Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests

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Abstract

An increasing number of studies have reported on forest declines and vegetation shifts triggered by drought. In the Swiss Rhone valley (Valais), one of the driest inner-Alpine regions, the species composition in low elevation forests is changing: The sub-boreal Scots pine (*Pinus sylvestris* L.) dominating the dry forests is showing high mortality rates. Concurrently the sub-Mediterranean pubescent oak (*Quercus pubescens* Willd.) has locally increased in abundance. However, it remains unclear whether this local change in species composition is part of a larger-scale vegetation shift. To study variability in mortality and regeneration in these dry forests we analysed data from the Swiss national forest inventory (NFI) on a regular grid between 1983 and 2003, and combined it with annual mortality data from a monitoring site. Pine mortality was found to be highest at low elevation (below 1000 m a.s.l.). Annual variation in pine mortality was correlated with a drought index computed for the summer months prior to observed tree death. A generalized linear mixed-effects model indicated for the NFI data increased pine mortality on dryer sites with high stand competition, particularly for small-diameter trees. Pine regeneration was low in comparison to its occurrence in the overstorey, whereas oak regeneration was comparably abundant. Although both species regenerated well at dry sites, pine regeneration was favoured at cooler sites at higher altitude and oak regeneration was more frequent at warmer sites, indicating a higher adaptation potential of oaks under future warming. Our results thus suggest that an extended shift in species composition is actually occurring in the pine forests in the Valais. The main driving factors are found to be climatic variability, particularly drought, and variability in stand structure and topography. Thus, pine forests at low elevations are developing into oak forests with unknown consequences for these ecosystems and their goods and services.

Keywords: climate change, generalized linear models, inner-Alpine dry valleys, land-use change, mixed-effects models, Pinus sylvestris, Quercus pubescens

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Introduction

In recent years an increasing number of studies have reported on forest declines and shifts in species composition in response to changing climatic conditions. Temperature-induced changes include the upward shift of the alpine treeline (Kullman, 2002; Shiyatov, 2003; Gehrig-Fasel *et al.*, 2007; Devi *et al.*, 2008), the poleward shift of the northern treeline (Esper & Schweingruber, 2004; Lloyd, 2005), the invasion of evergreen oaks into higher situated mesic broadleaved forests in northeast Spain (Penuelas & Boada, 2003), the invasion of exotic evergreen broadleaves into mixed temperate

broadleaved forests at the southern fringe of the Alps (Walther *et al.*, 2002) and the shift of the upper respective northern distribution limit of temperature-sensitive plant species such as *Viscum album* ssp. *austriacum* (see Dobbertin *et al.*, 2005a).

In addition to temperature-related changes, drought has also been identified as an important trigger for forest decline and decline-induced vegetation shifts (Allen & Breshears, 1998; Penuelas & Boada, 2003; Breshears *et al.*, 2005). A global overview on drought-induced forest decline was recently presented in Allen *et al.* (2010). Drought may directly cause mortality via hydraulic failure in extreme drought events (Bréda *et al.*, 2006; McDowell *et al.*, 2008), or indirectly, as a persistent weakening of trees by reducing carbon storage (McDowell *et al.*, 2008; Eilmann *et al.*, 2010). Therefore,

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these weakened trees are increasingly vulnerable to additional stressors like insects (Rouault *et al.*, 2006; Wermelinger *et al.*, 2008), fungi (Giordano *et al.*, 2009; Heiniger *et al.*, 2011), nematodes (Polomski *et al.*, 2006), and mistletoes (Dobbertin & Rigling, 2006; Rigling *et al.*, 2010; Zweifel *et al.*, 2012).

Drought is also a limiting factor in forest ecosystems in inner-Alpine valleys such as the Valais, Switzerland. Scots pine (*Pinus sylvestris* L.) dominates forest stands in the driest parts of the valley, i.e. from 700 to 1100 m a.s.l., but recently high mortality rates of Scots pine have been observed in this region (Dobbertin *et al.*, 2005b; Bigler *et al.*, 2006) and in other inner-Alpine valleys with similar climatic conditions such as the Italian Aosta valley (Vertui & Tagliaferro, 1998; Vacchiano *et al.*, 2012) or the Austrian Inn valley (Oberhuber, 2001). Concurrently, deciduous tree species, in particular pubescent oak (*Quercus pubescens* Willd.) are becoming locally more abundant and are increasingly competing with Scots pine on dry sites (Weber *et al.*, 2007, 2008a). The question arises whether these observed changes indicate a general shift in species composition or whether these changes are restricted to a few extreme sites only.

The Valais is among the driest inner valleys of the European Alps (Braun-Blanquet, 1961; Ozenda, 1985). On south-facing slopes with shallow soils Scots pine forests give way to steppe-like vegetation. On these sites a change in climate conditions is expected to have a strong effect on tree growth and tree survival as well as on the persistence of forest cover (Moser *et al.*, 2010). Regional climatic conditions significantly changed within the last 100 years. Whereas the precipitation regime was relatively constant (Begert *et al.*, 2005), the increase in temperature (Begert *et al.*, 2005) and frequency of hot days during the summer months (Rebetez & Dobbertin, 2004) intensified the evapotranspiration and led to increasing drought stress for the plants, particularly in dry years when water is limited (Rebetez & Dobbertin, 2004). This aggravation of water shortage is expected to have a strong impact on tree survival and regeneration.

