An increase in the upper tree-limit of silver fir \textit{(Abies alba Mill.)} in the Alps since the mid-20th century: A land-use change phenomenon

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Abstract

Global environmental changes observed during recent decades are likely to have had an impact on the distribution of species. Currently, silver fir (\textit{Abies alba}) is becoming established in the subalpine forests of the west central Alps at elevations higher than 2000 m a.s.l.; prior to the 1970s its upper altitudinal limit was 2000 m. Several hypotheses could explain this recent expansion of the upper tree-limit. Silver fir regeneration could be linked (1) to land-use changes or (2) to current climatic warming. Using dendrochronology, the age structure of 31 forest plots containing at least one silver fir was examined in order to elucidate the population dynamics of subalpine communities. This allowed us to decipher the timing of fir regeneration in relation to the mean age of the stands examined and of the other tree-canopy species present. The majority of the firs germinated sporadically since 1950, before the regional temperature increase. The pattern of fir recruitment did not appear to relate to altitude, but followed a pattern characteristic of secondary succession. The age structures identified showed an exponential increase in tree-density during the 20th century; the stands were first dominated by \textit{Larix decidua} during the 18th and 19th centuries, and then by \textit{Pinus cembra} during the 20th century. In most stands, fir regeneration occurred after \textit{Larix} and before \textit{P. cembra} dominated, following a similar pattern to \textit{Pinus abies} regeneration. The number of local inhabitants and temperature both exhibited a negative relationship with fir tree recruitment, thus supporting the land-use change hypothesis. There has been a significant upward shift of the altitudinal range of fir, amounting to an increase of about 300 m since 1950. This followed the abandonment of low-productivity land. This trend is likely to continue during the 21st century, because of new agricultural and forestry practices which involve limited intervention in low-productivity areas and may be because of the effects of global warming.

1. Introduction

Unfavourable climatic conditions, e.g. such as low temperatures or drought, may govern the limits of species’ ranges and any change in environmental conditions can lead to significant changes in a species’ demographic patterns (Grace et al., 2002; Breshears et al., 2009). There is some indication that recent climatic change has affected tree species; there is evidence from individuals, for example radial and height growth increases (Paulsen et al., 2000; Motta and Nola, 2001; Gamache and Payette, 2004) and from population patterns, for example shifts in forest composition or plant distribution (Camarero and Gutiérrez, 2004; Beckage et al., 2008; Lenoir et al., 2008). In mountain regions, climate change in the form of warming may lead to an upward movement of the treeline and the upper altitudinal limit for particular species. Recent land-use and management changes may also explain upward shifts of the maximum altitudinal range of tree species (Gehrig-Fasel et al., 2007; Albert et al., 2008). Indeed, mountainous areas in Europe have been influenced by man’s activities for centuries or perhaps even millennia: since the middle of the 19th century, however, such land has been abandoned as a result of a rural exodus (Didier, 2001; Motta and Garbarino, 2003; Chauchard et al., 2007) resulting in a significant expansion of mountain forests (MacDonald et al., 2000; Conti and Fagarazzi, 2005; Gellrich et al., 2007). The current organisation and composition of the forest landscape in the mountains of Europe are strongly determined by legacies of past land-use and management (Koerner et al., 1997; Flinn and Marks, 2007). The current increase in temperature combined with land abandonment should result in an upward shift of species’ maximum altitudinal limit (Dinnböck et al., 2003), and changes in forest diversity and properties (Lloyd and Fastie, 2003; Parmesan and Yohe, 2003; Walther et al., 2005). However the...
dynamics and rhythm of this upward expansion remain unelucidated. Indeed, communities and populations may be resilient thus creating an inertia, whereas individual species may be able to react more or less rapidly. In order to plan how to manage the effects of such environmental changes, it is necessary (i) to understand the characteristics of tree-limit shifts and (ii) to distinguish between the effects of land abandonment and climatic change on tree population dynamics.

Silver fir (Abies alba Mill.) is widely distributed across the European mountains (Rol, 1937) and is generally found in areas where annual precipitation exceeds 1000 mm. Many experimental and dendrochronological studies have reported the susceptibility of fir first to atmospheric and edaphic drought (Guicherd, 1994; Aussenac, 2002; Maclas et al., 2006; Peguero-Pina et al., 2007) and, second, to sudden frost, and very low winter and spring temperatures (Desplanque et al., 1998; Rolland et al., 1999).

