Ungulate herbivory modifies the effects of climate change on mountain forests

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Abstract Recent temperature observations suggest a general warming trend that may be causing the range of tree species to shift to higher latitudes and altitudes. Since biotic interactions such as herbivory can change tree species composition, it is important to understand their contribution to vegetation changes triggered by climate change. To investigate the response of forests to climate change and herbivory by wild ungulates, we used the forest gap model ForClim v2.9.6 and simulated forest development in three climatically different valleys in the Swiss Alps. We used altitudinal transects on contrasting slopes covering a wide range of forest types from the cold (upper) to the dry (lower) treeline. This allowed us to investigate (1) altitudinal range shifts in response to climate change, (2) the consequences for tree species composition, and (3) the combined effect of climate change and ungulate herbivory. We found that ungulate herbivory changed species composition and that both basal area and stem numbers decreased with increasing herbivory intensity. Tree species responded differently to the change in climate, and their ranges did not change concurrently, thus causing a succession to new stand types. While climate change partially compensated for the reductions in basal area caused by ungulate herbivory, the combined effect of these two agents on the mix of the dominant species and forest type was non-compensatory, as browsing selectively excluded species from establishing or reaching dominance and altered competition patterns, particularly for light. We conclude that there is an urgent need for adaptive forest management strategies that address the joint effects of climate change and ungulate herbivory.

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1 Introduction

The general anthropogenic warming trend (IPCC 2007) may be causing tree species to shift to higher latitudes and altitudes (Davis and Shaw 2001; Theurillat and Guisan 2001; Walther et al. 2002). It is expected that some previously unforested regions at high latitudes and altitudes (cold treeline) may become more suitable for tree growth, whereas some low-latitude and low-altitude areas may not sustain forest cover any more due to an increase in droughts (Cairns et al. 2007; Gehrig-Fasel et al. 2007). However, the range shifts of tree species depend, in addition to climate, on various other natural and anthropogenic factors such as seed availability, resource availability and land use (Walther et al. 2002; Thuiller et al. 2005). Feeding on aboveground plant tissue by wild ungulates such as deer and reindeer has been identified as an important driver for the local position of treelines in mountain and high-latitude ecosystems (e.g., Kullman 2001; Grace et al. 2002; Moen et al. 2004). In these, but also in other forest ecosystems, ungulate herbivores can prevent tree establishment entirely or modify the tree species mix and thus influence long-term forest development (Augustine and McNaughton 1998; Côté et al. 2004).

Forest development in response to changes in climate has been explored in a wide range of modeling studies (e.g., Wallentin et al. 2008; Bugmann 2003; Lexer et al. 2002). However, the role of ungulate herbivores as a driver of forest succession in response to a changing climate has, to our knowledge, not been addressed in modeling studies. We aimed to fill this gap by using the forest gap model ForClim (Didion et al. 2009c) to simulate forest development under climate change and different ungulate browsing pressure.

The objective of this study was to examine the combined effects of climate change and ungulate browsing along elevation transects. We selected three climatically different valleys in the Swiss Alps to investigate (1) altitudinal range shifts in response to climate change, (2) the consequences for tree species composition, and (3) the combined effect of climate change and ungulate browsing.

2 Material and methods

2.1 Study area

We selected transects across three valleys in climatically different regions of the Swiss Alps: (1) Western Central Alps (dry, warm summers and cold winters); (2) Northern Central Alps (moist, cool summers and cold winters); and (3) Southern Alps (wet, warm summers and mild winters). All transects ran from a predominantly south-facing to a predominantly north-facing slope via the valley bottom.

2.1.1 Western Central Alps

The Anniviers valley (*Val d'Anniviers*) is a side valley of the Rhone River valley in the Valais, Western Central Alps. The catchment is ca. 255 km^2 in size and ranges from 500 to 4,400 m a.s.l. The transect crosses the valley in a north-east to south-west direction from a small peak near Mt. Illhorn (ca. 2,300 m; 46°15′ N, 7°36′ E) to Mt. La Brinta (ca. 2,600 m; 46°13′ N, 7°32′ E) via the village of Fang in the valley bottom (ca. 850 m). This valley is characterized by a continental climate with cold winters and

relatively dry and warm summers (Table 1). In the valley bottom where precipitation is low (i.e., annually ca. 500–700 mm) and the dry treeline is approached, current forests are composed mainly of drought-resistant species, such as *Quercus* spp. and *Pinus sylvestris* (Lock et al. 2003). With increasing elevation, the dominant species change to *Picea abies* (high-montane to subalpine, ca. 1,000–1,800 m) and further up to *Larix deciduas–Pinus cembra* (upper subalpine ca. 1,800 m to treeline ca. 2,500 m; Gödickemeier 1998; Ott et al. 1997). The transition between *Pinus* and *Picea* forests is found around 200–400 m lower on the colder north-facing slope than on the warmer south-facing slope (Ott et al. 1997).

2.1.2 Northern Central Alps

The Tuors valley (*Val Tuors*) is located in the transition zone between the northern pre-alpine and the central alpine area in Graubünden. The catchment is ca. 57 km^2 in size and ranges from 1,350 to 3,350 m a.s.l. in altitude. The transect runs in a straight north-south direction from Piz Valmela (ca. 2,700 m; 46°39′ N, 9°47′ E) via the village of Tuors Davant in the valley of the Tuors (ca. 1,700 m) to Piz Darlux (ca. 2,600 m; 46°37′ N, 9°47′ E). Cold winters with high amounts of snow (Table 1) restrict the species diversity and successional pathways in the montane and subalpine forests (Ott et al. 1997). The dominant species change with elevation from *P. abies* at the high-montane and lower subalpine region (i.e., up to ca. 2,000 m) of the valley (Didion et al. 2009b; Ott et al. 1997) to *L. decidua* and *P. cembra* in the upper subalpine level up to treeline (ca. 2,500 m; Ott et al. 1997).

2.1.3 Southern Alps

The Maggia valley (*Valle Maggia*) is located in the northern part of the Ticino in the Southern Swiss Alps. The catchment covers ca. 574 km^2 and ranges from 200 to 3,200 m a.s.l. The transect runs in a north–south direction from Piz Spluga (ca. 2,200 m; 46°19′ N, 8°39′ E) via the Maggia River (ca. 400 m) to Piz Güi (ca. 2,200 m;

Table 1 Long-term mean seasonal temperature (°C) and precipitation sum (cm) of the current climate (1961–2000) and mean anomalies (°C and % precipitation, respectively) for future steady state climate (cf. Section 2.3.2)

	Temperature				Precipitation			
	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
Anniviers valley								
800 m	8.0	16.7	8.6	−0.2	15.5	19.0	17.2	19.1
2650 m	−3.6	5.5	0.3	−7.2	26.8	33.5	26.0	25.9
Anomalies	+4.1	+5.9	+4.8	+3.6	−6.3	−15.7	−8.3	−1.4
Tuors valley								
1650 m	1.7	10.8	3.8	−5.1	21.4	36.7	25.5	15.9
2700 m	−4.7	4.7	−1.1	−9.6	25.8	44.0	29.3	21.0
Anomalies	+3.9	+5.1	+4.7	+3.6	+0.4	−10.0	−3.0	+4.8
Maggia valley								
350 m	11.0	19.7	11.3	2.5	47.8	49.9	60.1	22.7
2200 m	−1.1	8.2	2.2	−5.7	60.8	57.9	67.1	37.5
Anomalies	+4.1	+5.3	+4.6	+3.8	+5.1	−27.6	+3.3	+11.9

Data were presented for the lowest and highest point of each transect

46°15′ N, 8°37′ E). The climate in this part of the Southern Alps is characterized by warm summers, mild winters and high annual precipitation (Table 1) of uneven distribution including heavy rainfall events interrupted by extended periods of drought in spring and summer. This is characteristic of the so-called insubrian region; it allows for a diverse mix of deciduous tree species at low to medium elevations (Gobet et al. 2000). In the colline belt below ca. 700 m, *Castanea sativa*, *Fagus sylvatica* and *Quercus* spp. are expected to dominate (Ott et al. 1997). The montane belt (ca. 700–1,600 m) is dominated by *F. sylvatica* at the lower and *P. abies* together with *Abies alba* at the upper level (Didion et al. 2009b; Ott et al. 1997). The subalpine region between ca. 1,600 and 2,100 m is dominated mainly by *P. abies* and *L. decidua* (Ott et al. 1997).