At dry sites Scots pine and pubescent oak are competing for the same resources. Scots pine is a sub-boreal species with a wide distribution range, however, in the Valais, Scots pine is growing close to the southern distribution limit where it locally reaches its dry limits at lower elevations (Boratynski, 1991; Meusel, 1992). At lower latitudes Scots pine occurrence is restricted to higher altitudes only (Boratynski, 1991). In contrast, pubescent oak has a sub-Mediterranean origin with a much smaller distribution range (Meusel, 1992). In the Valais pubescent oak grows close to its northern distribution limit. Hence, both species must be considered as

highly sensitive to direct and indirect effects of the ongoing and expected future climate changes (Zweifel *et al.*, 2009) and the question arises whether pubescent oak will replace or displace upward Scots pine in the Valais, when considering the tree-specific physiological capabilities (Zweifel *et al.*, 2006, 2007, 2009).

The aim of this study was to analyse the dynamics of the Scots pine forests in the Valais during two decades with respect to driving factors leading to these changes. We focused on the spatial and temporal changes in forest structure, species composition, tree mortality, and tree regeneration. Because of the varying spatial and temporal dimensions of the forest changes, two approaches differing in scale (space and time) and methodology were combined: Firstly, we resampled the Swiss national forest inventory (NFI) on the regular 1 × 1 km grid in the Valais, consisting of 201 grid points between the valley bottom at 430–700 m a.s.l. and 1600 m a.s.l. At each grid point 20-year mortality (1983/1985 to 2002/2003) of Scots pine was analysed and the actual state of tree regeneration in 2002/2003 was surveyed and related to climate and site parameters. Secondly, tree mortality from a long-term experimental site at Visp and climate data with high temporal resolution were interrelated.

The following questions were addressed: (1) Is the shift from Scots pine to pubescent oak a general pattern in the Valais or is it restricted to extreme sites only? (2) What factors impact tree mortality and regeneration of the two species?

Materials and methods

Study area

The Swiss Rhone valley is an inner-Alpine dry valley (Fig. 1). The surrounding mountain ranges, with altitudes exceeding 4000 m, shelter the inner part of the valley from the moist oceanic air masses transported with westerly and southerly winds. As a result a steep precipitation gradient exists with yearly precipitation of 1046 mm in Bex in the west to 871 mm in Martigny and 599 mm in Sion and Visp in the central and eastern part of the Valais (period 1961–1990, MeteoSwiss). In addition, there is also a gradient in the seasonal distribution of precipitation: from the west with a distinct maximum of precipitation in summer to the central area of the valley with an even distribution of precipitation over the year (Fig. 1). Drought years with yearly precipitation below 500 mm are frequent in central Valais (20 drought years occurred in the last century in Visp). Cloudiness is generally very low and, as a consequence, solar radiation is high. Mean annual temperature in Sion is 9.2 °C (norm period 1961–1990, MeteoSwiss). The steep climatic gradient is well reflected by the forest composition: European beech (*Fagus sylvatica*), an indicator species of the temperate deciduous forests (Mayer, 1984; Ozenda, 1985),
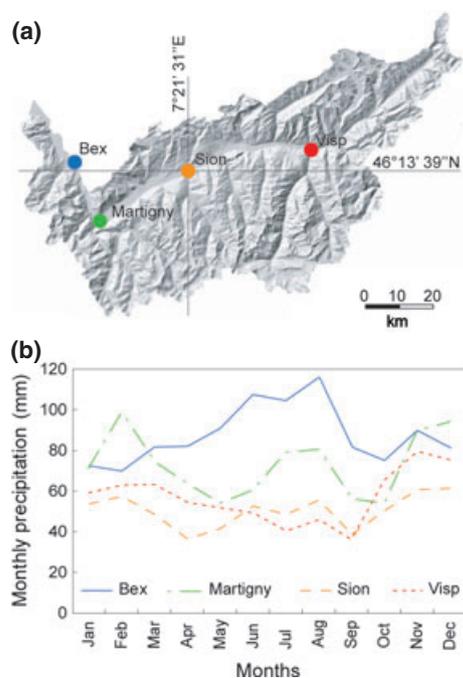
Fig. 1 (a) Map of the study area Valais including the four weather stations Bex, Martigny, Sion and Visp. The long-term monitoring plot is located in Visp. (b) Variability of monthly precipitation over the year (period 1961–1990) for the four weather stations within the study area.

tends to dominate forests in the atlantic western part, but lacks in the drier central part of the main valley, where more drought-resistant pine and oak forests at lower elevations and various coniferous forests from 1000 m a.s.l. to the tree-line dominate (Brändli, 2010).

Inventory data and description of predictor variables

Swiss forests are inventoried every decade on a grid of permanent plots (Bachofen & Mahrer, 1988; Brassel & Brändli, 1999; Brändli, 2010). The first Swiss NFI was conducted from 1983 to 1985 on a regular 1 × 1 km grid. From 1993 to 1995 the inventory was repeated on half of the original plots with a random selection of plots on an additional 0.5 × 0.5 km grid. To study recent changes in the Scots pine forests of the Valais, existing NFI plots served to reassess the presence and state of trees and document natural tree regeneration in 2002 and 2003. For this purpose 201 plots (186 plots on the 1 × 1 km grid plus 15 plots on the 0.5 × 0.5 km grid) were selected up to the approximate limit of Scots pine dominance at about 1600 m a.s.l. (Fig. 2).