Indeed the growth of fir is greatly influenced by the water balance of the previous summer, and April and February temperatures during the current year (Desplanque et al., 1998; Rolland et al., 1999). In the western Alps, the upper tree-limit of silver fir is conventionally considered to be situated at ca. 1800 m a.s.l. on north-facing slopes and, 1950 m a.s.l. on south-facing slopes (e.g. Bartoli, 1966; Gensac, 1972, 1974; Rameau et al., 1994). However, small silver fir trees can be observed above 2000 m a.s.l. in subalpine woodlands. Their presence at this altitude is remarkable on the basis of the species’ generally accepted distribution and in light of paleoecological studies that describe stability of the fir tree-limit at the millennial-scale (Carcaillet and Muller, 2005). Although recently acquired paleological data have demonstrated that the species has long been present in mixed stone pine–larch forest above 2000 m (Genries et al., 2009b; Blarquez et al., in press), it was much more common during the mid–Holocene, from 7000 to 5000 cal yr BP, and was generally found below 2000 m in the western Alps (Muller et al., 2007). Using dendrochronology to determine the population dynamics of silver fir and its associated tree community should set the current presence of the species at elevations above 2000 m in context. Because silver fir is known as a late-successional species, age structure analysis should demonstrate whether the main process controlling the species’ expansion was the result of post-abandonment dynamics. Indeed, if population dynamics mirror altitudinal expansion irrespective of the successional status of the firs within stands, then this would suggest that climate may be the factor controlling the expansion of the species’ maximum altitudinal limit. Moreover, if climate is the main factor affecting fir expansion, we hypothesise that altitudinal expansion of the species resulting from a temperature increase would be associated with a decrease in fir ages with altitude. In contrast, no altitudinal age pattern is expected if land-use change is the principal process affecting the range expansion. Using tree-ring data, this study aimed to analyse (i) the history of silver fir expansion above 2000 m a.s.l. and, (ii) the tree age structure of stands containing by silver fir, in order to determine the ecological mechanisms associated with forest transformations. The comparison of these dendrochronological data with climate and society predictors aims to decipher the causes of the fir expansion.

2. Methods

2.1. Study area

The study site is located in the upper Maurienne Valley (inner French Alps, Savoy, Fig. 1A). The valley represents the southern limit of the Vanoise massif in the northern French Alps. The area is located on the northern side of the Mont Cenis massif between 2000 and 2300 m a.s.l. (Fig. 1B). The climate is continental, with relatively low mean annual precipitation compared to that of the Alps (925 ± 233 mm; meteorological station of Lanslebourg-Val Cenis, 2042 m a.s.l, 1971–1999) and has a low mean annual temperature (3.5 ± 2.2 °C).

The woody vegetation is dominated by Larix decidua Mill. (European larch), Pinus cembra L. (Arolla pine) and Picea abies (L.) Karsten (Norway spruce). In addition, Salix caprea L., Alnus viridis DC., Sorbus aucuparia L. and, less frequently, Betula pendula Roth. occur in the avalanche corridors. The main understorey species are Rhododendron ferrugineum L., Vaccinium myrtillus L., V. uliginosum L., V. vitis-idaea L., Juniperus sabina Loddiges, Sorbus chamaemespilus Crantz and Lonicera caerulea L.
2.2. Sampling design

