgrund der umgebenden zwei Gletschern, die Einwanderung neuer Arten erschwert (Nunatak Isla Persa, Bernina, Schweiz). Die Zeitspannen der einzelnen Teilstudien variieren von vierzehn bis einhundert Jahren.

In jeder Teilstudie wurde ein Anstieg in der Höhenverbreitung der Vorkommen der Pflanzenarten beobachtet: für die 175 Waldpflanzenarten in den mediterranen Bergen lag sie bei +12,5 m/Dekade, für die Pflanzengesellschaft der Wälder der Maurienne bei +29,6 m/Dekade bei gleichzeitiger Verschiebung zu einer thermophileren Gesellschaft, für die Arten im Bernina-Tal bei +5,6 m/Dekade und auf dem Nunatak Isla Persa wurden Pflanzenarten beschrieben, die ursprünglich in tieferen Lagen heimisch sind. Allerdings gab es einige weitere Faktoren, die die beobachteten Änderungen erklären: in den mediterranen Bergen entwickelte sich ein Bestand mit stärker geschlossener Kronendecke, im Maurienne-Tal kam es zu einer Eutrophierung der Vegetation aufgrund ansteigenden Verkehrs und im Berninagebiet zur Habitatfragmentierung und Zerstückelung der Vegetation durch Klettertourismus. Diese Auswirkungen, entstanden durch direkte Einwirkung des Menschen, sind in Stärke und Zeitskala vergleichbar mit denjenigen des indirekten menschlichen Einflusses durch den Klimawandel. Beide müssen deshalb gleichermaßen bei der Analyse der derzeit ablaufenden Vegetationsveränderungen berücksichtigt werden.

Schlüsselwort: Wald; Unterwuchsvegetation; Gebirge; Höhenlage; Nunatak; ökologisches Nischen Model; Zeigerwert; Ellenberg; Landolt; Vegetationsdynamik; Untergrenze; Pflanzengesellschaft; Höhenoptimum; Artenveränderung; Globale Umweltveränderung; Klimaerwärmung; Eutrophierung; Landnutzungsänderungen; Landesforstinventar; verändernde Vegetationszusammensetzung; Nicht permanent Aufnahme; Alpen; Mittelmeergebirge; Maurienne-Tal; Bernina; Frankreich; Schweiz.

Résumé

La végétation herbacée est un bon indicateur des conditions environnementales. Pour cette raison, elle a souvent été utilisée pour mettre en évidence les changements environnementaux causés par les actions humaines, tels qu'eutrophisation, dépôts atmosphériques acides, changements de l'usage des sols ou de la pression d'herbivorie.

Depuis peu, on s'intéresse aux effets des changements climatiques sur les écosystèmes en général, et sur la végétation en particulier. Le choix des zones d'étude s'est naturellement porté sur la montagne, car le gradient thermique induit par le relief (-0,56°C pour 100 mètres d'altitude) y est mille fois plus élevé qu'en plaine le long du gradient latitudinal. D'autre part, les zones de montagne sont soumises à une urbanisation et une pression agricole moindre qu'en plaine, limitant ainsi les obstacles à la migration des espèces. Ces deux arguments font des régions de montagne une zone privilégiée pour l'étude de la réponse migratoire précoce de la végétation aux changements climatiques.

Jusqu'ici, les études effectuées se sont focalisées pour la plupart sur la limite supérieure des espèces, ou sur de petites zones géographiques, ou bien encore sur des zones où il est difficile de dissocier les effets du réchauffement de ceux des changements d'usage des sols, qui se produisent eux aussi à grande échelle. Une partie de cette thèse est consacrée aux milieux forestiers montagnards, dans lesquels l'effet du pastoralisme est réduit. D'autre part, une méthode basée sur la modélisation des changements de la réponse de la végétation au gradient d'altitude est développée, permettant le rééchantillonnage sur placettes non-permanentes, et ainsi d'étendre l'utilisation de données anciennes à des séries de relevés non géolocalisés. En s'appuyant sur cette méthode, deux caractéristiques de la végétation ont été analysées : la position de l'optimum d'espèces prises individuellement d'une part (données de l'Inventaire Forestier National dans les montagnes méditerranéennes du sud-est de la France), et les changements de la valeur indicatrice des communautés végétales d'autre part (vallée de la Maurienne, France). Par ailleurs, on a étudié les déplacements à long terme de la limite inférieure des espèces dans la vallée de la Bernina (Suisse), pour tester si la réponse des espèces en limite inférieure, peu étudiée jusque là, est identique à celle en limite supérieure de leur distribution. Enfin, on a étudié l'évolution de la flore d'une zone très localisée, mais par ailleurs protégée des migrations d'espèces par une large barrière physique constituée par deux glaciers (Nunatak Isla Persa, Bernina, Suisse) permettant de s'affranchir totalement des effets potentiels d'autres perturbations anthropiques concomitantes. Dans ces différentes études, les intervalles de temps entre chaque inventaire ou échantillonnage varient de 14 ans à un siècle.