Each plot consists of two concentric circles. In the 200 m^2 circle all overstorey trees with ≥ 12 cm stem diameter at breast height (DBH) and in the 500 m^2 circle all trees with ≥ 36 cm DBH were monitored. Any mortality and abundance data that were used in the analyses and presented in the results were based on weighted data, i.e. trees from the 200 m^2 circle were weighted with 2.5, trees from the 500 m^2 circle were weighted with 1.0. For the 186 plots on the

1 × 1 km grid we reported tree mortality and removal rates for the period from 1983/1985 to 2002/2003, whereas all plots assessed in 2002/2003 (i.e. including 15 plots on the 0.5 × 0.5 km grid) were used for comparison of the current forest structure and species composition. For trees that were cut between the two inventories we were not able to distinguish between regular management operations or salvage cuttings. Hence, we computed both tree mortality and the combined value of tree mortality and removal.

To assess the recruitment of Scots pine and pubescent oak we counted all saplings smaller than 20 cm height on a 50 m^2 circle on each grid plot. Canopy cover was estimated visually and was used as a surrogate for light availability for tree regeneration. Furthermore, we estimated the percentage cover of bare soil vs. soil with organic layers to characterize the seedbed of the saplings. Browsing damage on buds and shoots was assessed for each sapling.

For each plot, we derived additional variables that were related to climate variability, stand structure and topography. Climate variability was represented by a drought index and degree days. A monthly drought index as an estimate for water availability was calculated as the difference between monthly precipitation sum (P) and potential evapotranspiration (PET) according to Turc (1963). Degree days were calculated as the sum of mean daily temperatures above 5 °C. Annual values for the long-term period 1961–1990 were computed for all climate variables. All climatic data obtained from the climate stations of MeteoSwiss were interpolated for the inventory plots using an inverse weighted distance approach (Zimmermann & Kienast, 1999). Stand structure was characterized by stand basal area calculated over all species for all trees that were alive in 1983/1985. Topography was represented by aspect (north, south, east, west), slope steepness and elevation.

Modelling tree mortality and tree regeneration

For Scots pine, we quantified the effects of climate, stand structure and topography on individual-tree mortality (i.e. including dead and removed trees) between 1983/1985 and 2002/2003. Only Scots pine were considered that were alive in 1983/1985. Generalized linear mixed-effects models (GLMMs) were fitted with a binomial distribution (Pinheiro & Bates, 2000; Zuur *et al.*, 2009) defined by the density function:

$$f(y; p) = \binom{N}{y} \times p^y \times (1 - p)^{N-y} \qquad (1)$$

where N is the number of dead and living trees and y the number of living trees. The survival probability p of a tree is modelled with the logit-link function:

$$\ln\left(\frac{p}{1 - p}\right) = X\beta \qquad (2)$$

where ln is the natural log, X is a matrix that contains the predictor variables and β is a vector with the regression coefficients. To estimate model parameters the 'lmer' function of the 'lme4' package (version 0.999375-40) in the statistical computing software R (version 2.12.0; R Development Core Team,
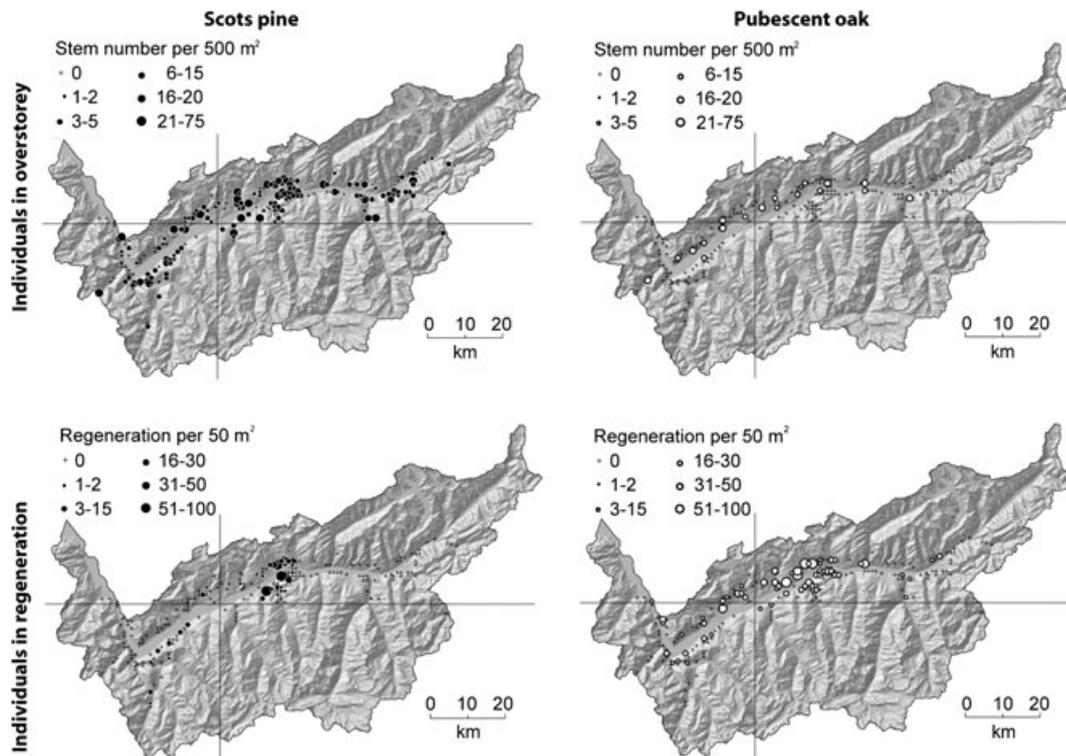
Fig. 2 Spatial distribution of Scots pine and pubescent oak individuals in the overstorey (number of trees per 500 m^2) and in the regeneration (number of saplings per 50 m^2); observations from 2002/2003 (© 2005 BFS GEOSTAT/swisstopo).