In order to locate silver fir trees, a systematic survey of ca. 100 ha of subalpine forests and woodlands between 2000 and 2300 m a.s.l. was performed in 2005 (Fig. 1). Around each fir tree, a 10-m-radius (= 314 m²) circular sampling plot was defined (Fig. 1C). For each plot we noted the geographic coordinates and the altitude, determined using a GPS. In order to examine the minimal sampling area, we targeted 31 plots (Fig. 1B), each centred on a fir tree and with two other fir trees situated close (< 10 m) to the central fir in plot J. All the sample plots had the same aspect. The cumulative sampled area was 9734 m²; an area of ca. 1 ha is generally considered sufficient for examining forest structure and dynamics (e.g. Motta and Lingua, 2005; Genries et al., 2009a). All individual trees of each species were identified and sampled to determine the age structure of the stand. For seedlings and saplings (Ø < 5 cm at 30 cm), a disc was sawn from the trunk at the root-collar, whereas a core was taken from non-fir trees (Ø > 5 cm at 30 cm) at a height of 30 cm using an increment borer; fir trees were cored at the root-collar. For all individuals (seedlings, saplings and trees), the circumference was measured, and the height of individuals <180 cm tall was recorded. Circumference was used to estimate the tree diameter and the basal area. The height was used to establish a height–age model to calibrate the ages of trees cored at 30 cm.

2.3. Age estimation

Cores and basal sections were air-dried and a smooth surface obtained by the use of progressively finer sandpaper. To determine tree ages, tree-rings were counted and cross-dated using a skeleton plot under a dissecting microscope (Schweingruber, 1988; Chauchard et al., 2006). For incomplete cores, where the pith was not traversed, we estimated the length of the missing radius by matching the curvature of the innermost rings to concentric circles drawn on paper (Arno and Sneck, 1977; Chauchard et al., 2006). The number of missing rings was estimated by calculating the mean number of rings for radii of corresponding lengths from basal sections of saplings (larch, spruce, Arolla pine) or from complete cores (silver fir). The resulting age correction factors were added to the number of visible rings in the incomplete cores to estimate age at coring height.

To estimate total age, we assessed the number of years to reach coring height by determining the age–height relationship for each tree species (Mast et al., 1998; Kajimoto et al., 2002). The method assumes that the growth conditions of extant seedlings and saplings are similar to those that were experienced by the existing trees when they were the same age (Wong and Lertzman, 2001). The large number of sampling (23 spruces, 144 larches, and 665 stone pines) used to determine the age-height regressions should be representative of all the growing conditions experienced (density, competition amplitude, etc.). The regression should thus reduce the overall errors in age determination. The final age of each tree was obtained by adding our estimates of ages at coring height to the estimated number of years required to reach 30 cm.

2.4. Community structure and dynamics analysis

To account for composition variability between the stands, the number of individuals per species is displayed as a box-plot for saplings and trees (see Fig. 2). In order to assess community and the species dynamics, age structure was plotted for all individuals of the three main species (larch, spruce and pine), all understorly tree species, all tall broadleaf deciduous shrub species (willow, alder, rowan and birch), and silver fir. The individuals, used to reconstruct the forest dynamics were those that had survived both natural disturbances and land-use impacts (grazing, clear-cutting, etc.). Missing or low numbers of trees in a particular age-class could be due to lack of regeneration, to a high mortality rate in trees regenerating at the relevant time or to clear-cutting (Johnson et al., 1994). Dead individuals, stumps (N = 83) and core showing damaged wood (N = 28) were excluded from the analysis. To account for age structure variability between the stands, the numbers of individuals per age-class are presented in a box-plot (see Fig. 3).

To compare fir recruitment to the dynamics of the surrounding tree populations, we calculated the relative fir age as follows:

\[ \delta x_j = \frac{\text{Abies } x_j - \bar{x}_j}{C_0} \]

where \( \delta x_j \) is the relative age of fir trees in the circular-plot \( j \), Abies \( x_j \) is the age of the central fir in the circular-plot \( j \) when the plot contained a single fir and the mean age of firs when the plot contained three firs (plot J). \( \bar{x}_j \) is the arithmetic mean age of \( x_j \), i.e. all main tree species in the plot \( j \). Relative ages of all stands versus altitude were plotted. To account for any error in the age estimation, we considered that fir recruitment was concomitant with the mean age of the stand (\( \bar{x}_j \)) when −20 years < \( \delta x_j \) < +20 years. When \( \delta x_j < -20 \) years, fir was recruited after \( \bar{x}_j \); and when \( \delta x_j > +20 \) years, fir was recruited before \( \bar{x}_j \).