2.2 Gap model ForClim

The gap model ForClim simulates the establishment, growth, and mortality of trees on multiple small forest patches to derive stand-scale dynamics (Bugmann 1996). Tree growth is specified as a species-specific maximum that is reduced to a realized growth rate by taking into account key limiting factors (temperature, drought, light availability, and nitrogen availability). Trees are established as saplings with a diameter at breast height (dbh) of 1.27 cm, whereby the number of new trees is a function of species-specific responses to winter temperature, light availability, growing degree-days, and browsing pressure (Bugmann 1994). ForClim performed well in several studies comparing simulated forests with local, site specific forest data (Didion et al. 2009b, c; Risch et al. 2005), and also with potential natural vegetation along large temperature and precipitation gradients within and between various mountain regions (Didion et al. 2009c; Bugmann and Solomon 2000; Shao et al. 2001). As input the model requires monthly means and standard deviations of temperature and precipitation as well as their cross-correlation (Bugmann 1994).

The model allows to account for the effect of slope and aspect on the amount of incident radiation, which affects evapotranspiration (cf. Section 3.3.3 in Bugmann 1994 and references therein). The parameter $kSlAsp$ [−2..+2] is used to modify potential evapotranspiration (PET; Bugmann 1994, eq.[3.74]) by decreasing PET by a maximum of 12.5% on steep north-facing slopes ($kSlAsp = −2$) and by increasing PET by a maximum of 25% on steep south-facing slopes ($kSlAsp = +2$).

In our study, we revised ForClim model version 2.9.5 (Didion 2009; Didion et al. 2009a) by refining the relationship between browsing pressure and browsing-induced mortality. This resulted in the new model version 2.9.6 (for a detailed description see Appendix I and III in Didion 2009). In the new model version, the relationship between browsing pressure ($kBrPr$) and browsing-induced mortality of seedlings and saplings ($kBrP$) is

$$kBrP = \left(\frac{kBrPr}{100}\right)^{a_{\text{kBrow}}} \tag{1}$$

where $kBrPr$ ranges from 0% (no browsing) to 100% (heavy browsing where no sapling establishment is possible) and a_{kBrow} is the exponent for five levels of tree species browsing sensitivity ($kBrow = [1..5]$). The parameter $kBrow$ is a measure of the browsing related survival probability of seedlings and saplings before reaching a dbh of 1.27 cm, which is the size at which trees establish in ForClim. This corresponds

to a tree height of at least 1.40 m, which is above the browsing limit of ungulates in the European Alps (Eiberle and Nigg 1987). *kBrow* was revised based on an extensive literature search and expert opinion, and considers (a) the browsing preference of ungulates (*BPU*), (b) the rate of height growth of seedlings (*RHG*), (c) the ability of a tree species to compensate for tissue losses (*CA*), and (d) the survival probability after browsing (*SP*, Table 2; cf. Appendix III in Didion 2009). The exponent a_{kBrow} (Eq. 1) was set to 4, 2, 1, 0.5 and 0.25 for *kBrow* values of 1 to 5, respectively (Fig. 1; for details see Appendix III in Didion 2009).
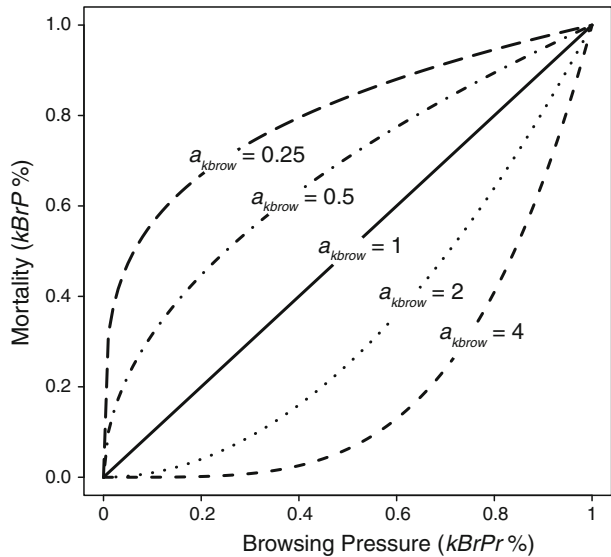
The model includes 30 European tree species (Fig. 1, Table 2) and assumes unlimited seed availability of all species. As *C. sativa* is mostly absent in the northern part of the Swiss Alps (Brassel and Brändli 1999; EAFV and BFL 1988), we assumed that this species will remain absent due to its heavy seeds. Thus, we excluded *C. sativa* from the species pool at the two transects in the Western (i.e., Anniviers valley)

Table 2 Species-specific sensitivity to browsing: Estimations of "*BPU*": browsing preference by ungulates with 1 (unpalatable) and 5 (highly palatable and preferred browsed)

Species	BPU	RHG	CA	SP	μ	kBrow
Abies alba	5	4	5	4	4.60	5
Larix decidua	3	2	3	5	3.20	3
Picea abies	1	3	4	5	2.80	2
Pinus cembra	3	5	4	4	3.80	4
Pinus montana	1	4	4	5	3.00	3
Pinus sylvestris	2	3	4	5	3.20	3
Taxus baccata	5	5	5	3	4.60	5
Acer campestre	5	3	3	2	3.60	4
Acer platanoides	5	2	3	3	3.60	4
Acer pseudoplatanus	5	2	3	3	3.60	4
Alnus glutinosa	2	1	3	1	1.80	1
Alnus incana	2	1	3	1	1.80	1
Alnus viridis	2	1	3	1	1.80	1
Betula pendula	2	1	1	2	1.60	1
Carpinus betulus	4	2	2	1	2.60	2
Castanea sativa	1	3	1	1	1.40	1
Corylus avellana	4	1	1	1	2.20	2
Fagus sylvatica	3	3	4	4	3.40	3
Fraxinus excelsior	5	2	3	2	3.40	3
Populus nigra	4	1	3	1	2.60	2
Populus tremula	4	1	3	1	2.60	2
Quercus petraea	4	2	3	5	3.60	4
Quercus pubescens	4	3	3	4	3.60	4
Quercus robur	4	2	3	5	3.60	4
Salix alba	5	1	1	1	2.60	2
Sorbus aria	5	4	3	3	4.00	4
Sorbus aucuparia	5	2	3	3	3.60	4
Tilia cordata	3	3	2	3	2.80	2
Tilia platyphyllos	3	3	2	3	2.80	2
Ulmus glabra	5	2	2	3	3.40	3

RHG rate of height growth with 1 (fast growing) and 5 (slow growing); *CA* compensation ability regarding tissue losses with 1 (high) and 5 (low); *SP* survival probability after browsing with 1 (high) and 5 (low); μ weighted mean of BPU (double weight), RHG, CA and SP; *kBrow* derived from μ as used in the current ForClim v2.9.6. For details see Appendix III Didion (2009)

and Eastern (i.e., Tuors valley) Central Alps. However, in the Southern Alps (i.e.,
Maggia valley) *C. sativa* is a common tree species and was therefore included in the
species pool for the simulations. Since the three *Quercus* species that are included
in the model, i.e., *Quercus petraea*, *Quercus pubescens* and *Quercus robur*, have
similar traits and are known to hybridize (Aas and Friedrich 1991), we subsumed
them under *Quercus* spp. in the presentation of the results. Similarly, we combined
Acer campestre and *Acer platanoides* as *Acer* spp.

