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ORIGINAL ARTICLE

The impact of climate change and its uncertainty on carbon storage in Switzerland

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Abstract Projected future climate change will alter carbon storage in forests, which is of pivotal importance for the national carbon balance of most countries. Yet, national-scale assessments are largely lacking. We evaluated climate impacts on vegetation and soil carbon storage for Swiss forests using a dynamic vegetation model. We considered three novel climate scenarios, each featuring a quantification of the inherent uncertainty of the underlying climate models. We evaluated which regions of Switzerland would benefit or lose in terms of carbon storage under different climates, and which abiotic factors determine these patterns. The simulation results showed that the prospective carbon storage ability of forests depends on the current climate, the severity of the change, and the time required for new species to establish. Regions already prone to drought and heat waves under current climate will likely experience a decrease in carbon stocks under prospective 'extreme' climate change, while carbon storage in forests close to the upper treeline will increase markedly. Interestingly, when climate change is severe, species shifts can result in increases in carbon stocks, but when there is only slight climate change, climate conditions may reduce growth of extant species while not allowing for species shifts, thus leading to decreases in carbon stocks.

Keywords Biomass · Carbon · Climate change · Dynamic vegetation models · LPJ-GUESS

Introduction

Carbon storage by vegetation is controlled by climate (Beer et al. 2010). Already short-term events such as heat waves and droughts can markedly reduce carbon uptake and lead to some forests being a carbon source, as shown in Europe for the year 2003 (Ciais et al. 2005). However, in the same period, trees in temperature- but not precipitation-limited areas, i.e., at high elevations, benefited in terms of growth (Jolly et al. 2005). Thus, increasing temperatures and changing precipitation patterns as expected for the remainder of the twenty-first century (Seneviratne et al. 2012) are likely to affect ecosystem dynamics and, among others, alter global vegetation carbon pools (Heimann and Reichstein 2008).

The different climatic tolerances of tree species regarding, e.g., frost or drought lead to competitive advantages for certain species and thus favor species shifts under climate change (Fuhrer et al. 2006). For instance, in an inner-Alpine dry valley (Swiss Rhone valley, Valais) *Pinus sylvestris* L. forests are turning into oak forests due to the higher drought tolerance of *Quercus pubescens* Willd. (Rigling et al. 2013). Similarly, in the Western United States, abrupt vegetation shifts due to climate-driven mortality of *Populus tremuloides* Michx. (Anderegg et al. 2013) and *Pinus edulis* (Breshears et al. 2005) have been reported. Meanwhile, trees at the cold treeline have already shifted upwards due to both land use change and global warming (Gehrig-Fasel et al. 2007).

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In general, different regions vary in their sensitivity to climate change (Gonzalez et al. 2010). Ecosystem susceptibility to climate change is *inter alia* controlled by spatial and temporal climate variations (Lindner et al. 2010). Therefore, particularly areas that feature large climatic gradients over small spatial scales, such as mountain regions, require a high spatial resolution (<5 km) of climate projections to make reliable predictions of possible climate change impacts (Trivedi et al. 2008).

Many previous assessments of climate change impacts were based on ecosystem models that have been applied either at coarse spatial resolution on continental to global scales (e.g., Bachelet et al. 2003; Cramer et al. 2001; Hickler et al. 2012; Morales et al. 2007; Sitch et al. 2008; Zaehle et al. 2007) or at local to regional scales (e.g., Elkin et al. 2013; Morales et al. 2005; Wolf et al. 2008). However, there is a need for assessments at the regional to national scale of vegetation and soil carbon storage; particularly in areas that are characterized by high topographic variability, a high spatial resolution of the assessment is required that allows policy makers to analyze climate change risks and to develop national adaptation and mitigation strategies. To date, such studies at the national scale are quite rare (e.g., Koca et al. 2006).

Furthermore, although most previous simulation studies have covered a broad range of greenhouse gas emission scenarios (based on Nakicenovic et al. 2000), they did not investigate the 'lower edge' of climate change, i.e., assuming high intervention intended to stabilize the temperature increase compared to pre-industrial values at 2°, as internationally agreed upon (United Nations Framework Convention on Climate Change). Elkin et al. (2013) recently presented one of the first such studies for two valleys in Switzerland. Here, we use a novel gridded daily climate change data set (spatial resolution ~2 km) (CH2011 2011; Fischer et al. 2012) to extend this study to the national scale. The dynamic vegetation model LPJ-GUESS (Sitch et al. 2003; Smith et al. 2001) is used to estimate the potential future carbon stocks for the entire of Switzerland. In contrast to the approach proposed by Elkin et al. (2013), we include the uncertainty range of three climate projections gained by the probability distribution for changing temperature and precipitation (Fischer et al. 2012). This allows covering a broad range of possible climate change impacts on carbon storage, providing a more differentiated view on the future development of carbon stocks in Switzerland than in Elkin et al. (2013). Moreover, we also differentiate vegetation and soil carbon storage, which allows a better characterization of carbon sinks and the carbon cycle.