![Fig. 2](image-url) Box-plot of the composition of the 31 circular-plots (A) for all individuals and (B) separated into seedlings and saplings (Ø < 5 cm, S) and trees (Ø > 5 cm, Tree). The middle line indicates the median value of the number of individuals, the upper extent of the box indicates the 75th percentile, and the lower extent indicates the 25th percentile.
2.5. Climate variation

In order to test for any relationships between fir recruitment and climate change, we used several climatic variables: annual mean temperature and annual sum of precipitation for the longest regional meteorological series from Geneva, Switzerland (46°12'N, 6°20'E, 405 m a.s.l., 1850–2008); seasonal temperature and precipitation were determined from a grid-based dataset 0.5° x 0.5° resolution (Luterbacher et al., 2004; Pauling et al., 2006) for the Maurienne valley and the surrounding area (44°45'–45°40'N and 6°00'–7°10'E) using Climate Explorer (http://climexp.knmi.nl).

To describe climatic trends, we identified significant inflections in the temperature and precipitation trends (Kendall, 1976) using the “turnpoints” function of the “pastecs” package in the R software (see Ibanez et al., 2009 for details). The climatic trend for each period identified was tested using a Mann–Kendall test (Mann, 1945; “Kendall” package in R software, McLeod, 2009).

2.6. Former land-use

In 1733, 23 circular-plots (74.2%) were located in municipality’s forest: five were in bush (16.1%) and only three (9.2%) in grazing land (“Mappe Sarde”: the first land-register of the Savoy Duchy, Sardinian Kingdom). The successive land-registers (“Mappe Sarde”, Napoleon’s land-registers and modern land-registers since 1861) were not used directly to determine the date of land abandonment because the municipality’s land remains classified as municipality’s forest, and its status in the registers has not changed. Forest in this area was probably grazed in the past but it is difficult to quantify precisely the extent and intensity of grazing, both spatially and temporally. In order to assess land-use change in the study area, therefore, we used human population inventories at the municipality level and livestock inventories at the valley level (upper Maurienne valley) over the last 260 years. The numbers of permanent inhabitants and transient shepherds in the two villages closest to the study site (Lanslevillard, Bessans) were obtained.

Fig. 3. Age structure of the 31 circular-plots combined (~1 ha) for (A) Abies alba; under the box-plots the number of individuals per circular-plot and per 10-year class are given for (B) all living trees, (C) Larix decidua, (D) Picea abies, (E) Pinus cembra and (F) deciduous broadleaved species.
from demographic databases (http://cassini.ehess.fr), from the Archives Départementales de Savoie, combined with published data (Jail, 1969; Rambaud and Vincienne, 1964). The number of cattle and sheep/goats in the upper Maurienne Valley was obtained from the Archives Départementales de Savoie, from the agricultural census (“recensement généraux agricole”) and from published data (Jail, 1969; Rambaud and Vincienne, 1964). Inflections in the land-use variables (local population, cattle and sheep) were assessed in the same way as the climate variables.

2.7. Explanation of fir regeneration

The analysis of the effects of climate, land-use change and plot characteristics on fir regeneration was limited to the period for which reliable land-use change proxy data was available, namely 1750–2005. To assess the effect of the three types of variables on fir establishment, generalised regression models with a binomial distribution and a logistic link function (i.e. logistic regression) were used. The number of fir trees established was calculated for each decade for each circular-plot. The following explanatory variables were tested: (i) plot characteristics: altitude, present plot status (i.e. forest, avalanche patch, presence of logging), ancient land-uses (i.e. ancient forest, bush or pasture); (ii) weather variables: seasonal and mean annual temperature anomalies, seasonal and annual precipitation anomalies and (iii) proxies of land-use change: number of inhabitants, sheep/goat numbers, and cattle numbers. Time series based on decadal means (weather variables and land-use change proxies) was used in our models. Several models were tested, notably models introducing a time lag. A major problem when considering human land-use, topographic and climatic predictors jointly in a model is that these are often correlated (Randin et al., 2009). To select an appropriate model, all correlations between explanatory variables were thus tested in order to adjust the model to account for collinearity of predictors. Each independent variable was centred and scaled to test the regression model.

3. Results

All firs (A. alba) observed within the ~100 ha survey area were clustered into two spatial groups (Fig. 1B). However, this distribution did not determine our survey strategy, but is probably the result of natural seed dispersal patterns, related to seed-sources and local regeneration conditions.