2010) was used. Combinations of the following predictor variables were included as fixed effects in the models: drought index, degree days, aspect, slope steepness, stand basal area and DBH (as measured in 1983/1985). To reduce numerical instabilities and increase convergence in the model fitting process, the variable degree days was divided by 10. Elevation was not considered in the models because of the high correlation with the two climate variables. To take into account plot-to-plot variability, the intercept was included as random effect. After removing observations with missing values, the data set was reduced from 1014 Scots pines in 139 plots to a total of 985 Scots pines in 137 plots, which were included in the mortality models. A weight argument in the model formulation allowed to consider whether a tree was observed in the 200 m^2 or 500 m^2 circle without inflating the number of observations.

For both Scots pine and pubescent oak, the effects of climate, topography, canopy cover and bare soil on tree regeneration as determined in 2002/2003 were quantified. These count data were modelled with generalized linear models using a negative binomial distribution (Zuur *et al.*, 2009; Van der Burght *et al.*, 2012) defined by the density function:

$$f(y; \theta, \mu) = \frac{\Gamma(\theta + y)}{\Gamma(\theta) \times y!} \times \frac{\mu^y \theta^\theta}{(\mu + \theta)^{\theta + y}} \qquad (3)$$

where y is the number of regeneration, Γ is the gamma distribution and θ the dispersion parameter taking into account overdispersion (i.e. the variance is greater than the mean; Zuur *et al.*, 2009). The mean μ is modelled with the log-link function:

$$\ln(\mu) = X\beta \qquad (4)$$

where X is a matrix with the predictor variables and β is a vector with the regression coefficients. The 'glm.nb' function of the 'MASS' package (version 7.3–8) in the statistical computing software R (R Development Core Team, 2010) was used to fit the models. The following predictor variables were combined in the models: drought index, degree days, aspect, slope steepness, canopy cover and bare soil. After removing observations with missing values, the data set was reduced for both Scots pine and pubescent oak from 201 to 193 plots, which were included in the regeneration models.

For both the mortality models and regeneration models, we followed an information-theoretic model selection approach based on the AIC$_c$ (corrected Akaike Information Criterion; Burnham & Anderson, 2002; Stauffer, 2008). In both cases, we defined a priori 14 models using different combinations of predictor variables (Supporting informations Table S1, S2 and S3). The models were ranked according to the AIC$_c$, i.e. the model with the lowest AIC$_c$ was considered to be the best-fitting model within each selection of 14 models. For each model, we calculated the Akaike weight (Burnham & Anderson, 2002), which is the probability that a specific model is the best-fitting model within these 14 models.

Long-term monitoring at research plot

Annual variation in Scots pine mortality was studied based on data from a research plot established in 1996 close to the

community of Visp (Fig. 1). The plot belongs to the Swiss long-term forest research network, which is part of the European level II monitoring network of ICP forests (Lorenz, 1995). In this 2 ha plot all trees were geo-referenced and tree sizes were measured. Each August between 1996 and 2011, mortality of every single Scots pine was assessed (Dobbertin & Rigling, 2006). The MeteoSwiss climate station Visp is located in 2 km distance from the plot.

Results

Presence of Scots pine and pubescent oak in the overstorey

A total of 2010 living Scots pines ≥ 12 cm DBH (200.0 trees per ha) was found on 153 of the 201 plots in 2003, whereas living pubescent oaks in the overstorey were only present on 19 plots with an estimated total of 114 individuals (11.3 trees per ha; Table 1). For both species there were no distinct longitudinal–latitudinal trends in species distribution (Fig. 2). In contrast the altitudinal distribution differed. Scots pine was evenly distributed within the studied sites (up to 1600 m a.s.l.), whereas pubescent oak peaked at 800–1000 m a.s.l. and was rarely found above 1200 m a.s.l. (Fig. 2).

The survey of 1983/1985 (Table 1) accounted for 139 plots with 2254 Scots pines (242.3 trees per ha) and 11 plots with 41 pubescent oaks (4.4 trees per ha) in the overstorey. Compared with the survey in 1983/1985 the abundance of pubescent oak increased in the overstorey until 2002/2003 by 160.7% in contrast to the decreasing abundance of Scots pine (−17.5%).

Table 1 Occurrence of dead and living Scots pine and pubescent oak in the overstorey (1983/1985 and 2002/2003)

	Scots pine	Pubescent oak
Plots with individuals in overstorey (1983/1985) out of 186 plots, count	139	11
Plots with individuals in overstorey (2002/2003) out of 201 plots, count	153	19
Individuals in overstorey (1983/1985) out of 186 plots, count/ha	242.3	4.4
Individuals in overstorey (2002/2003) out of 201 plots, count/ha	200.0	11.3
Dead trees from 1983/1985 to 2002/2003, count/ha	33.2	0.4
Dead and removed trees from 1983/1985 to 2002/2003, count/ha	78.8	0.6
Mortality from 1983/1985 to 2002/2003 (%)	13.7	8.6
Mortality & removal from 1983/1985 to 2002/2003 (%)	32.5	14.8
Change in number of individuals in overstorey from 1983/1985 to 2002/2003 (%)	−17.5	160.7

Tree mortality

Within the two decades of investigation a total of 33.2 Scots pines and 0.4 pubescent oaks died per ha (Table 1). The percentage of mortality was almost 60% higher in Scots pine (13.7%) than in pubescent oak (8.6%). The 20-year rate for mortality and removal was more than twice as high for Scots pine (32.5%) than for pubescent oak (14.8%). A majority of the dead and removed Scots pines were observed in the interior part of the Valais. Mean rates of mortality and removal increased with decreasing altitude, however, variability at altitudes ≤ 600 m was high (Fig. 3). In altitudes below 1000 m a.s.l., Scots pine mortality was about twice the mean mortality in Switzerland (0.3–0.5% per year). The mean rate of mortality and removal in low altitude was four times higher than the nationwide average mortality (Fig. 3). Due to small absolute numbers, oak mortality was not further analysed.