Specifically, we focus on the following research questions: (1) Under which conditions do Swiss forests remain a carbon sink with respect to climate change in the coming decades and centuries? (2) Which variables, in terms of the various elements of climate and atmospheric CO_2 concentrations, are driving the change in carbon storage? (3) Which other factors may counteract climate change impacts? (4) How does the inherent uncertainty of the climate models and thus climate scenarios affect the simulation results?

Materials and methods

The dynamic vegetation model

We used the dynamic vegetation model LPJ-GUESS (Lund–Potsdam–Jena General Ecosystem Simulator) that captures tree population dynamics on small patches of land (typically 0.1 ha) based on mechanistic descriptions of the underlying physiological and biogeochemical processes (Sitch et al. 2003; Smith et al. 2001). Individuals of each species are represented in age cohorts, i.e., they establish on one patch in the same year, experience the same resource competition and have the same growth rate. Each species has specific properties regarding growth, establishment, mortality, metabolic rates, shade tolerance, and bioclimatic limits (Smith et al. 2001). Here, we used the species parameterization compiled by Hickler et al. (2012) that represents the 20 most common European tree species as well as several plant functional types (PFTs) representing shrubs and grasses.

Physiological processes such as photosynthesis and respiration as well as carbon and water fluxes are updated with a daily time-step, whereas growth (carbon allocation), the turnover of leaves and fine roots, sapwood-heartwood conversion, and vegetation dynamics are simulated annually (Sitch et al. 2003). Carbon of dead vegetation enters a litter pool from that 70 % is respired annually to the atmosphere whereas the remaining 30 % is transferred to the soil carbon pool, 29.55 %, to an 'intermediate' and 0.45 % to a 'slow' pool (Sitch et al. 2003). Decomposition is modeled as a function of soil moisture and temperature. At 10 °C and ample soil water, the turnover time is 2.85 years for the litter pool, 33 years, for the 'intermediate,' and 1,000 years, for the 'slow' carbon pool. A detailed description of the model is provided in Sitch et al. (2003).

Soil hydrology is simulated with a multi-layer 'bucket' model based on site-specific soil layer information for water holding capacity and soil texture to better reflect dry conditions as described by Manusch et al. (submitted). Rain and snowmelt infiltrate the upper 500 mm of the soil until field capacity is reached; excess water is lost as runoff (Gerten et al. 2004). The lower layers are fed by percolation from surplus water of the upper layers. Percolation from the lowest layer is considered runoff. Roots penetrate the whole soil column, but their mass declines exponentially (Jackson et al. 1996). Thus, transpiration occurs from all soil layers. Evaporation is extracted from the upper 200 mm of the soil only (Gerten et al. 2004).

LPJ-GUESS and the related LPJ-DGVM have been successfully applied to simulate species composition as well as carbon storage at numerous sites, regions, and globally for past, current, and prospective climate conditions (Hickler et al. 2012; Leuzinger et al. 2013; Poulter et al. 2009; Wolf et al. 2012; e.g., Elkin et al. 2013). In this study, we applied an improved (in terms of depicting the underlying processes) version of the standard model (Sitch et al. 2003; Smith et al. 2001) that features carbon sink limitation under cold conditions (Leuzinger et al. 2013) and a size- instead of the former age-dependent mortality (Manusch et al. 2012).

Study sites

The Forest Soils and Biogeochemistry Unit of the Swiss Federal Institute for Forest, Snow and Landscape Research WSL (hereafter called WSL) maintains a soil data set of more than 1,000 forested sites located all over Switzerland comprising, among many other variables, layer-specific information on depth, grain size, and water holding capacity (whc), i.e., maximum plant-available water storage (defined as the difference between field capacity and the permanent wilting point). Grain size was derived with hand texture measure and by the sedimentation method (Gee and Bauder 1986); whc was defined based on Teepe et al. (2003) with density classes of fine earth, soil texture classes, and humus content. In this study, we excluded all soils that are fed by groundwater and that are shallower than the assumed evaporation depth of 20 cm (Gerten et al. 2004) to allow for comparable climatic driving conditions and to ensure a minimum rooting depth. We prepared the soil data for the model as described in Manusch et al. (submitted) using the package *The soil texture wizard* for the statistics software R (Moeys 2012). In total, we used 915 sites covering a broad climatic gradient from low- to high altitudes (286 m–2188 m a.s.l.) with whc ranging from 19 to 972 mm. Historic climate data for 1980–2009 were provided by Meteotest (Remund 2011). Within this period, the mean annual temperature of all sites varied from 0.6 to 12.9 °C and annual precipitation ranged from 633 to 2470 mm. Atmospheric CO_2 concentrations were derived from the Mauna Loa record (Keeling et al. 2009).