3.1. Stand characteristics

In total, the 31 plots contained 1735 individuals; the cumulative basal area was 36.5 m² ha⁻¹. The number of individuals per plot varied between 17 and 112. Silver fir was scarce, representing 2% of the individuals, at most. Indeed, the sampled areas were circular-plots centred on individual fir trees, so the estimated fir abundance is artificially high for the study area. Across the ~100 ha of subalpine woodlands that were surveyed, in which all stands containing a fir were sampled, the actual density of fir was about 0.3 ind. ha⁻¹. Arolla pine (P. cembra) was the most abundant species (Fig. 2A) with 928 individuals, including seedlings, saplings and trees. Arolla pine represented 53% of the total number of individuals and was the only species present in all stands. European larch (L. decidua) was the second most abundant species with 590 individuals, corresponding to 34% of the total number of individuals. Larch was found in almost all stands (98%). Norway spruce (P. abies) was less frequent, representing only 6% of the total number of individuals, but was relatively widely distributed, occurring in 71% of stands. Broadleaved tree species, i.e. S. caprea, A. viridis, S. aucuparia and B. pendula, were less frequent (accounting for 5% of the total number of individuals) and, occurred irregularly, being present in only 48% of stands. Only one Scots pine (P. sylvestris) was recorded, but this was not plotted in Figs. 2 and 3.

Arolla pine dominated the seedling and sapling category (ø < 5 cm), representing 71% of the total number of individuals, but this high abundance varied greatly between the stands (Fig. 2B). Although larch accounted for only 18% of the seedlings and saplings, it dominated the tree category (ø > 5 cm, 62% of trees). Spruce and fir were better represented in the tree category than in the seedling–sapling category (Fig. 2B). Broadleaved deciduous species were more common as seedlings or saplings than as trees (Fig. 2B).

3.2. Age structure

Based on the height–age analysis, allometric equations were determined from linear regressions for the three main species, allowing us to calculate the time taken for a tree to grow to the coring height. The age to reach coring height was estimated to be 17 ± 7 years (N = 23, r = 0.59, p < 0.001) for spruce, 13 ± 9 years (N = 144, r = 0.57, p < 0.001) for larch and 10 ± 5 years (N = 665, r = 0.64, p < 0.001) for Arolla pine. Silver firs regenerated sporadically since 1849, with the rate increasing since 1950 (Fig. 3A).

The oldest firs were located at lower elevations, just above 2000 m a.s.l. (Fig. 4). During the last 50 years, fir regeneration was evenly distributed across the altitudinal range and the age of fir trees was not correlated with altitude (Fig. 4). Of the five firs that regenerated before 1950, four were located below 2050 m a.s.l., and the other one at 2188 m.

The number of other tree species individuals recruited during the 18th and 19th centuries was rare (Fig. 3B), but an increase in recruitment was observed during the 20th century, particularly marked after 1950. Larch and Arolla pine were present in few stands before the end of the 19th century, but their recruitment then increased. First, larch recruitment increased after the end of the 19th century (Fig. 3C), then Arolla pine after 1950 (Fig. 3E). The increase in recruitment was more distinct for pine than for larch. Recruitment of spruce and broadleaved trees occurred since the 1960s and 1980s, respectively (Fig. 3D and F).

3.3. Silver fir age compared to the rest of the community

In 10 stands (32%) fir ages tallied with mean ages of the surrounding community (Fig. 5A); in 12 stands (39%) fir ages were higher than mean ages of the surrounding community; and in nine stands (29%) fir ages were lower than mean ages of the community. Within each stand, an asterisk indicates whether fir ages were higher (*) or lower (**) than those of the surrounding community. Even if the mean age of fir trees in the study area was 11 ± 7 years, the age of fir trees in the upper Maurienne Valley was still considerably lower than in the surrounding community.
surrounding community. This 32/39/29 distribution exhibits that any relationship between fir ages and mean age of the stands exists. In 50% of the plots, the fir ages tallied with the mean ages of the surrounding larch population and in 37% they were younger (Fig. 5B), indicating that, broadly, the firs regenerated at the same time as or after the larches. In 48% of the plots, the fir ages matched the mean ages of the surrounding Arolla pine population and in 39% the firs were older (Fig. 5C), indicating that the firs generally regenerated at the same time as the pines or were already established when the pines regenerated. In 86% of the plots, the fir ages tallied with the mean ages of the surrounding spruce population and in 14% the firs were older than mean age of surrounding spruce population (Fig. 5D).