2.3 Climate data

2.3.1 Current climate

We obtained monthly data for mean temperature and precipitation sum from the
database of the Land Use Dynamics Research Group at the Swiss Federal Institute
for Forest, Snow and Landscape Research. The database contains climate data for
the period from 1960 to 2006 interpolated to a 1-ha grid across Switzerland based
on the DAYMET model (Thornton et al. 1997). In order to derive temperature
and precipitation data representing the current climate along each valley transect,
we used the following procedure: First we selected from the respective catchment
area those 1-ha grid cells that were within the altitudinal range of the transect
and aggregated them into 50-m elevation bands. This resulted in a dataset of daily
temperature and precipitation sum representative for each 50-m elevation band. We
then calculated for each of those elevation bands the long-term monthly means
(1961–2006), standard deviations and cross-correlations of mean temperature and
precipitation sum (Fig. 2, Table 1). This approach eliminated potential inaccuracies
occurring when single grid cells (i.e., only those intersected by a transect) are chosen
from interpolated climate data. Due to differences in topography, the transects in the
three valleys comprised different numbers of 50-m elevation bands: 68 bands (leading
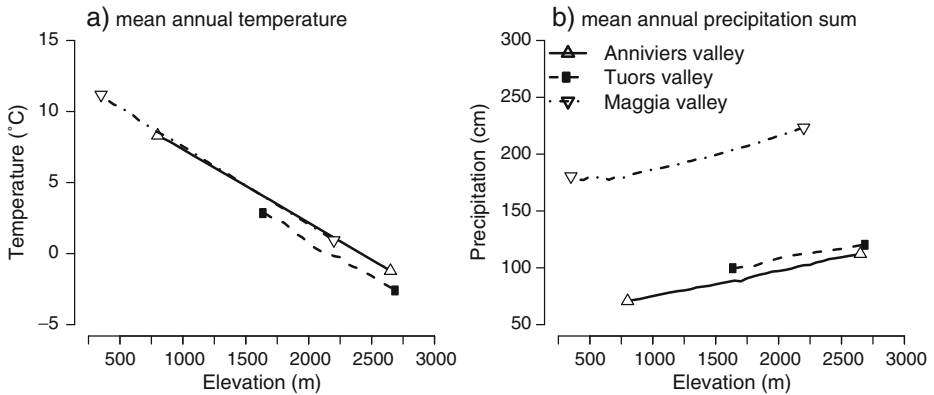
Fig. 2 Long-term annual mean temperature and precipitation sum by 50-m elevation bands in the three examined catchments based on interpolated climate data from 1960 to 2006 obtained from the Land Use Dynamics Research Group at the Swiss Federal Institute for Forest, Snow and Landscape Research

to simulation plots) for the transect in the Anniviers valley, 42 in the Tuors valley and 75 in the Maggia valley.

To represent the change in aspect and slope along the transects, we used the model parameter *kSlAsp* (cf. Section 2.2). Using the different number of 50-m elevation bands on the north- and south-facing slopes, we linearly interpolated the range of *kSlAsp* on each slope from north facing top (*kSlAsp* = −2) passing the valley bottom (*kSlAsp* = 0) to the south-facing top (*kSlAsp* = +2).

2.3.2 Future climate

To represent the anticipated change in climate in each of the three study regions, we used the regionalized climate change projections of the Institute for Atmospheric and Climate Science, ETH Zürich provided within the ENSEMBLES project (Hewitt and Griggs 2004; http://ensembles-eu.metoffice.com). For this dataset, projected climate change for the A1B scenario of the IPCC AR4 (IPCC 2007) was regionalized to a 10 × 10 km grid, and transient climate change was simulated until the year 2099.

We derived climate change scenarios for each transect based on the data from the nine 10 × 10 km cells of the ENSEMBLES dataset that covered and surrounded each study area. We used the periods from 1961 to 1990 as baseline and the years 2075 to 2099 as representative years for the future climate and calculated the following climate anomalies based on the average monthly temperature and precipitation sum of these two periods:

1. Temperature anomalies for the seasonal mean (Table 1) and the standard deviation of the seasonal mean using the absolute difference between baseline and future temperatures;
2. Seasonal precipitation anomalies as the relative difference (percent; Table 1) between the baseline and the future precipitation both for the mean and the standard deviation;

3. The anomalies of the monthly cross-correlations using the absolute difference
    between the corresponding values for the two periods (baseline and future
    climate).

The anomalies of the means, standard deviations, and cross-correlations were added
(in case of absolute differences) and multiplied (in case of relative differences) to the
current climate (Section 2.3.1), and the weather generator of ForClim (cf. Bugmann
1996) was used to derive realizations of a future climate in the plots along the
three transects. As future climate is typically not projected by GCMs post-2100,
we assumed here that it remains constant after 2100, thus simulating the long-term
impact of the generally predicted warming trend.

2.4 Simulation experiments

Forest succession for a total of 6,100 years was simulated for each plot along the three
transects (Section 2.3.1), as follows:

2.4.1 Spin-up for 3,000 years under current climate

Starting from bare ground, forest succession was simulated for 3,000 years under
current climate to ensure that the simulated forest was in equilibrium with climate
prior to imposing scenarios of changes in browsing and climate. The browsing
pressure (*kBrPr*) was assumed to amount to 20% (cf. Eq. 1, Fig. 1), which represents
a moderate intensity that approximates an average browsing intensity in Swiss forests
(Didion et al. 2009c). This spin-up simulation was used for all of the following
scenarios in order to have identical starting conditions for the browsing and climate
change scenarios.

2.4.2 Browsing and climate change scenarios

Following the spin-up, browsing pressure (*kBrPr*) was varied in a one-step fashion
using three settings:

•   Continuation of the 20% for a "moderate" browsing intensity;
•   80% for an "elevated" browsing intensity to approximate conditions in Swiss
    forests where ungulate population size is above average (Senn and Suter 2003);
    and
•   95% for a "high" browsing intensity to illustrate effect of further increasing
    ungulate populations (Senn and Suter 2003).

According to the aim of current ungulate management practices to maintain animal
populations constant (Senn and Suter 2003), we assumed constant browsing intensity
over time.

    In order to separate the effects of browsing and climate change, one set of
simulations was done only varying browsing pressure but using current climate
conditions. A second set of simulations was performed by varying browsing pressure
in combination with a change in climate.

    We assumed the changes in climate to occur in a linear fashion, whereby the
transient climate change was simulated over a period of 100 years, i.e., starting
after the spin-up (year 3000) and reaching the new steady climate (future climate,
Section 2.3.2) in the simulation year 3100. The simulations were then continued with

this new climate state for another 3,000 years to obtain forests that are in equilibrium with this specific realization of future climate.