Climate scenarios

To depict prospective climate change, we used gridded daily change signals for temperature and precipitation in Switzerland that were obtained from the Center for Climate Systems Modeling (C2SM) at ETH Zurich (CH2011 2011). These projections with a spatial resolution of 2 km are based on the two non-intervention emission scenarios A1B, A2 (Nakicenovic et al. 2000), and a mitigation scenario, in which emissions are reduced by 50 % until 2050 (RCP3PD), that limits global warming to $<2°$ by the end of this century relative to pre-industrial conditions (Meinshausen et al. 2011; Moss et al. 2010). The baseline data set refers to the period 1980–2009, and the scenario data represent the annual cycle of daily changes for three 30-year periods (time slices) centered around 2035, 2060 and 2085 (Fischer et al. 2012). The scenario data were derived as an ensemble from 20 GCM-RCM combinations and therefore allowed for uncertainty estimations expressed with a probability distribution where the 2.5, the 50 and 97.5 % quantiles are interpreted to be possible lower, medium, and upper estimates for climate change (hereafter called anomalies) (Fischer et al. 2012). A detailed description of the data set and its derivation was provided by Fischer et al. (2012).

We applied linear interpolation between the central year anomalies of each time slice and thus generated continuous daily anomalies for the period 1994–2100 (Table 1). Using these data, we created continuous daily data sets from 1994 to 2100 by drawing sample years randomly from the reference period (1980–2009) and adding the daily anomalies of temperature differences and proportional change of precipitation. Beyond 2100, we assumed a hypothetical, constant climate until the end of the simulation period in 2300 to create a likely equilibrium of carbon pools. To this end, we added the 2100 anomalies to randomly drawn reference years and used a constant atmospheric CO_2 equivalent concentration of 703 ppm (A1B), 856 ppm (A2), and 450 ppm (RCP3PD), respectively. To minimize the risk of favoring single years and to allow for comparability across all data sets, we used the same random set of reference years for generating all time series.

Percentage sunshine was derived as in Elkin et al. (2013) by converting solar radiation from observed data (1975–2010) to percentage sunshine assuming that the maximum solar radiation of each day throughout all observed years corresponds to 100 % of bright sunshine for this day of the year. Thereafter, we drew the same random years for the whole simulation period as mentioned above. We confirmed that annual carbon uptake is similar in amount and distribution using observed daily values, randomly sampled observation years, and the mean over all observed values for percentage sunshine (C. Manusch, unpublished data).

Simulation experiments

Model calibration

As mentioned above, the model described in section "The dynamic vegetation model" was based on the species parameterization according to Hickler et al. (2012).

Table 1 Mean anomalies for projected climate change in 2100 averaged across all 915 study sites in Switzerland (CH2011 2011) for annual mean temperature and growing season (gs) precipitation (April–October)

Scenario	Temperature change (annual, °C)			Precipitation change (gs, %)		
	Low ('Moderate')	Medium ('Medium')	Upper ('Extreme')	Low ('Extreme')	Medium ('Medium')	Upper ('Moderate')
A2	3.3	4.7	6.1	−30.9	−14.6	1.7
A1B	2.7	3.8	5.0	−26.0	−12.0	2.1
RCP3PD	0.8	1.4	2.0	−13.4	−3.9	5.6

Anomalies refer to the reference period 1980–2009. Low, medium and upper changes cover the uncertainty range of the projections, i.e., reflecting the 2.5, 50 and 97.5 % percentiles of the probability distribution of projected change (cf. Fischer et al. 2012)

However, the newly introduced parameters by Manusch et al. (2012) that are relating tree size to mortality rates were validated based on five sites only (Manusch et al. 2012). Therefore, we recalibrated them and cross-compared the results with above- and belowground vegetation carbon stock from the latest Swiss National Forest Inventory at nine more sites (NFI, Speich et al. 2011). In more detail, we used the mean values for five sub-regions of Switzerland that are characterized by similar growth conditions (so-called 'Production Regions'): Jura, Plateau, Pre-Alps, Alps, and Southern Alps as target values. For the calibration, we selected all sites per production region where simulated vegetation carbon stock for the observation period equaled the mean simulated vegetation carbon stock for the according region. Then, we changed one parameter at a time and evaluated the result at all nine sites against the observed mean of each region. In the final setting, the optimal parameter *dbhdeath* was 50 cm larger and the shape parameter of the function 0.5 larger for all species compared to Manusch et al. (2012), e.g., 260 cm and 2.8 for boreal/temperate shade-tolerant needle-leaved evergreen species, and 290 cm and 3.3 for temperate shade-tolerant broadleaved summergreen species (Fig. SI). Thus, trees can grow larger with the new parameterization because mortality increases less fast with diameter compared to the original settings.