The mortality model SMP10 (Table 2, Supporting informations Table S1) had a probability of 45% to be the best-fitting model among the 14 models explaining survival probabilities of Scots pine. The model included the predictor variables drought index (P-PET, positive correlation with survival probabilities), stand basal area in 1983 (negative correlation) and DBH in 1983 (positive correlation). Hence, mortality in Scots pine was increased at drier sites, in stands with high stand basal area and in trees with small DBH.

The data from the long-term monitoring plot at Visp showed a negative correlation between summer drought (drought index, April–August) and Scots pine mortality, which was assessed in the following summer (end of July to beginning of August) (Spearman rank correlation between drought index and subsequent annual mortality rate: −0.72, $P < 0.01$; Fig. 4).

Tree regeneration

The spatial distribution of tree regeneration (0–20 cm; Fig. 2) differed between the two species: Scots pine saplings were only found in the central and western part of the Valais. In the eastern part, the driest area, Scots pine regeneration was basically absent. Pubescent oak saplings were almost evenly distributed over the entire valley with a maximum in abundance in the western and central parts.

Scots pine saplings were found on 34 of 201 plots, whereas pubescent oak regeneration occurred on nearly twice as many plots (67 plots; Table 3). Five times more pubescent oak saplings ($n = 2343$; 2331.3 saplings per ha) were recorded than Scots pine saplings ($n = 486$; 483.6 saplings per ha). When comparing regeneration at the plot level, more saplings were found for
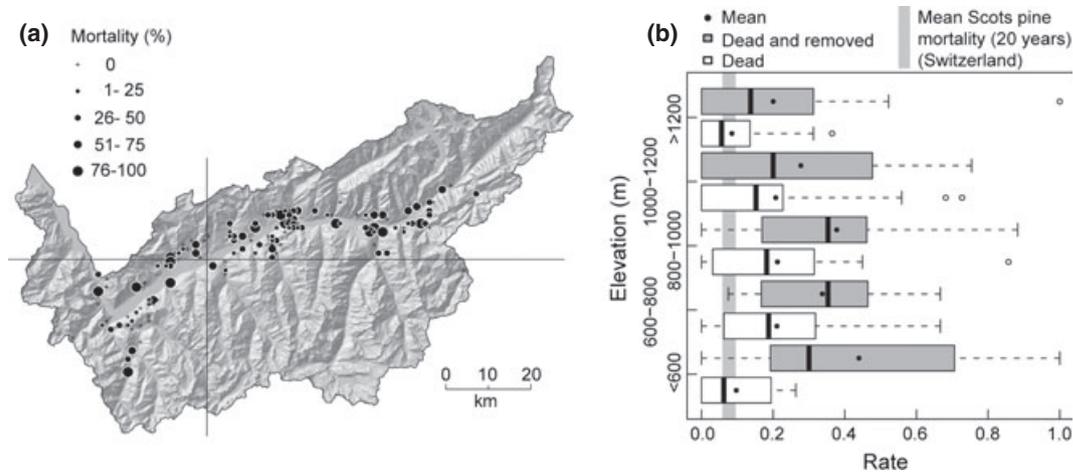
Fig. 3 (a) Longitudinal–latitudinal distribution and (b) boxplots of the altitudinal distribution of Scots pine mortality including tree removal for the period from 1983/1985 to 2002/2003. Only plots with at least five trees present in the overstorey during the first survey were considered. The vertical grey bar represents the Swiss average (© 2005 BFS GEOSTAT/swisstopo).

Table 2 Model description of the best-fitting Scots pine mortality model (SMP10; see Table S1 in the Supppoting Information). Survival probabilities were calculated for 985 Scots pine in 137 plots with a generalized linear mixed-effects model using a binomial distribution [Eqn (1)] and a logit-link function [Eqn (2)]

Fixed effects: estimates ± SE (*P*)				Random effect: SE
Intercept	Drought index (mm)	Stand basal area (m² ha⁻¹)	DBH (cm)	Intercept
0.365 ± 0.516 (0.479)	0.0015 ± 0.0007 (0.033)	−0.037 ± 0.017 (0.032)	0.058 ± 0.009 (<0.0001)	2.009

SE, standard error; Maximum likelihood estimation was used to fit the model.

pubescent oak than for Scots pine (*P* = 0.00052; paired Wilcoxon signed rank test). In only 20% of the plots with Scots pine in the overstorey saplings of the species were observed. In contrast, on 74% of the plots with pubescent oak overstorey also oak saplings occurred. In plots without the two tree species in the overstorey, saplings of Scots pine and oak were found in 8% and 79% of the plots respectively.