3 Results

The results presented here for simulated forests under current and future climatic conditions refer to the respective equilibrium conditions. Generally, the model produced an accurate representation of the expected forest types for the current climate (cf. Section 2.1; Figs. 3a, 5a, 6a). Exceptions were the lack of the *P. abies* belt on the south-facing slope of the Anniviers (Fig. 3a, Section 3.1.1) and the underestimation of *Quercus spp*. in the Maggia valley (Fig. 6a, Section 3.3.1). Our estimations of basal area, stem numbers and species compositions are not predictions or projections, but represent a few possible scenarios of forest development, assuming the three different browsing scenarios and one realization of climate change.

3.1 Western Central Alps

3.1.1 Current climate

Based on the control run with no change in browsing and climate, drought-resistant *P. sylvestris* and *Quercus* spp. dominated the forests at the valley bottom of the Val d'Anniviers (basal area [BA] ca. 20 to 25 m^2/ha, Fig. 3a) and up to the montane zone of the south-facing slope (BA ca. 25 to 30 m^2/ha, Fig. 3a). On the north-facing slope, *Quercus* spp. and *P. sylvestris* were replaced with increasing elevation by deciduous species such as *F. sylvatica* intermixed with *A. alba* (BA ca. 30 m^2/ha, Fig. 3a), and further up by *P. abies*, which dominated the high-montane and subalpine plots up to ca. 2200 m a.s.l. (BA ca. 35 m^2/ha, Fig. 3a). On both slopes, *P. cembra* and to a lesser extent *L. decidua* formed the forests at higher elevations (BA < 1 to ca. 20 m^2/ha, Fig. 3a).

3.1.2 Effect of changes in browsing

On many plots along the transect, changes in browsing pressure led to shifts in the relative and absolute abundance of the dominant and sub-dominant species (Fig. 3b, c), whereby *A. alba*, *F. sylvatica* and *P. cembra* were affected most. The resulting loss in basal area was not uniform (i.e., 1–15 m^2/ha, Fig. 3b, c) and it was only partially compensated by other species. Interestingly, although *Quercus* spp. are sensitive to browsing (*kBrow* = 4, Table 2), they remained part of the forest community even under high browsing pressure. As light-demanding species, they profited from the increased light availability in the intensively browsed forests (Fig. 3c).

3.1.3 Effect of changes in climate

Keeping browsing pressure constant at a moderate intensity but changing the climate resulted in a collapse of the forest in the valley bottom (Fig. 4c), where only *P. sylvestris* was able to survive in some plots with a resulting drop in basal area from >20 to <5 m^2/ha (Fig. 3d). Compared to conditions under current climate, climate change forced an upslope shift of species ranges (Fig. 3d): (1) on the south-facing slope, the *Quercus* spp.–*P. sylvestris* forests were found at much higher elevations (up to upper current treeline); (2) on the north-facing slope *P. abies* with some *A. alba*, both typical species of the current montane level (cf. Fig. 3a) were found at the
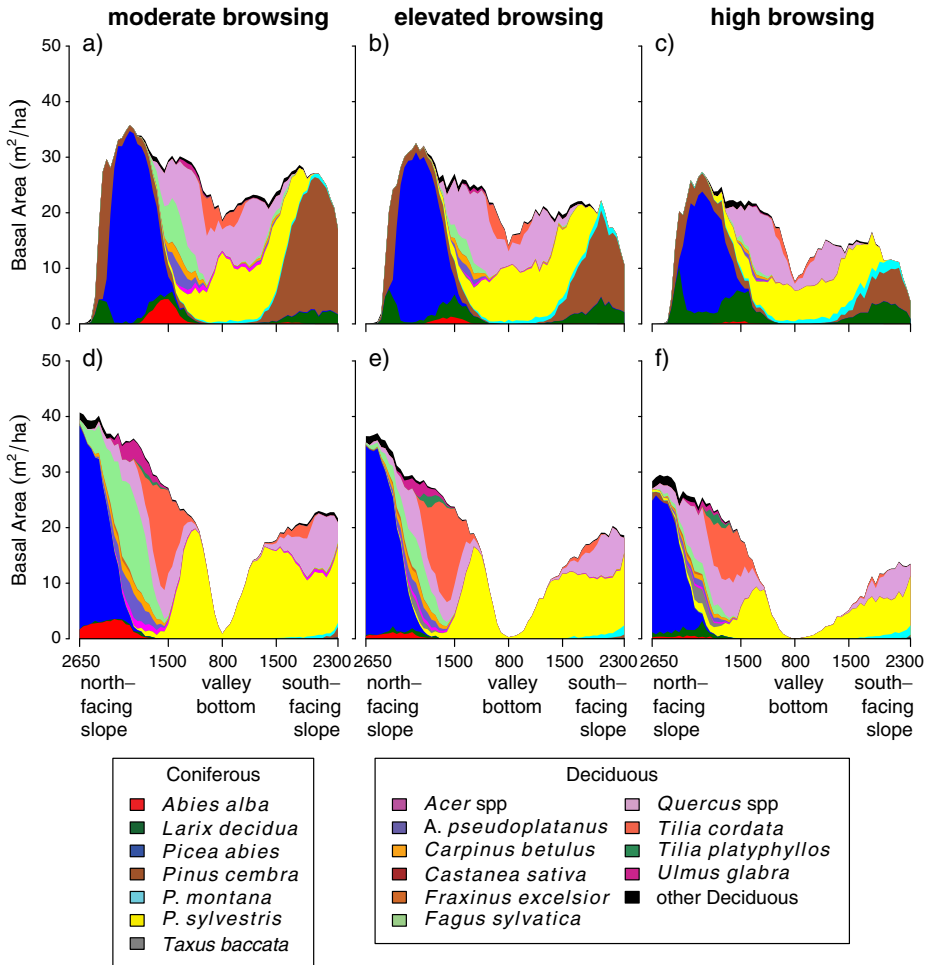
Fig. 3 Basal area along the transect in the Anniviers valley (dry and continental climate) after 3,000 years of spin-up under current climate and moderate browsing pressure (*kBrPr*) for: **a–c** additional 3,100 years under current climate for three different browsing pressures and; **d–f** after 100 years of climate transition +3,000 years under the new climate for three different browsing pressures. "Other deciduous" include: *Alnus glutinosa*, *A. incana*, *A. viridis*, *Betula pendula*, *Populus nigra*, *P. tremula*, *Salix alba*, *Sorbus aria*, *S. aucuparia*. The graph displays the results of 68 independent simulations for the elevation plots along the transect (cf. Section 2.3)

elevation of the current treeline and above; (3) due to this increase of *P. abies* and *A. alba*, species forming the current upper treeline (*P. cembra* and *L. decidua*) declined; and (4) on the north-facing slope new forest types, dominated by *Tilia cordata* and *Quercus* spp., formed in what is currently the lower montane belt.

3.1.4 Effect of changes in browsing and climate

An increase in browsing pressure in addition to climate change led again to a strong reduction in *A. alba* and *F. sylvatica* but not of *Quercus* spp. (Fig. 3e, f).