Model initialization

We ran the model from bare ground for 1,000 years of 'spin-up' to create an equilibrium state of carbon pools in vegetation and soils. The simulation experiment was performed on 200 patches per site to control for stochastic variations in simulated vegetation dynamics (Smith et al. 2001). Climate data for the spin-up period were derived randomly, year-wise drawn climate data, from the reference period (1980–2009). Thereafter, the historic data for 1980–2009 were used to simulate this reference period followed by the projections for 2010–2300 as explained further above. We wanted to cover a wide range of possible future climate outcomes and its consequences for ecosystems. Thus, we exploited the uncertainty ranges that are provided with the CH2011 (2011) scenarios using: (1) the lower estimate of temperature change with the upper estimate of (negative) precipitation change (hereafter called 'Moderate'); (2) the medium estimates of climate change ('Medium'); and (3) the upper estimate of temperature change with the lower estimate of precipitation change ('Extreme') for the scenarios RCP3PD, A1B, and A2, i.e., in total nine possible climate outcomes (cf. Table 1). To disentangle the effect of climate change and CO_2 increase, we additionally ran three control scenarios: one scenario without climate change and without CO_2 increase, i.e., temperature anomalies were assumed to be 0 and precipitation anomalies to be 1, and CO_2 was kept constant at the 2012 level of 394 ppm (hereafter called *CTR*); one scenario without climate change but including the CO_2 increase (A2 scenario, *CTR_CO2*); and one scenario that employed the A2 'Extreme' anomalies for temperature and precipitation but constant CO_2 from 2012 onwards (*CTR_CLIM*).

Model application

Forest management pursues different targets at different sites (e.g., protection from gravitational natural hazards in mountain regions vs. timber production in low-elevation areas). We therefore decided not to include management in this study but to focus on the impact of varying climatic influences on carbon storage, and not of varying management practices.

We evaluated the impact of the three climate change scenarios with their three possible variants (Table 1) on carbon pools for potential natural vegetation, their dynamics and species composition at the 915 sites where WSL soil profile information is available (see above). To derive a synopsis at the national scale, we interpolated the results using co-kriging with topography (digital terrain model with spatial resolution of 25 × 25 m) as external driver and aggregated the data to a grid with a cell size of 0.1 ha (Aertsen et al. 2012). We assessed vegetation and soil carbon pools in forests for (1) a potential full

Table 2 Simulated carbon stock (Mt) in forest vegetation (Veg) and soils of Switzerland for potential full forestation (below current treeline) and simulated versus observed carbon stock for the currently forested areas in the observation period 1980–2009, and simulated changes (Δ, Table 1) for both compartments

Period	Compartment	Fully forested (Mt)	Current forest cover (sim./obs.) (Mt)
1980–2009	Veg	429	158/143
	Soil	484	179/160
2070–2099	ΔVeg	0–54	0–20
	ΔSoil	−53 to 17	−19 to 7
2271–2300	ΔVeg	18–125	6–45
	ΔSoil	−101 to 8	−37 to 3

Simulations were done with LPJ-GUESS, range indicates range of results for all climate scenarios. Observations are based on NFI data for vegetation carbon and BUWAL and WSL (2005) for soil carbon. The first two rows show simulated and observed values while the later rows show ranges due to climate scenarios

forestation below current, in most areas anthropogenically induced treeline (simplistically assumed at 2200 m a.s.l., Leuzinger et al. 2013) and (2) for the currently forested area according to NFI (Table 2, Speich et al. 2011). Based on these results, vegetation and soil carbon stocks were analyzed with regard to the CTR, CTR_CO2, and CTR_CLIM simulation results to investigate the relative effects of climate change and CO_2. As these effects were strongest for the most extreme climate scenario (A2, 'Extreme'), we additionally analyzed the impact of temperature change (expressed as Δ growing degree-days, GDD) and water availability change (Δ growing season precipitation) on carbon storage and species composition for this particular climate scenario in more detail.

Results

Present state of simulated carbon storage and species composition

Under current climate conditions (1980–2009), vegetation carbon stocks simulated for the five Swiss production regions were within observed ranges for these regions, although management was excluded in the simulations, which is in contrast to current forest management (Fig. 1). In the regions Plateau (P) and Jura (J), deviations between simulated and measured vegetation carbon were lowest with 1 % (P) and 3 % (J), while it was by 9 % lower in the Pre-Alps (PA), and in the Alps (A), and Southern Alps (SA) it was by 21 % (A) and even 63 % (SA) higher than the measured values. For the whole of Switzerland, simulated vegetation carbon stock for the current forest cover was 10 % higher than observed (Speich et al. 2011) (Table 2), and simulated soil carbon storage was 12 % higher than observations (data from: BUWAL and WSL 2005).

In all regions, both needle- and broadleaved species occurred (Fig. 1). However, compared to observations, the simulated proportion of broadleaved species in the total vegetation carbon stock was notably higher, especially in the regions that are characterized by low- to medium elevation but much less so in the Alps (Fig. 1): 20–31 % (Jura, Plateau, Pre-Alps) versus 10 % (Alps) and 5 % (Southern Alps).

Simulated changes in vegetation and soil carbon due to climate change

For most of the Swiss area, an increase in carbon storage in vegetation from the beginning toward the end of this century is simulated by all scenarios (Fig. 2). Carbon storage would be even higher at the end of the simulation period (2271–2300, Fig. 3). The increase in vegetation carbon stock was characterized by an increase in broadleaved and a decrease in needle-leaved species starting in the middle of the twenty-first century in all NFI production regions (Fig. 4), indicating the onset of species shifts.