3.4. Climatic variation

Since the beginning of the 19th century, we identified 12 inflections in the temperature trend, with four occurring during the 20th century: 1901 (turn point test, \( p < 0.01 \)), 1937 (\( p < 0.01 \)), 1941 (\( p < 0.01 \)) and 1975 (\( p < 0.05 \)). The trend in temperature anomalies showed a significant gentle increase between 1901 and 1937 (Mann–Kendall test, tau = 0.09, \( p < 0.01 \), Fig. 6), followed by a short cold period between 1937 and 1941. After 1941, a rapid temperature increase was observed, with a peak in 1949, and then temperature decreased significantly until 1975 (tau = -0.51, \( p < 0.001 \)). Since 1975 there appears to be a temperature increase (tau = 0.53, \( p < 0.001 \)).
Since the beginning of the 19th century, 11 inflections in the precipitation trend have been detected, with four during the 20th century: 1960 (p < 0.05), 1974 (p < 0.05), 1977 (p < 0.01) and 1981 (p < 0.05). The trend in precipitation anomalies showed a significant gentle decrease between 1898 and 1960 (tau = -0.07, p < 0.05, Fig. 6). Precipitation was then relatively low until 1974, followed by a short period (1974–1977) of high levels. After 1981, an increase in precipitation was observed (tau = 0.48, p < 0.01).

3.5. Land-use history

The number of local inhabitants reached a maximum around the mid-19th century in the two municipalities surrounding the study site (Fig. 7A). In the Bessans municipality, the number of inhabitants was highest during the 1880s, whereas in Lanslevillard the maximum occurred between the 1800s and 1870s. Thereafter, the number of local inhabitants decreased until the 1950s in Bessans (Mann–Kendall test, tau = -1, p < 0.001) and until the 1940s in Lanslevillard (tau = -1, p < 0.001). After the middle of the 19th century, the number of inhabitants remained low in the two municipalities (tau = -0.06, non-significant p > 0.05 for Bessans; tau = 0.8, non-significant p > 0.05 in Lanslevillard). The number of farmers in the municipalities began to decrease at the beginning of the 20th century (Fig. 7A). In the upper Maurienne valley, the resident livestock numbers remained high until the 1860s (Fig. 7B). Thereafter, numbers decreased until the 1930s, although this decreasing trend was not significant (tau = -1, p = 0.09). Resident livestock then increased slightly, but the increase was not significant (tau = 0.4, p = 0.46). Although livestock numbers exhibited two significant trend changes, no significant changes were found for cattle: cattle numbers have continued to decrease over the last two centuries (tau = -0.53, p < 0.01).

Since the middle of the 20th century, new agricultural practices have resulted in land-use changes: farmers progressively abandoned low-productivity or inaccessible areas but intensified production elsewhere. Furthermore, the creation of cheese labels (e.g. “Beaufort” and “Tomme de Savoie”) of high value (“Appellation d’Origine Contrôlée”) promoted cattle farming until the European Union (EU) dairy crisis of the 1980s. Since then, cattle numbers have dropped to a minimum (Fig. 7B).

Conversely, during the 1990s, the local sheep economy was stimulated as a result of both the dairy crisis of the 1980s, and specific grants from France and the EU (1992 and after) for shepherds to conserve a local breed of sheep (“Thones et Martod”). This conservation action explains the recent high density of sheep (Fig. 7B). However, this sheep production does not really affect the subalpine grassland and woodlands because the “Thones et Martod” sheep are generally kept around farms in the valleys, or in the most easily accessible lowland grasslands. Although the valley still remains in agricultural production in order to produce high value cheeses, the cattle and sheep density at elevations above 2000 m has dropped severely since the 1950s.