Chacun des cas étudiés montre une remontée des espèces en altitude : remontée moyenne de +12,6 m/décennie des optimums de 175 espèces forestières dans les montagnes méditerranéennes, communautés des forêts de Maurienne évoluant vers une végétation plus thermophile à une altitude donnée équivalent à une remontée moyenne de +29.6m/décennie, retrait de la limite inférieure des espèces en Bernina de +5,6 m/décennie, arrivée d'espèce d'étages inférieurs sur le nunatak Isla Persa. Mais d'autres phénomènes expliquant la réponse observée de la végétation sont clairement mis en cause dans cette étude : fermeture et maturation du couvert forestier relativement plus importante à basse altitude dans les montagnes méditerranéennes, eutrophisation importante de la végétation en vallée de la Maurienne probablement due à l'augmentation du trafic routier, probable fragmentation de l'habitat ou dispersion par les randonneurs en Bernina. Ces perturbations anthropiques directes jouent à des échelles de temps et d'espace comparables à l'effet anthropique indirect du changement climatique. Il est donc primordial de les prendre en compte dans les changements de végétation observés, avant de conclure à un effet du réchauffement climatique seul.

Mot-clefs : forêt ; végétation du sous-bois ; montagne ; altitude ; nunatak ; modèle de niche ; valeur indicatrice ; Ellenberg ; Landolt ; dynamique de la végétation ; limite inférieure ; optimum d'altitude ; communauté végétale ; déplacement d'espèce ; changement global ; réchauffement climatique ; eutrophisation ; changement d'usage du sol ; inventaire forestier national ; placette non permanente ; Alpes ; montagne méditerranéenne ; vallée de la Maurienne ; Bernina ; France ; Suisse.

Abstract

Herbaceous vegetation is a good bio-indicator of environmental conditions. For this reason, it was often used to detect and to put in evidence environmental changes caused by anthropogenic activities, like eutrophication, acid atmospheric deposit, land-use change and herbivory pressure.

More recently, the interest had focused on the impacts of climatic change on ecosystems in general, and on vegetation in particular. Mountains were naturally chosen as study areas, as the thermal gradient induced by the relief (-0.56°C for 100m a.s.l.) is thousand times higher than in lowlands along the latitudinal gradient. Moreover, mountain regions undergo weaker urbanisation and agricultural pressure than lowlands, thus limiting obstacles to species' migration. Both these arguments make mountain regions a privileged area for the study of early migratory response of vegetation to climatic changes.

Until now, existing studies mostly focused on upper species' limits, or on limited geographic zones, or else on areas where the warming effect is difficult to disentangle from land-use change, which also occur at a large spatial scale. A part of this PhD is devoted to mountain forest habitat, where pastoralism effects are reduced. Furthermore, a method is developed, based on the modelling of changes in vegetation response to elevation gradient, allowing the reinventory of non-permanent plots, and thus to extend the use of historical data to non-geolocalized dataset. With this method, two characteristics of vegetation were analysed: the optimum position of individual species on the one hand (data from French National Forest Inventory in Mediterranean mountains of southeastern France), and changes in the indicator value of plant communities on the other (inner alpine Maurienne valley, France). Moreover, the long-term shift of species' lower limit is studied in the Bernina valley (Switzerland), to test if the species response at their lower limit, rarely studied until now, is similar to the response reported from the upper limit. The last part focuses on changes in the flora of a really localised area, that is protected from species migrations by a broad physical barrier formed by two glaciers (Nunatak Isla Persa, Bernina, Switzerland), and thus, almost free from potential effects of other parallel anthropogenic disturbances. Time intervals between each inventory or sampling in these different studies vary from 14 years to one century.

Every studied case shows a shift of species toward higher elevations: mean shift of 12.6m/decade of the optimums of 175 forest species in Mediterranean Mountains, communities of Maurienne forests changing to more thermophilous vegetation at a given elevation equivalent to a mean shift in elevation of +29.6m/decade, retreat of the species' lower limit in the Bernina valley of +5.6m/decade, arrival of species from lower vegetation belts on the Nunatak Isla Persa. However, other phenomena explaining the observed vegetation response became also evident in our study: forest closure and maturation relatively more important at lower elevations in Mediterranean mountains, important eutrophication in vegetation of Maurienne valley probably due to increasing road traffic, probable habitat fragmentation and dispersal by hikers in Bernina. These direct anthropogenic disturbances play a role comparable in space and time to the indirect anthropogenic impact of climate change. Thus, it is essential to consider them in the observation of vegetation changes, before assigning the effects to climate warming only.

Keywords: Forest; understorey vegetation; mountain; elevation; nunatak; niche model; indicator value; Ellenberg; Landolt; vegetation dynamics; lower limit; elevation optimum; plant community; species shift; global change; climate warming; eutrophication; land-use change; national forest inventory; non-permanent plot; Alps; Mediterranean mountain; Maurienne valley; Bernina; France; Switzerland.