However, also under the most extreme scenario (A2, 'Extreme'), until the end of this century, almost all sites were still dominated by the currently dominant vegetation type (needle- or broadleaved, Fig. 5). Toward the end of the simulation period with this scenario, most sites currently dominated by needle-leaved trees turned into broadleaved-dominated sites and experienced an increase in carbon storage. In the same period, currently broadleaved-dominated sites remained broadleaved dominated and showed similar rates of increase or decrease as 200 years earlier (Fig. 5).

Sites with an increase in precipitation and a low absolute GDD increase, but a high relative GDD increase for the A2 'Extreme' scenario, showed an increase in carbon storage of up to 12 kg C m^{-2} until the end of this century (Fig. 5). All these sites are located at altitudes above 1,900 m a.s.l., i.e., close to the current cold treeline. At sites with the same low increase of absolute GDD but a lower relative increase, carbon stock increase was lower, and needle-leaved trees were still dominant at the end of the simulation period.

Under certain climate scenarios (cf. "Impact of different climate change scenarios on simulation results" section) some regions experienced a decrease in vegetation carbon storage (Figs. 2, 3). The maximum decrease in the carbon stock over all scenarios was −6.6 | −8.8 kg C m^{-2} (2070–2099 | 2271–2300, both A2 'Extreme'), while the absolute maximum increase was 12.2 | 16.0 kg C m^{-2} (A1B 'Medium' | A2 'Extreme,' all values refer to the 915

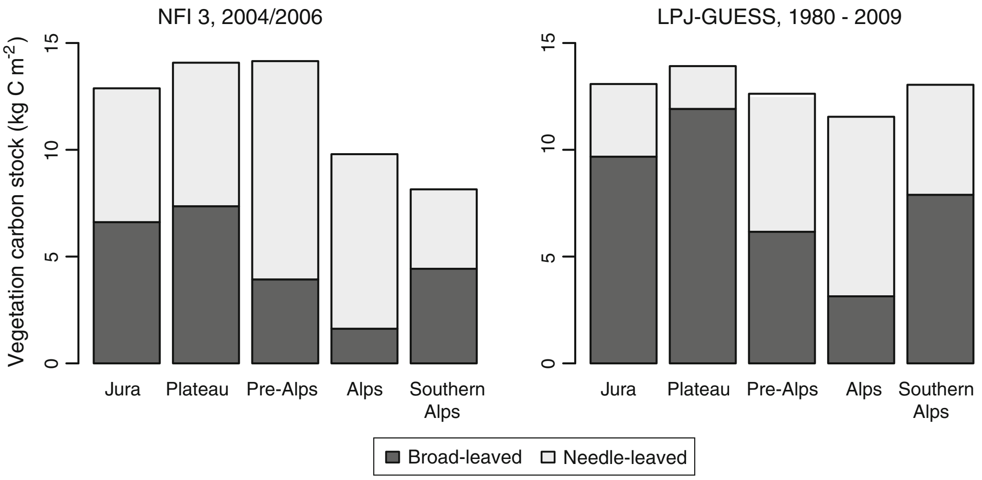


Fig. 1 Observed versus simulated vegetation carbon stocks of broadleaved and needle-leaved tree species for the NFI production regions in Switzerland (Speich et al. 2011)

study sites). Sites that featured high GDD and a low growing season precipitation before climate change (i.e., low relative but high absolute GDD increase, and high relative but low absolute precipitation decrease, Fig. 5) were especially prone to vegetation carbon losses.

The average results across the 915 sites extrapolated over the total area of Switzerland, showed constant or increasing vegetation carbon stocks for all scenarios until the end of this century and increases until the end of the simulation period (Tables 2, 3). For CTR_CO2, it started to increase at the end of the twenty-first century and leveled off toward the end of the twenty-second century (Table 3). Without an increase in CO_2 (CTR_CLIM), vegetation carbon pools decreased toward the middle of the next century and then slightly increased again. Without climate change and atmospheric CO_2 increase (CTR), they were nearly constant.

Soil carbon stocks were decreasing for most climate scenarios. This decrease was highest at the end of the simulation period in 2300 (Table 2). When climate did not change but CO_2 increased (CTR_CO2), soil carbon stocks increased notably (Table 3), while they decreased when CO_2 was constant and only climate change occurred (CTR_CLIM). In accordance with vegetation carbon stocks, soil carbon stocks were constant when climate and CO_2 did not change (CTR).

Impact of different climate change scenarios on simulation results

The simulation results depended strongly on the underlying assumptions regarding climate (Figs. 2, 3). In general, RCP3PD was the scenario that featured the lowest increase in vegetation carbon for the whole simulation period. The A1B and A2 scenarios, however, showed a similar increase in vegetation carbon over time. Surprisingly, RCP3PD was the only scenario, under which in some regions, a marked loss in vegetation carbon was predicted, irrespective of the level of that scenario (‘Moderate’ to ‘Extreme’). This loss increased with the severity of climate change. Across all scenarios for the twenty-first and the twenty-third century, the ‘extreme’ variant with highest temperature increase and highest precipitation loss in summer featured regions where vegetation carbon stocks decreased strongly compared to the reference period (Rhone valley, Engadin, Basel, and Schaffhausen, Figs. 2, 3). Yet, with the same ‘extreme’ variants other regions experienced the highest increase in vegetation carbon by the end of the twenty-third century compared to the ‘medium’ and ‘moderate’ variants. In contrast, at the end of the twenty-first century, the highest vegetation carbon increase nationwide was simulated for A1B and A2 under a ‘moderate’ climate.