3.6. Explanation of fir regeneration

Several logistic regression models intended to explain fir recruitment both spatially and temporally were tested. Due to a high correlation between the four seasonal temperature variables and between the four seasonal precipitation variables, we choose to represent weather by two variables in our regression model: mean decadal temperature and mean decadal precipitation. Moreover, due to high autocorrelation of several temporal variables (mean temperature, precipitation, numbers of local inhabitants, livestock and cattle numbers), the assumption of time independence was not supported by our data. It is, thus, difficult to test the time lag effect of temporal variables in our regression model. Finally a simple preliminary model, including site characteristics, mean decadal temperature, mean decadal precipitation, mean decadal number of inhabitants, mean decadal number of livestock and mean decadal number of cattle, was tested. Temperature and number of local inhabitants had a significant effect (coef. = -0.93, p < 0.01; coef. = -2.63, p < 0.01, respectively). In this first model, 51.4% of the observations were omitted from the model due to incomplete livestock and cattle time series.

Fig. 7. (A) Human population census (circles) and farmer census (triangles) for both municipalities surrounding the study area [http://cassini.ehess.fr] and fir recruitment (bars); (B) resident sheep/goats and cattle numbers in the high Maurienne valley over the last 260 years (Jail, 1969). Vertical lines indicate significant trend inflections (* p < 0.05, ** p < 0.01, *** p < 0.001).
A second model excluding these two variables and including 86.9% of observations was tested. Temperature and number of local inhabitants had a significant effect, as in the first model (coef. $= -0.65$, $p < 0.01$; coef. $= -1.17$, $p < 0.001$, respectively).

4. Discussion

Subalpine forests within the study area have undergone great changes since the beginning of the 20th century. The upper altitudinal limit of silver fir has increased by about 300 m during the last 50 years (Fig. 4), i.e. since the last vegetation studies in this area, which reported an upper-limit for the species around 1800–1950 m a.s.l. (Bartoli, 1966; Gensac, 1972). Moreover, the present-day forest shows a bimodal structure, with the canopy dominated by larch, but with abundant Arolla pine seedlings and saplings (Fig. 2). Before analysing the fir dynamics, we will discuss this community transformation.

4.1. Canopy composition echoes former management: land-use legacies

In most alpine forests, past human activities have greatly altered the structure and dynamics through forestry, forest litter collection and grazing (Motta and Lingua, 2005; Gimmi et al., 2008). In our study area, the recruitment of all species was very low until the 20th century (Fig. 3B) when the human population and grazing activities, notably livestock grazing, were locally important (Fig. 7A and B). Despite overall low tree recruitment during the 18th and the 19th centuries, there was significant recruitment of larch. Larch is an earlier successional species and is generally favoured by shepherds because it is compatible with grazing activities. The deciduous foliage of larch, comprising soft needles, plus a low tree-density ensure high grass productivity and offer shelter for cattle and sheep from rain and intense sunlight. In contrast other tree species, i.e. Arolla pine and silver fir that were late-successional species, were actively removed from subalpine areas by shepherds (Carrer and Urbinati, 2001; Motta and Lingua, 2005). Furthermore, larch is probably more resistant to trampling than Arolla pine and silver fir and its wood is valued for its natural decay resistance, high density and aesthetic value. The limited recruitment of trees until the 20th century (Fig. 3B) and the current dominance of larch in the canopy (Fig. 2B) seem thus reflect past management of the area, i.e. grazing by domestic animals and forest management.

4.2. Recent forest dynamics mirror land abandonment

The decrease in the human population, resident livestock and cattle that began in the 1870s–1880s (Fig. 7A and B) should have lead to an increase in tree recruitment during the 20th century. Although tree establishment did increase during the 20th century, the expected acceleration of establishment was delayed until after the 1960s (Fig. 3B). A great increase in the numbers of transient livestock during the first half of the 20th century (Rambaud and Vincienne, 1964) may have partially replaced the effects of resident livestock and may explain the observed delay. Indeed, Jail (1969) reported a transient livestock rise of +47% between 1928 and 1964 in the upper Maurienne valley. This increase amounted, in the Savoy department (covering a larger area), to +96% between 1913 and 1928 and +52% between 1928 and 1964 (Jail, 1969). The increasing recruitment trend was probably the result of progressive land abandonment that began at the end of the 19th century. Specifically, tree community dynamics followed the expected pattern of secondary succession resulting from land abandonment, i.e. establishment of larch followed by Arolla pine in the subalpine belt (Krüsi and Moser, 2000; Didier, 2001; Motta and Nola, 2001; Motta and Lingua, 2005). Seed dispersal by wind and the light requirements of larch explain its rapid expansion in open areas after grazing reduction (Rameau et al., 1994; Motta and Lingua, 2005), whilst long-distance seed dispersal by the nutcracker (Nucifraga caryocatactes) and the capacity to grow in the shade may explain the recent Arolla pine expansion and establishment.