Furthermore, browsing exacerbated the collapse of the forests in the valley bottom (Fig. 3e, f and 4c, d). Elevated browsing pressure delayed forest development above current treeline on the north-facing slope, so that at the end of the climate transition (100 years after spin-up), simulated basal area was about twice as high under moderate browsing (Fig. 4e) compared to elevated browsing (Fig. 4f). On the south-facing slope, the climate change-induced transition from the current subalpine *L. decidua*–*P. cembra* forest to a *Quercus* spp.–*P. sylvestris* forest took place over several centuries as *P. cembra* was gradually replaced by new species irrespective of the browsing scenario (Fig. 4a, b).
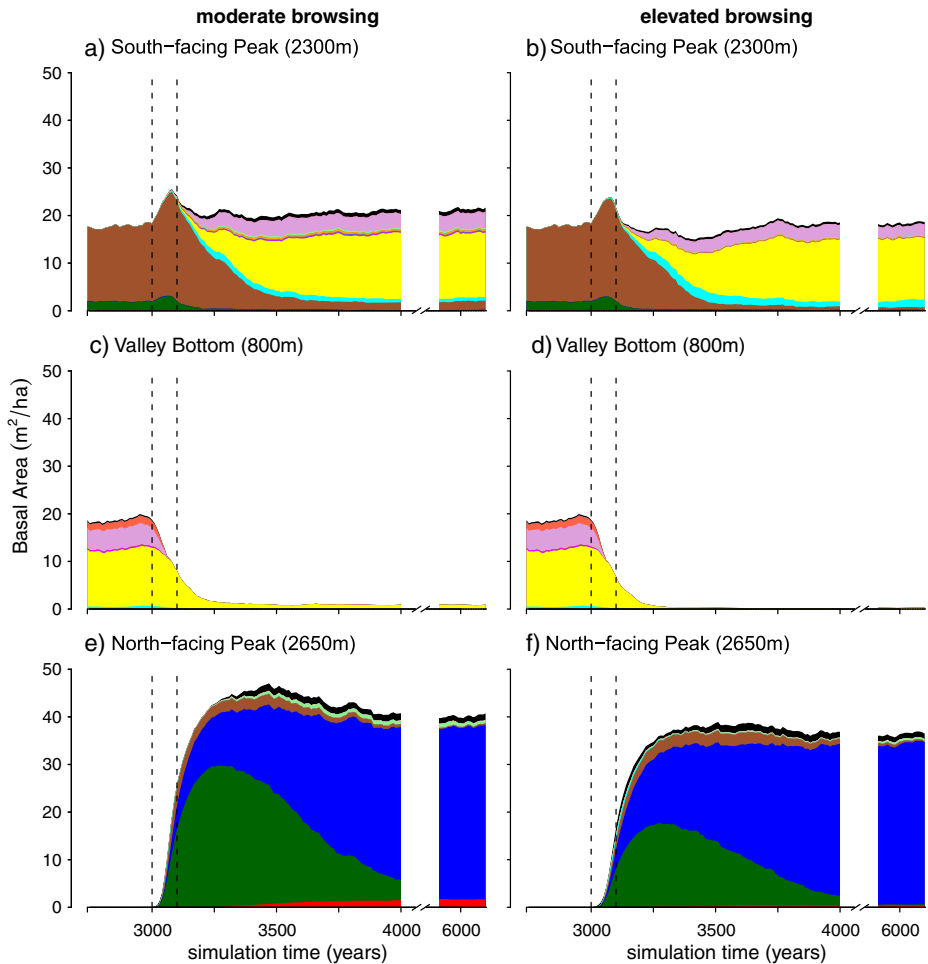

Fig. 4 Forest succession over time in the Anniviers valley for moderate ($kBrPr = 20\%$) and elevated browsing pressure ($kBrPr = 80\%$) on the two highest plots on the south-facing (**a**, **b**) and the north-facing slope (**e**, **f**), and for the lowest plot in the valley bottom (**c**, **d**). *Dotted lines* indicate the end of the spin-up period under current climate coinciding with the start of the climate transition (i.e. first line at simulation year 3000) and end of the climate transition period in simulation year 3100 (*second line*). Species legend as in Fig. 3

Total stem numbers differed by a factor of more than two between moderate and elevated browsing pressure at the south-facing slope and in the valley bottom (Table 3). Model behavior near the north-facing peak was different, as it was above treeline under current climate; although basal area was developing at a lower rate under high browsing pressure (Fig. 4e, f), stem number was not affected by browsing after 100 years of climate transition (Table 3). The 115 trees per hectare that were estimated by the model for the north-facing peak (Table 3) are an artifact of the model simulations due to the representation of the establishment process: small trees are established as soon as climate permits, even though they may not be able to grow; their total basal area amounted to merely 0.03 m^2/ha.

3.2 Eastern Central Alps

3.2.1 Current climate

In the Tuors valley, forests did not grow along the whole transect, as the cold treeline was reached on both the south-facing and the north-facing slopes at ca. 2,400 m (Fig. 5a). Treeline forests were formed by *L. decidua* and *P. cembra*, while *P. abies* dominated the forests towards the valley bottom (Fig. 5a). Basal area reached a maximum of approximately 38 m^2/ha in the valley bottom and gradually decreased until treeline was reached (Fig. 5a). Similarly to the Anniviers valley, trees were able to establish above treeline (Table 3), but unable to grow.

3.2.2 Effect of changes in browsing

Higher browsing pressure led to a ca. 25% decrease in the basal area of the dominant *P. abies* (Fig. 5c). The concurrent increase in available light resulted in a considerable 50% gain in basal area of *P. cembra* and *L. deciduas*, which are more light-demanding

Table 3 Total stem numbers per hectare on the two highest plots on the south-facing and north-facing slopes and on the plot in the valley bottom for all three transects under moderate (i.e., 20%) and elevated (i.e., 80%) browsing pressure

Year	3000	3100		6100	
Browsing pressure	Moderate	Moderate	Elevated	Moderate	Elevated
Anniviers valley					
South-facing (2,249 m)	504	905	435	1671	802
Valley (854 m)	1820	525	215	246	73
North-facing (2,564 m)	115[a]	1213	1160	838	603
Tuors valley					
South-facing (2,715 m)	9[a]	1776	1076	810	561
Valley (1,717 m)	836	1713	1002	2006	1318
North-facing (2,540 m)	20[a]	1666	1174	707	547
Maggia valley					
South-facing (2,091 m)	807	961	682	1736	1108
Valley (367 m)	2128	2161	1312	1819	986
North-facing (2,061 m)	748	964	645	1698	1073

Data are presented for current climate (i.e., year 3000), after the transition to the new climate (i.e., year 3100) and after additional 3,000 years under the future climate (i.e., year 6100)