Discussion

To fulfill the emission reduction aims of the Kyoto Protocol (United Nations Framework Convention on Climate Change) and to develop adaptation and mitigation strategies at the national scale, decision-makers need nation-wide information on above- and belowground carbon storage capacities under both current and future climates. However, to date studies at national scale are scarce (e.g., Koca et al. 2006). We provided a vegetation model-based national assessment of current and future vegetation and soil carbon stocks for Switzerland for potential natural vegetation. In a next step, the additional influence of varying management practices should be investigated to provide more concrete recommendations for policy makers.

LPJ-GUESS somewhat simulated higher total vegetation biomass for Switzerland compared to observed NFI data

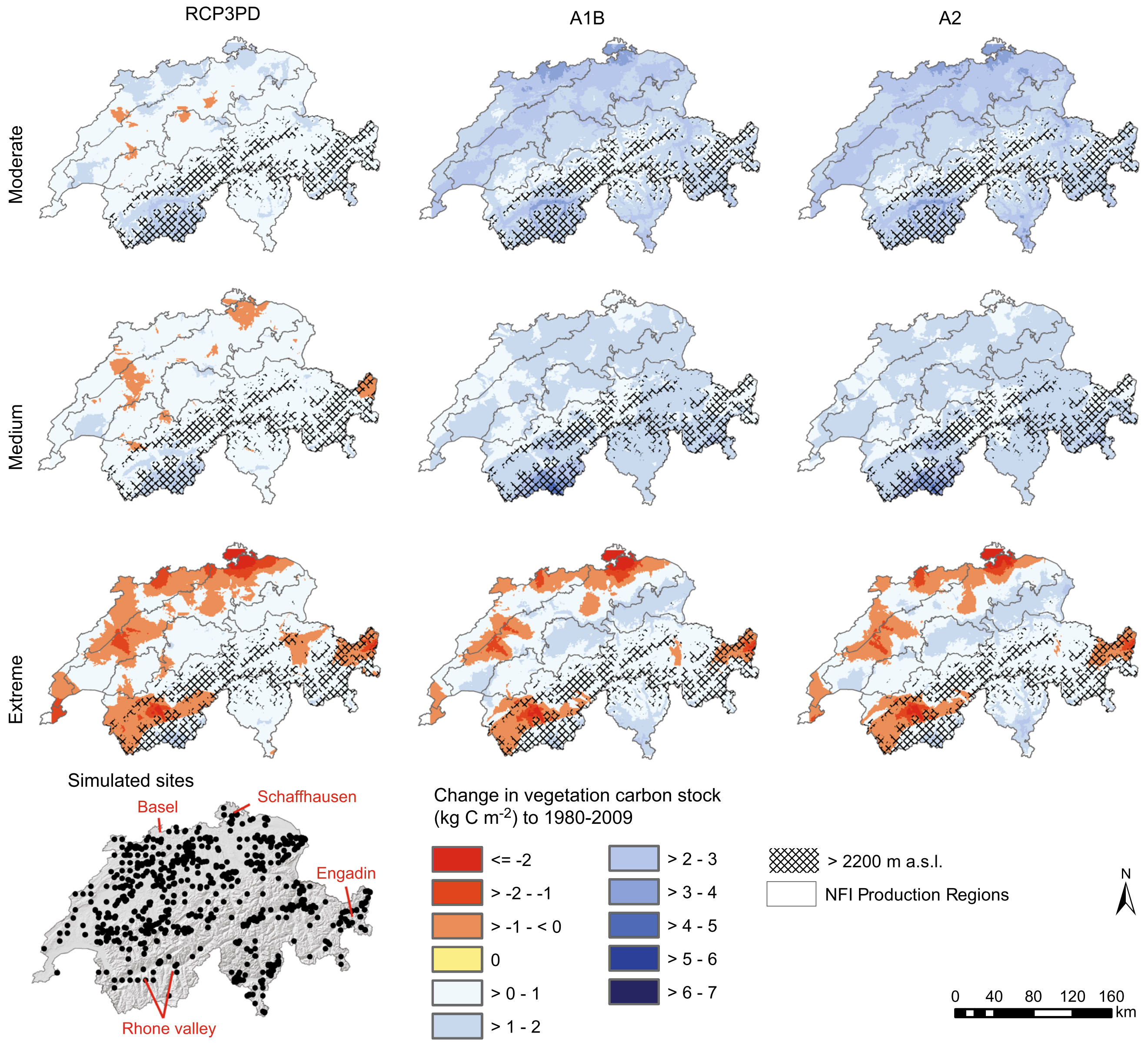


Fig. 2 Simulated change in vegetation carbon stocks (kg C m^{-2}) between the reference period (1980–2009) and the end of the present century (2071–2099) for the climate scenarios RCP3PD, A1B, and A2, each with three possible outcomes: low annual temperature increase and low precipitation decrease in summer ('Moderate'); medium annual temperature increase and medium summer precipitation loss ('Medium'); and high temperature increase and high precipitation loss in summer ('Extreme'), always assuming a full forestation of Switzerland. Simulation results were interpolated based on the 915 study sites shown in the lower left panel. *Shaded areas* correspond to areas above treeline, simplistically assumed to occur at 2,200 m a.s.l (cf. Leuzinger et al. 2013), *gray zoned* areas are the production regions of the Swiss National Forest Inventory (NFI)