For Scots pine the number of regeneration was best modelled with model RMP07, which had a probability of 52% to be the best-fitting model among the 14 models. The model included the predictor variables drought index and degree days, both were negatively correlated with regeneration (Table 4; Supporting informations Table S2). For pubescent oak the best fit showed model RM012 with a probability of 84% (Table 4; Supporting

informations Table S3), which was based on the explaining variable drought index (negative correlation) and the positively correlated variables degree days, aspect and slope steepness. Hence, regeneration of both species was more frequent on drier sites. Scots pine was more frequent on cooler sites (i.e. higher altitudes), whereas oak was more successful at warmer sites (i.e. sites at lower altitudes). In addition, oak regeneration was more frequent on steep slopes that were facing east, south or west. Canopy cover (negative correlation) and bare soil (positive correlation) were included in the second best-fitting model for Scots pine (Table S3).

On average, deciduous tree species were browsed two to four times more often (12–22%) than conifers (5–10%, see Fig. 5). Browsing pressure was lowest for saplings of Scots pine, common juniper (*Juniperus communis*) and shrubs with thorns (5–7% of the saplings were browsed). The highest pressure was on saplings of maple (*Acer* sp.), common whitebeam (*Sorbus aria*) and shrubs without thorns (18–21% of the saplings were browsed). In pubescent oak 16% of the saplings were browsed.

Discussion

Driving factors of tree mortality

The combined results of the two approaches using data sets, which differ in their spatial coverage (grid analysis vs. long-term monitoring plot) and temporal resolution (decadal vs. yearly), revealed the importance of the joint effects of drought, stand structure and tree size on the observed Scots pine decline in inner-Alpine forests. Scots pine mortality was increased on dry plots with
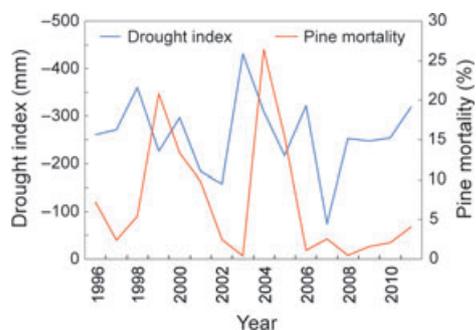
Fig. 4 Temporal variability in drought (drought index calculated for April to August, blue line) and Scots pine mortality (current August to August in the following year, red line) surveyed on the long-term monitoring plot Visp. Note the inverse scale for the drought index.

Table 3 Occurrence of Scots pine and pubescent oak regeneration in relation to the overstorey (n = 201 plots)

	Scots pine	Pubescent oak
Plots with regeneration, count	34	67
Total regeneration, count	486	2343
Regeneration per ha (only on plots with regeneration), count/ha	483.6	2331.3
Plots without regeneration, but with individuals in overstorey, count (%)	122 (80)	5 (26)
Plots with regeneration and with individuals in overstorey, count (%)	31 (20)	14 (74)
Plots with regeneration, but without individuals in overstorey, count (%)	3 (8)	53 (79)

high stand competition as represented by stand basal area (Table 2), particularly following dry years (Fig. 4) and for small-diameter trees (Table 2). High stand competition implies increased water consumption, hence, in this dry environment drought stress is increased in denser stands (Weber *et al.*, 2007, 2008a). This coincides with a study by Oberhuber (2001) of a Scots pine stand near Innsbruck (Austria), where the highest mortality rates occurred on the most drought exposed sites. Our data showed for the dryer sites below 1000 m a.s.l. almost three times higher mortality rates compared with the mean mortality of Scots pine nationwide, and even four times higher rates when including tree removal. At low elevations most pine forests have little economic value due to slow tree growth and poor stem quality. As a consequence these forests have never been regularly managed (Gimmi *et al.*, 2010) and therefore, most cutting operations likely occurred to remove dead trees. If these removed trees are not added to the mortality data, pine mortality is rather underestimated at lower altitudes. Actual mortality was probably close to

the estimated values of mortality including tree removal. However, at high elevations timber quality is improved and regular cuttings for economic reasons are practiced. Thus, above 1000 m a.s.l., the actual Scots pine mortality might be well described with our observed mortality data only (without tree removal).

The sub-Mediterranean pubescent oak seems to cope better with severe drought than Scots pine resulting in lower mortality rates (Table 1). This might be explained by the ability of pubescent oak for long-lasting stomata opening under drought compared with Scots pine (Zweifel *et al.*, 2005, 2006, 2009) resulting in higher photosynthetic activity. However, during the summer heat wave 2003, also pubescent oak reached its physiological limits and showed a complete leaf shedding already in July (Zweifel *et al.*, 2006). Both Scots pine and pubescent oak completely ceased their assimilation during that period (Zweifel *et al.*, 2009), which might be the reason for the drastic growth depression in Scots pine (Oberhuber *et al.*, 1998; Rigling *et al.*, 2001, 2002, 2003; Eilmann *et al.*, 2011) but also in pubescent oak during extreme dry years (Eilmann *et al.*, 2006, 2009; Weber *et al.*, 2007).

Repeated drought might lead to progressive depletion of stored carbohydrates because freshly produced assimilates cannot cover carbon needs for the trees' metabolism, defence and growth (Bréda *et al.*, 2006; McDowell *et al.*, 2008). Whereas carbon starvation was identified as a relevant process in Scots pine decline in northeast Spain (Galiano *et al.*, 2011) and in the Valais (Eilmann *et al.*, 2010), Gruber *et al.* (2012) and Oberhuber *et al.* (2011) could not show any reductions in carbon reserves of Scots pines in a dry year nor on a dry site near Innsbruck (Austria). Beside carbon starvation, hydraulic failure is another limiting process weakening trees during drought (McDowell *et al.*, 2008; McDowell, 2011) and increasing the trees' vulnerability against additional stressors such as (i) the semiparasite pine mistletoe (*Viscum album* ssp. *austriacum*) aggravating the drought stress of the host tree (Dobbertin & Rigling, 2006; Rigling *et al.*, 2010), or (ii) pests and insects (Braasch & Enzian, 2004; Polomski *et al.*, 2006; Dobbertin *et al.*, 2007; Wermelinger *et al.*, 2008). These attacks by additional stressors might gain importance because increasing warming is expected to speed up insect reproduction and development, which finally might increase the infestation pressure (e.g. Wermelinger & Seifert, 1999; Bale *et al.*, 2002; Gan, 2004).