[a] Plots above treeline where trees can establish but not persist, which resulted in the reported numbers of very small stem
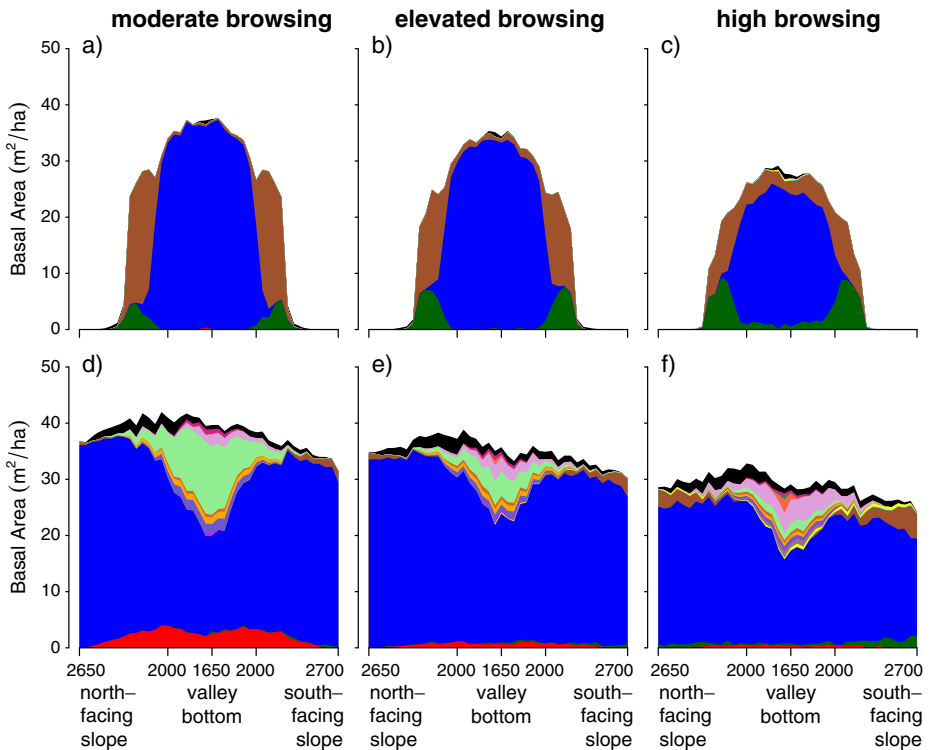
Fig. 5 Transect in the Tuors valley (moist and cold climate); for details and species legend see Fig. 3. The graph displays the results of 42 independent simulations for the elevation plots along the transect (cf. Section 2.3)

than *P. abies* (Fig. 5b, c), thus leading to a co-dominance by *P. cembra* at lower elevations.

3.2.3 Effect of changes in climate

Climate change caused a shift of tree species by approximately 1,000 m upslope. The forest that developed at current treeline (i.e., ca. 2,400 m, Fig. 5a) is typical for forests found today at the transition from high-montane to subalpine conditions, i.e., dominance of *P. abies* with some *P. cembra* (Fig. 5a, d). Under the changed climate, forests covered the entire transect, as the cold treeline moved beyond the highest elevations of the transect. In the valley bottom, forest types developed that were dominated by *F. sylvatica* and *P. abies* (Fig. 5d). The temporal development of forests above current treeline under the assumed change in climate proceeded in a similar way as on the north-facing peak in the Anniviers valley (Fig. 4e), moving through an early-successional *L. decidua* forest to dominance by *P. abies* interspersed with *P. cembra* trees (results not shown). Below ca. 2,500 m, deciduous species including *F. sylvatica*, *A. pseudoplatanus*, *Quercus* spp., and *T. cordata* together with *A. alba* started to replace *P. abies* with the onset of climate change.

3.2.4 Effect of changes in browsing and climate

Browsing pressure had a strong influence on the change in tree species composition following climate change. The increase in browsing pressure led to a decrease of *F. sylvatica* (Fig. 5e, f). Additionally, the abundance of browsing-sensitive but relatively shade-tolerant tree species such as *A. alba* and *A. pseudoplatanus* was reduced strongly, whereas the browsing-sensitive but more light-demanding *Quercus* spp. and *P. cembra* gained importance with increasing browsing pressure (Fig. 5e, f). An increase in browsing pressure from a moderate to a high level led to a reduction in stem numbers by ca. 30% (cf. Table 3).

3.3 Southern Alps

3.3.1 Current climate

Under current climate the simulated subalpine *P. abies* forest in the Maggia valley extended down to ca. 1,700 m on both slopes (Fig. 6a). With decreasing elevation, the forest changed gradually to an *A. alba–F. sylvatica–P. abies* forest, and eventually to a deciduous forest dominated by *F. sylvatica*, *C. sativa*, *A. pseudoplatanus*, *Tilia*
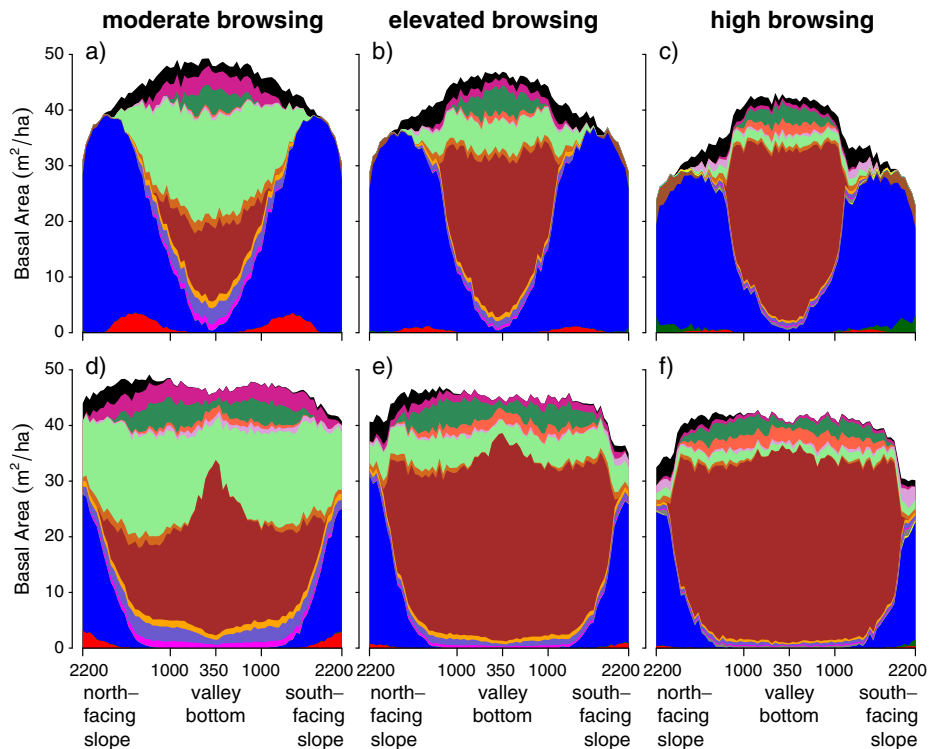

Fig. 6 Transect in the Maggia valley (moist and warm climate); for details and species legend see Fig. 3. The graph displays the results of 75 independent simulations for the elevation plots along the transect (cf. Section 2.3)

platyphyllos and *Ulmus glabra* at elevations below ca. 1,000 m (Fig. 6a). In the model, favorable climatic conditions allowed the establishment of a forest with a total basal area ranging between approximately 30 m^2/ha at the highest elevations to approximately 50 m^2/ha in the valley bottom (Fig. 6a).

3.3.2 Effect of changes in browsing

Leaving climate constant while increasing browsing pressure converted the mixed deciduous forests in the valley bottom to stands dominated by *C. sativa* below ca. 1,000 m. At higher elevations, *P. cembra* became a more abundant species (Fig. 6b, c). *A. alba*, *F. sylvatica*, *A. pseudoplatanus* and *U. glabra* declined with an increase in browsing pressure. The effect of a changing browsing pressure was not linear as the increase from moderate to elevated browsing resulted in an average decrease of basal area by 3 m^2/ha (or 7%), while an increase from elevated to high browsing induced an average basal area decrease by 5.5 m^2/ha (or 14%).