(Speich et al. 2011). This was not surprising, as the observed values represent mostly managed forests, whereas the LPJ-GUESS simulation experiments were set up to describe potential natural vegetation, thus assuming an equilibrium state of carbon pools in the absence of management (Smith et al. 2001). Using old-growth forest data for the comparison instead of the NFI data was not feasible as only very few forest stands are completely unmanaged or fall into the class of old-growth forests in Switzerland. At the same time, however, it should be noted that the management of Swiss forests is 'light' compared to most other European countries (C stock in Swiss forest biomass is about twice as high as in central Europe, and three to four times as high compared to all of Europe), and the management aims to mimic natural conditions ('close-to-nature sylviculture') (McEvoy 2004; de Turckheim and Bruciamacchie 2005). Therefore, the observed values can only be understood as a benchmark. Additional information

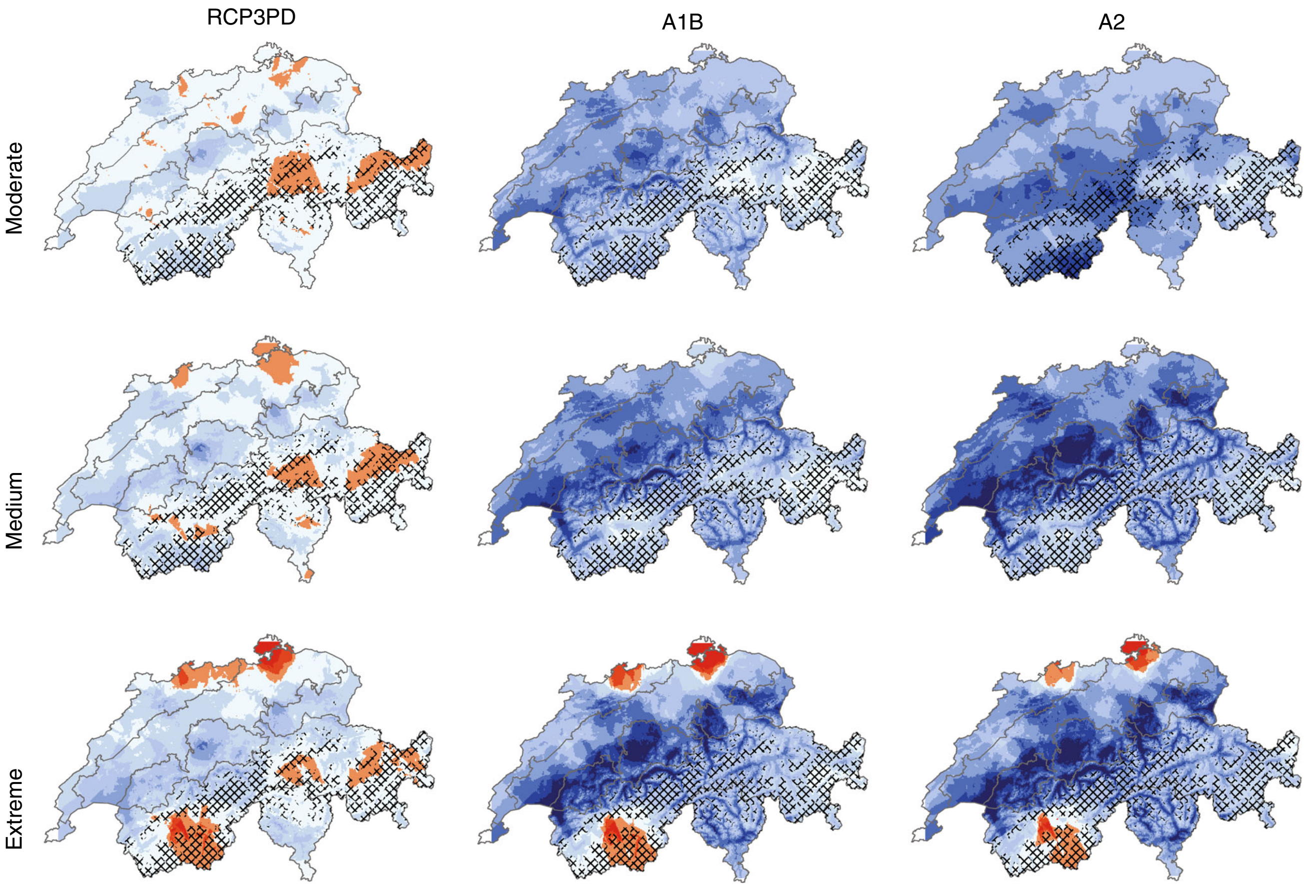


Fig. 3 Simulated change in vegetation carbon stocks (kg C m^{-2}) between the reference period (1980–2009) and the end of the simulation period (2271–2300). For explanations cf. Fig. 2