Occurrence and ecology of tree regeneration

Even though Scots pine dominates the overstorey its recruitment is generally poor (Fig. 2; Table 3). In stands without dominant Scots pine, its regeneration was

Table 4 Model description of the best-fitting regeneration models (Scots pine: RMP07; pubescent oak: RMO12; see Supporting information Tables S2 and S3). The generalized linear models were fitted to 193 plots using a negative binomial distribution [Eqn (3)] and a log-link function [Eqn (4)]

| | Estimates ± SE (P) | | | Aspect | | | | |
Model	Intercept	Drought index (mm)	Degree days (°C)	East	South	West	Slope (%)	Dispersion parameter
RMP07	15.085 ± 3.609 (<0.0001)	−0.0068 ± 0.0016 (<0.0001)	−0.0039 ± 0.0010 (<0.001)					0.059 ± 0.012
RMO12	−11.100 ± 2.451 (<0.0001)	−0.0033 ± 0.0011 (0.003)	0.0036 ± 0.0007 (<0.0001)	4.463 ± 0.676 (<0.0001)	4.561 ± 0.660 (<0.0001)	1.335 ± 0.619 (0.031)	0.0089 ± 0.0103 (0.390)	0.154 ± 0.024

SE, standard error; Models were fitted using maximum likelihood. For the variable aspect, north was set as reference level (i.e. the estimates for east, south and west are deviations from north).

essentially absent. Pubescent oak shows an opposite pattern with still relatively few trees in the overstorey but a large sapling bank, even in stands without seed trees. This situation is remarkable considering the reproductive strategy of the two species (e.g. Bran *et al.*, 1990; Keeley & Zedler, 1998; Lanner, 1998) with Scots pine producing a high amount of light and winged seed, which easily disperse, whereas pubescent oak produces relatively few and heavy seeds, which are dispersed by animals. Based on these differing strategies one would expect Scots pine predominantly colonizing new areas, which was obviously not the case in recent years in the Valais. A potential bottleneck for Scots pine recruitment, particularly for germination and establishment, is dry and warm springs as shown by Moser *et al.* (2010) for tree regeneration after a stand replacing fire. Obviously, current site conditions seem to be less favourable for Scots pine than for pubescent oak regeneration (Gimmi *et al.*, 2010). Furthermore, pubescent oak regeneration will increase in the near future due to the increasing ingrowth in the overstorey and subsequent increasing numbers of seed trees (cf. Table 1).

Both species regenerated more frequently with increasing dryness of the site. This is likely caused by increased competition by less drought-tolerant tree species on moister sites. Although Scots pine and pubescent oak recruitment were both more frequent on dry sites, significant differences exist between the two species (Table 4): Scots pine regeneration was favoured on cooler sites at higher altitudes (negative correlation with degree days), whereas pubescent oak was more frequent on warmer sites at lower altitudes (positive correlation with degree days) at west-, east- and south-facing aspects, which tend to be warmer and dryer compared with north-facing aspects. This is in accordance with the results of Moser *et al.* (2010) on a nearby study site demonstrating that postfire Scots pine regeneration success was hindered on warm-dry sites at low altitudes, whereas broadleaved pioneer tree species were able to establish on the driest sites. These findings fully correspond with studies from Spain showing for Scots pine regeneration drought as a main mortality factor (Castro *et al.*, 2005) and a reduced postfire regeneration success (Vila-Cabrera *et al.*, 2012). The lower abundance of pubescent oak saplings at higher altitudes might also be caused by its high sensitivity to late frost (Thomas *et al.*, 2002). In addition, pubescent oak was slightly more frequent on steep slopes (positive correlation), which often feature higher run-off and generally more shallow soils.

In contrast to studies from southern Spain, where establishment of Scots pine seedlings was reduced under the canopy of Scots pine and increased on bare soils (Castro *et al.*, 2004), these two factors turned out to

be less important in the Valais (Supporting informations Table S2).

Beside site conditions, browsing by domestic animals and game is another important limitation for tree regeneration (e.g. Zamora *et al.*, 2001). Our results showed that the current browsing pressure on Scots pine is relatively low in the Valais (Fig. 5), which is probably due to the high availability of more attractive broadleaves and shrubs. Thus, Scots pine regeneration in the Valais was hindered less by grazing compared with degraded Mediterranean forests with predominantly thorny shrubs where Scots pine seedlings are generally more frequently browsed (e.g. Hodar *et al.*, 1998; Gomez *et al.*, 2001). By contrast, pubescent oak is more attractive for browsing compared with Scots pine (Fig. 5). Hence, browsing cannot explain the differences in sapling occurrence between Scots pine and pubescent oak. However, previous land-use practices might partly explain the more abundant regeneration of pubescent oak, as past forest management including intensive forest pasture (browsing) and litter raking (seed removal) created environmental conditions, which hindered regeneration of deciduous trees (Weber *et al.*, 2008b; Gimmi *et al.*, 2010). Thus, the abandonment of these practices had a positive effect on the regeneration of pubescent oak as reflected by its current expansion (Fig. 2, Table 3).