3.3.3 Effect of changes in climate

Similar to the results for the Tuors valley, climate change led to an upslope shift of tree species by approximately 1,000 m. This species shift resulted in a replacement of the former *P. abies* forest by an *A. alba–F. sylvatica–P. abies* forest at the highest plots and below by a deciduous forest dominated by *F. sylvatica* and *C. sativa*, intermixed with *Acer* spp., *A. pseudoplatanus*, *Carpinus betulus*, *Fraxinus excelsior*, *T. platyphyllos*, and *U. glabra* (Fig. 6d). Furthermore, climatic change resulted in an increase in basal area at these elevations (Fig. 6d). In the valley bottom, *C. sativa* replaced *F. sylvatica* as the dominant species (Fig. 6d).

3.3.4 Effect of changes in browsing and climate

Similar to the simulations with an elevated browsing pressure alone (Fig. 6c), combining higher browsing pressure with climate change resulted in a more pronounced dominance of *C. sativa* leading to almost pure *C. sativa* stands (Fig. 6e, f), whereby *C. sativa* reached higher elevations (Fig. 6c, f). Plots at elevations higher than ca. 2,000 m were an interesting exception regardless of the level of browsing pressure. At these elevations *C. sativa* growth was strongly limited due to low winter temperature and low degree-day sums. On these plots, the decrease of *F. sylvatica* due to the increase in browsing was not compensated by other species, which resulted in a reduction of total basal area (Fig. 6e, f).

3.4 Common pattern

With increasing browsing pressure, basal area decreased (Figs. 3, 4, 5 and 6), and so did total stem numbers (Table 3). Generally, the effect of browsing was not linear; the decrease in basal area was typically stronger in response to a change from elevated to high browsing pressure (i.e., average ca. 14–40% depending on the study region) than from moderate to elevated browsing pressure (i.e., average ca. 7–25% depending on the study region). Along the transects the impact of browsing varied depending on the prevalent species composition and the respective species' sensitivity to browsing. In all three valleys, browsing pressure led to a reduction of the abundance of *A. alba* and *F. sylvatica*, while interestingly some browsing-sensitive

but more light-demanding species such as *P. cembra* and *Quercus* spp. did not suffer correspondingly.

Climate change led to an upslope shift of species and of the cold treeline. In the valley bottom the current forest types were substituted by deciduous trees in the two valleys with moist and wet climate and non-forest vegetation in the dry Anniviers valley. Furthermore, climate change resulted in the formation of new forest types along all transects (Figs. 3, 5 and 6).

Browsing partially counteracted the effects of climate change, for example by retarding forest development at the cold treeline (Fig. 4e, f), but it did amplify the effects of climate change in other plots, for example by exacerbating the collapse of forests near dry treeline (Fig. 4c, d).

4 Discussion

4.1 Current climate

Generally, the model simulated the expected forest types for the current climate accurately (cf. Sections 2.1, 3.1.1, 3.2.1 and 3.3.1). The dominant species of the different elevation bands from the colline, the montane to the subalpine level were reproduced accurately with two exceptions. First, at mid-elevations on the south-facing slope in the Anniviers valley, *P. abies* forests would have been expected (Gödickemeier 1998; Ott et al. 1997). The missing *P. abies* belt on this south-facing slope was either due to an overestimation of drought, which in the model strongly limits the establishment and growth of this species, or to an underestimation of its drought tolerance (cf. Table A-10 in Bugmann 1994; Ellenberg 1996). Second, at low elevations in the Maggia valley, the proportion of *Quercus* spp. should have been higher, reflecting the extended dry periods in summer that limit the competitiveness of other deciduous species, particularly *F. sylvatica*. This anomaly was probably due to the fact that the monthly climate data used in the model do not fully capture the very high variability of summer precipitation in this part of the Alps, where short thunderstorms often bring heavy precipitation followed by extended periods of drought. See also Giesecke et al. (2010) for the significance of inter-annual climate variability as driver in simulations of vegetation change.

4.2 Effect of changes in browsing

First and foremost, increased browsing caused a reduction in total basal area in all three valleys (Figs. 3, 5 and 6), whereby an increase in browsing pressure from "elevated" to "high" levels typically caused a greater decrease in basal area than a shift from moderate to elevated browsing pressure. This finding is not surprising, as it is based on a non-linear function in the model (Fig. 1), but it still corroborates results from other studies that changes in browsing can result in non-linear effects in forest attributes (e.g., Didion et al. 2009a; Kienast et al. 1999).

Second, the impact of changes in browsing pressure on the basal area of individual species and thus on the species composition differed strongly between regions. Particularly in the Anniviers and the Maggia valleys, changes in browsing intensity caused strong shifts in the composition of the dominant species: for example, forests

in the valley bottom in the Anniviers valley changed from a co-dominance by *P. sylvestris*, *Quercus* spp. and *T. cordata* to almost pure *P. sylvestris* stands (Fig. 3a–c); forests in the Maggia valley changed from *F. sylvatica* dominated stands to *C. sativa* dominated stands (Fig. 6a–f). In contrast, the effect of changes in browsing intensity was less pronounced in the Tuors valley although the simulated browsing intensities were identical in all three valleys. Thus we conclude that the impact of changes in browsing intensity on species composition cannot be extrapolated from one region to others but must rather be evaluated on a regional basis (cf. Didion et al. 2009a).

Third, we sometimes found a positive effect of an increase in browsing pressure on the basal area of shade-intolerant species such as *L. decidua* (Figs. 3a–c, 5a–c, 6a–c) and *P. montana* (Fig. 3a–c). These species profited more from the improved light conditions that were induced by the decrease in total basal area than they suffered from the direct effects of browsing. For similar reasons, the reduction in the basal area of the light-demanding *Quercus* spp. differed between the north-facing and the south-facing slopes in the Anniviers valley (Fig. 3a–c). On the north-facing slope, establishment and growth of *Quercus* spp. was limited under moderate browsing by low light availability due to the highly shade-casting canopy of *P. abies*, *A. alba* and *F. sylvatica* (Ellenberg 1996). Under higher browsing pressure, the growth of *Quercus* spp. profited from the higher light availability due to the decrease in the basal area of those shade-casting species. In contrast, on the south-facing slope *Quercus* spp. were not light-limited under moderate browsing because the co-occurring *P. sylvestris* had lower basal area and canopy density (Ellenberg 1996). Thus, on the south-facing slope *Quercus* spp. grew under similar light conditions in all three browsing scenarios, but establishment and hence basal area was increasingly limited when browsing increased. Thus, we conclude that species interactions can strongly modify the net response of tree species to changes in the browsing regime.

Lastly, our results indicate that browsing could cause a decrease in total stem numbers by a factor greater than two (Table 3). A reduction of stem numbers in response to browsing is typically accompanied by a change in the diameter structure of the forest both in the model (cf. Didion et al. 2009a) and in reality (Rossell et al. 2005; cf. Ammer 1996). Such structural changes influence the light regime and hence subsequent regeneration and growth dynamics (Didion et al. 2009a; Rossell et al. 2005; cf. Ammer 1996). Improved light conditions can favor light demanding tree species, as seen for *L. decidua*, *Pinus montana* and *Quercus* spp. Thus, browsing affects species diversity not only directly through the processes of selective feeding, but also indirectly by the alteration of the light regime (cf. Figs. 3, 4, 5 and 6; Ammer 1996; Rooney and Waller 2003; Vavra et al. 2007). These considerations are highly important because in mountain terrain, changes in species composition, forest structure and basal area affect key forest functions such as the protection against avalanches or rockfall (Brang et al. 2001; Dorren et al. 2004; Frehner et al. 2005).