4.3. Abies alba dynamics followed the secondary succession pattern

Today silver fir regenerates at altitudes up to 2226 m (Fig. 4); this is more than 300 m above the previously reported upper-limit in the valley (Bartoli, 1966; Gensac, 1974) or in the western Alps (Chas, 1994; Rameau et al., 1994). Two main factors may explain this observed upward shift of the upper-limit of fir regeneration, namely climatic changes or land abandonment.

In areas where water availability and the length of the growing season both impose restrictions on plant growth, the positive effect of temperature increase without an obvious increase in precipitation, as recently observed in the upper Maurienne valley, should not have an effect. Indeed, such a temperature rise without more precipitation should increase water stress and counteract any positive effect of temperature. Nevertheless, an increase in atmospheric humidity with altitude may counter soil drought and allow fir recruitment in the inner Alps, which are relatively drier than the outer Alps. The total annual precipitation is low and should not favour fir (Ausserac, 2002).

If recent temperature increase was the main factor explaining fir establishment, fir recruitment should have increased only since the end of the 1980s, following the net regional and global temperature increase. However fir recruitment began to rise after the 1950s when temperature was relatively low; at this time recruitment was significantly correlated to temperature decrease. It is amazing that silver fir was not restricted by low temperatures with respect to the limit of its altitudinal distribution. The effect of temperature on fir recruitment is low (coef. $< -1$) but was negative in both our tested regression models. These results indicate that the temperature increase hypothesis is not correct. Moreover, fir recruitment did not occur simultaneously at a given altitude and fir ages do not decrease with increasing altitude. Indeed young firs were not recorded much at the higher altitude. Altitudinal and temporal patterns of fir recruitment do not confirm the climatic change hypothesis and suggest that the land-use change hypothesis should be considered.

The land-use change proxies were related to regeneration in different ways. No significant effect of cattle or sheep/goat numbers was found; in contrast, number of inhabitants had a strong negative relationship with fir recruitment. Due to changes in agricultural and pastoral practices, namely intensification, the high number of sheep and goats present during the last decade did not reflect the spatial extent of grazing. Indeed grazing activities in the municipalities’ forest and surrounding areas has been abandoned even though the livestock numbers are high. The number of inhabitants should reflect the spatial extent of land abandonment in the study area and should explain its observed effects. A strong negative effect of the number of inhabitants suggests that land-use change influenced silver fir establishment. Finally, the temporal distribution of fir recruitment relative to the surrounding plant community supports the land-use change hypothesis. Indeed, fir recruitment and age structures for each species follow the expected pattern for secondary succession (the relay floristics model), i.e. fir recruitment occurred after or at the same time as larch recruitment and at the same time as or before Arolla pine recruitment. This pattern reflects the maturation of the ecosystem.
5. Conclusion

Most firs germinated after 1950; this suggests that data collectors (e.g. Bartoli, 1966; Gensc, 1974) were consistent in compiling their forest inventories and phytosociological relevés. Although the status of fir with regard to the dynamics of the all the surrounding trees was highly variable, fir establishment did, in part, follow the expected natural sequence of succession, i.e. firs established at the same time as or after larch, at the same time as or before stone pine, and at the same time as spruce. This pattern occurred in the majority of stands and supports the land-use change hypothesis, further evidence for which is provided by the strong negative effect of number of inhabitants on fir recruitment. A negative relationship was found between temperature records and fir regeneration. Clearly, the role of climatic warming cannot be ruled out, but land-use transformations obscure its possible effects on plant community structure.

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