Vegetation shift

Our results of the forest inventory definitely demonstrate that Scots pine is still dominating on the landscape scale at the dry low elevation sites, whereas pubescent oak is generally not yet abundant in the overstorey and basically absent above 1200 m a.s.l. (Figs 2 and 3). But changes in land-use practices will generally result in an increase in oak regeneration, and future climatic changes might result in more frequent drought (Schär *et al.*, 2004) and subsequent increased Scots pine mortality. Hence, in the long run the Scots pine forests at lower altitudes are likely to develop towards pubescent oak forests (Gimmi *et al.*, 2010).

In particular, in the region of Visp the proposed vegetation shift is already well advanced: A century ago the forests consisted essentially only of Scots pine with some pubescent oak-shrubs outside the closed forest (Christ, 1920; Schmid, 1936). In contrast, pubescent oak and other broadleaves are currently dominating the forests below approximately 1000 m a.s.l. where only a few Scots pines have remained (Gimmi *et al.*, 2010).

The findings of our study demonstrate that there is a significant change going on in forest vegetation below 1000 m a.s.l. in the Valais. In other inner-Alpine Scots pine forests in Switzerland (Schilli *et al.*, 2008), Italy (Minerbi, 1993; Vertui & Tagliaferro, 1998), France (Thabeet *et al.*, 2009) and Austria (Cech & Wiesinger, 1996; Cech & Perny, 2000; Oberhuber, 2001) similar mortality processes have been reported or are currently progressing. Thus, we assume that the conditions analysed in the Valais are representative for many of the dry inner-Alpine valleys. But also outside the Alps drought-induced vegetation shifts were reported, e.g. for northern Spain (Penuelas & Filella, 2001; Lloret
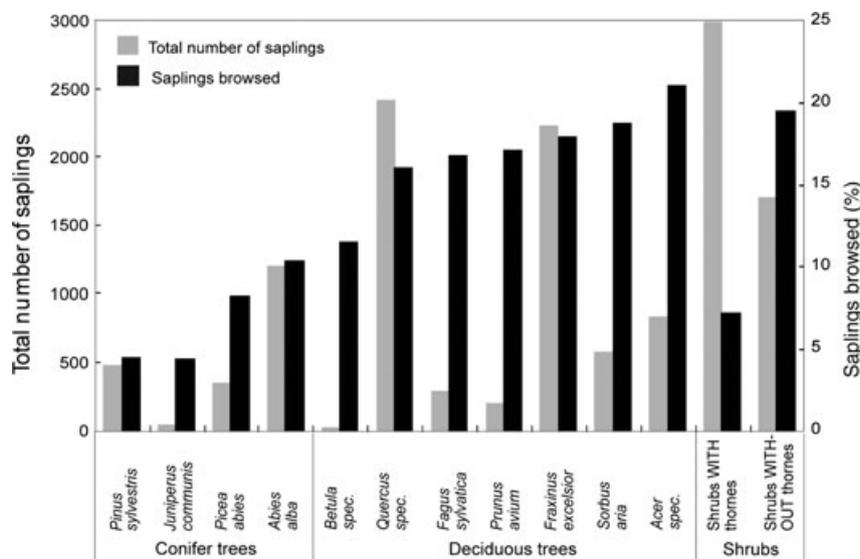

Fig. 5 Total number of saplings found on all sites (grey bars) and the percentage of browsing damage (black bars) of Scots pine and pubescent oak compared with different tree and shrub species (observations from 2002/2003).

et al., 2004), the Pyrenees (Galiano *et al.*, 2010) or for several regions in the United States (Allen & Breshears, 1998; Breshears *et al.*, 2005; Kelly & Goulden, 2008; Mueller *et al.*, 2005; van Mantgem *et al.*, 2009) and might gain in importance due to climate change (IPCC, 2007).

In conclusion, we revealed evidence of a vegetation shift in the Valais caused by increasing mortality after drought periods, a general decrease of Scots pine regeneration and an increasing regeneration success of pubescent oak. Hence, this is a clear indication that the vegetation shift was driven by both climate variability, with Scots pine mortality being affected by water shortage, and land-use change with increased stand competition aggravating the drought stress for Scots pine and with a stimulation of pubescent oak regeneration (Gimmi *et al.*, 2010).

Pubescent oak copes well with dry and warm conditions, and neither increased mortality rates nor a limitation of recruitment in response to drought have been observed so far. As pubescent oak is currently dominating the sapling bank in these dry forests in the Valais, the change from Scots pine forests to pubescent oak dominated forests seems to be inevitable at low elevations. However, there are indications that even the drought-tolerant pubescent oak may reach the limits of its physiological capacity in a drier future climate (Eilmann *et al.*, 2009). In addition, the extensive expansion of pubescent oak might generally increase the risk of species-specific biotic pests (Bale *et al.*, 2002). Hence, the long-term dynamics of these dry inner-Alpine forests remain open and so are the consequences for the concerned forest goods and services.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Model comparison of mortality models for Scots pine. Survival probabilities were calculated for 985 Scots pine in 137 plots with a generalized linear mixed-effects model using a binomial distribution (Eqn 1) and a logit-link function (Eqn 2).

Table S2. Model comparison of regeneration models for Scots pine. The generalized linear models were fitted to 193 plots using a negative binomial distribution (Eqn 3) and a log-link function (Eqn 4).

Table S3. Model comparison of regeneration models for pubescent oak. The generalized linear models were fitted to 193 plots using a negative binomial distribution (Eqn 3) and a log-link function (Eqn 4).

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