4.3 Effect of changes in climate

For the three climatically different valleys, the simulations showed that climate change caused shifts in tree species ranges towards higher elevations (Figs. 3, 5 and 6), which is congruent with observed changes in a variety of taxonomic groups and different geographic locations (Walther et al. 2002; Kullman 2001). The results indicate the absence of gradual movements of forest types (communities) along the

transects, thus leading to new forest types (e.g., Fig. 3a vs. 3d with a new *T. cordata*-dominated forest). Also, the legacies of the forests that had developed under current climate sometimes strongly affected successional dynamics during and after climate change (Figs. 3, 5 and 6). For example, on the south-facing peak in the Anniviers valley, *P. cembra* first increased in basal area under climatic change before decreasing to sub-dominant status (Fig. 4a, b). This initial increase, which is contrary to the fact that the species is less competitive under the new climatic conditions, is a legacy effect, which can delay the establishment of new species at given locations (cf. Davis 2001; Chauchard et al. 2010).

For a warming of 3.6°C to 5.9°C (Table 1), an elevational shift of 600 to 1,000 m could be expected for a lapse rate of 0.6°C per 100 m elevation (cf. Theurillat and Guisan 2001). The simulated species shifts were generally within this range (Figs. 3, 5 and 6). Since the model assumes unlimited seed supply, i.e., it does not address barriers to migration and seed dispersal (cf. Theurillat and Guisan 2001), establishment rates and thus the speed of the upslope shifts are certainly overestimated. Due to the model assumption that soils are always suitable for tree growth, colonization rates for areas well above the current climatic treeline may also be too high. However, land use has been a major driver for the position of the treeline in the Swiss Alps (cf. Gehrig-Fasel et al. 2007), and the existence of alpine meadows and pastures can be expected to be conducive to the establishment of forests after cessation of grazing (Ott et al. 1997). Indeed, Chauchard et al. (2010) found that in parts of the French Alps *A. alba* extended its range upslope by about 300 m during the last five decades. This is a much faster rate than in our simulations, despite unlimited dispersal in our model.

The replacement of the current high-montane and subalpine forests that are composed of relatively few species by more diverse mixed forests under a warmer climate (Figs. 3, 5 and 6) may be considered positive in terms of biodiversity. However, there will be strong reductions in the area available for alpine species, thus resulting in a higher risk of local extinctions of these species (e.g., *P. cembra*, Fig. 3d) due to the phenomenon of "summit traps" (cf. Pertoldi and Bach 2007; Theurillat and Guisan 2001). At the other end of the gradient, increasing drought risk can lead to the collapse of forests in some areas (Fig. 4c) as found in empirical studies (e.g., Bigler et al. 2006). The consequences thereof could be a loss of forest species and habitats in theses areas (cf. Davis and Shaw 2001; Theurillat and Guisan 2001) or an influx of invasive species (cf. Hampe and Petit 2005; McCarty 2001). The effects of these processes need to be considered with regard to the change of forest cover and stand types and the consequences for ecosystem services such as timber production and habitat (Millennium Ecosystem Assessment 2005), but also protection from avalanches and rockfalls (Brang et al. 2001; Dorren et al. 2004; Frehner et al. 2005).

4.4 Effect of changes in browsing and climate

Typically, the combined effects of climate change and browsing on total basal area along the transects were compensatory, as the reduction in basal area induced by an increase in browsing pressure was lower in the case of climate change than under current climate. The combined effects of climate change and browsing on species composition, however, suggested a dominance of non-compensatory effects. For

example, an increase in browsing enhanced the dominance by *C. sativa* that followed climatic change in the Maggia valley or led to a species shift (to *Quercus* spp. rather than to *F. sylvatica*) at low elevations in the Tuors valley. Thus, an evaluation of the joint effects of climate change and browsing needs to consider species-specific direct (e.g., selective browsing, climatic range) and indirect (e.g., light regime, competition) effects.

Browsing as a "bottom-up" driver of forest dynamics influences tree establishment and thus stem numbers (cf. Table 3; Cairns and Moen 2004) as well as species composition (Figs. 3, 5, 6 and 6). Climate change as a "top-down" process, however, primarily controls the suite of species that is able to establish and affects tree growth and productivity of a forest, as demonstrated by the changes in basal area (cf. Figs. 3, 4, 5 and 6; Motta et al. 2006). These different drivers controlling stem numbers, species composition and basal area led to the strong combined effect of browsing and climate change as shown in our modeling study, but also in field studies, e.g., in northern Sweden (Cairns and Moen 2004) and Canada (Tremblay et al. 2007). For the shift of species' ranges in response to climate change, browsing thus presents an important factor. Close to treelines, where forests are highly sensitive to disturbance (Davis and Shaw 2001; Hampe and Petit 2005), the effect of browsing can be expected to be most pronounced. For example, we found that browsing exacerbated the climate-induced collapse of forests at the dry treeline, (Fig. 4c, d), whereas it delayed the upward shift of the cold treeline by several decades (Fig. 4e, f).

4.5 Methodological considerations

We used only one regionalized data set for one climate change scenario (A1B, cf. IPCC 2007), because our focus was on the joint effects of climate change and browsing intensity rather than a comprehensive analysis of the range of responses under various climate scenarios. While it is likely that other climate scenarios would have shown somewhat different responses of forest ecosystems in the examined valleys, we expect that the demonstrated interactions of climate change and browsing pressure would not vary strongly between climate change scenarios. We therefore conclude that the results from our study characterize the importance of browsing when dealing with the response of forest ecosystems to climate change. Clearly, our results should not be mistaken as predictions of the future state of these systems, but rather as an evaluation of the importance of the processes shaping the long-term population dynamics of forests trees.

5 Conclusion

Our study showed that climate change can result in large changes in tree species composition, forest basal area and stem numbers, confirming results from previous modeling studies (e.g., Wallentin et al. 2008; Bugmann 2003; Lexer et al. 2002). We could substantiate and quantify the expected upward shift of tree species (Davis and Shaw 2001; Theurillat and Guisan 2001; Walther et al. 2002; Chauchard et al. 2010) by examining forest development along a continuous elevation transect in three climatically different zones of the Swiss Alps. We did not usually find a

concurrent movement of today's stand types, but rather remarkable changes in the species composition as well as the development of new stand types.

The simulated shift in tree species ranges due to changes in climate and browsing pressure resulted in changes in habitat types that present major challenges for the management of mountain forest ecosystems. Management practices designed for current forests based on the historical variability in the ecosystem may no longer be appropriate (Millar et al. 2007); alterations in the species composition and the succession to new stand types need to be investigated, and adaptive management strategies need to be developed.

Furthermore, by investigating different browsing regimes, we conclude that while climate change may partially compensate for browsing-induced reductions in basal area, the combined effect of climate change and browsing on the mix of tree species and forest types will probably differ between locations, as browsing selectively excludes species from establishing or reaching dominance (Côté et al. 2004; Rooney and Waller 2003). The responses we found ranged from compensation to enhancement, but they also involved unanticipated feedback loops (e.g., via light availability). Ungulate browsing is only one form of herbivory affecting tree regeneration; other forms of herbivory, for example by insects (Price et al. 2001; Payette and Delwaide 2003; Moen et al. 2004), are expected to add further to the impact of browsing. Since management decisions today have long-term implications with regard to forest succession under climate change (cf. Millar et al. 2007), there is an urgent need for adaptive management strategies that address the combined effects of climate change and both large and small-scale disturbances such as herbivory.

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