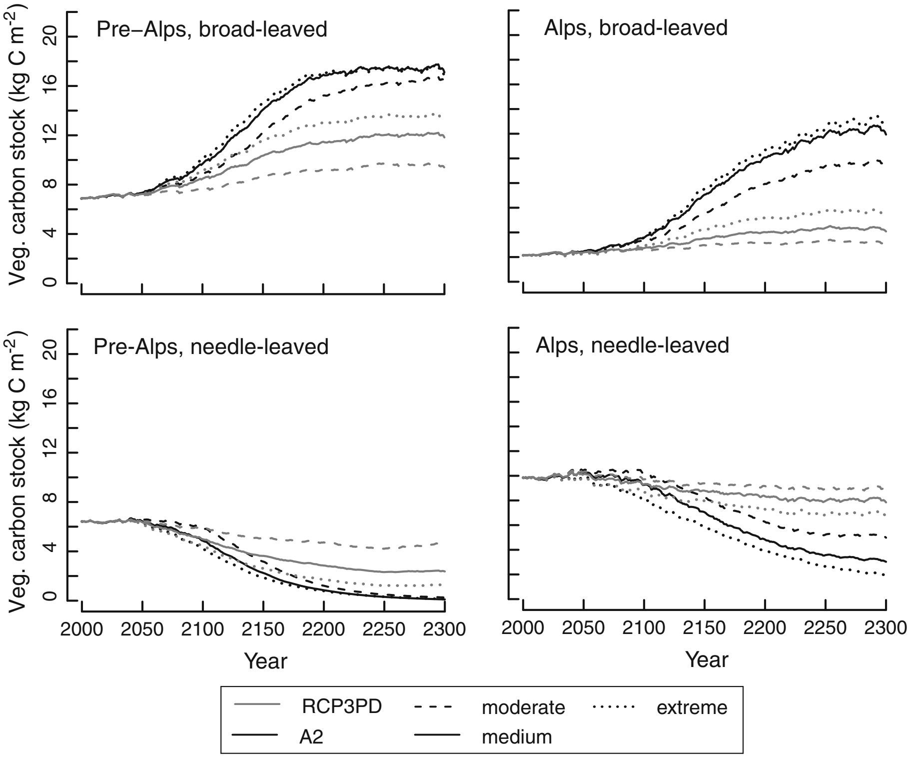
for the cross-comparison as potential natural vegetation maps (e.g., Brzeziecki et al. 1993) or different model studies was not possible due to missing data and would have raised additional uncertainties.

Most of the Swiss forests have an age between 60 and 120 years; thus they feature neither very old nor very young stands (BUWAL and WSL 2005), and the century-long harvesting practices most likely also imply that soil organic carbon is lower than under natural conditions (Gimmi et al. 2009, 2013). In the model, however, the higher biomass compared to the observations led to higher rates of carbon flow to the soil and thus to higher rates of soil carbon stocks than in reality (BUWAL and WSL 2005).

For centuries, forestry in Switzerland favored needle-leaved trees (mostly *Picea abies*); this started to change about 40 years ago only, as a result of efforts to render forest composition more natural (BUWAL and WSL 2005). Potential natural vegetation for most of the low-elevation regions (J, P and PA) is *Fagion* associations (Brzeziecki et al. 1993). Therefore, the simulated high proportion of broadleaved species (mainly *Fagus sylvatica*) in these regions (Speich et al. 2011) matches potential natural vegetation well, but fails to capture the details of land use history (Fig. 1). In contrast, in the high-elevation, alpine regions (A and SA), the simulated proportions of broad versus needle-leaved trees matches better the observed patterns. In these regions, management focuses on the protection against avalanches and rock fall instead of timber-production, which supports more natural species compositions.

Under climate change, the mean simulated vegetation carbon stocks for Switzerland increased for all scenarios (Table 2). This is consistent with simulation results at the global scale (Cramer et al. 2001; Levy et al. 2004; Sitch et al. 2008), for Europe (Zaehle et al. 2007) as well as with local empirical ecosystem studies at mid-latitudes in the Northern hemisphere (Norby et al. 2005). Higher atmospheric CO_2 concentrations have a fertilizing effect at least in the short term; net primary productivity and water use efficiency increase (Amthor 1995). This is reflected in the simulation results: when only CO_2 increased and climate was kept at historic values (CTR_CO2), vegetation carbon stock increased faster during the first 50 years than with

Fig. 4 Mean simulated broadleaved and needle-leaved vegetation carbon stocks (kg C m^{-2}) for all study sites of the Pre-Alps and Alps from 2000 to 2300 for the scenarios RCP3PD and A2



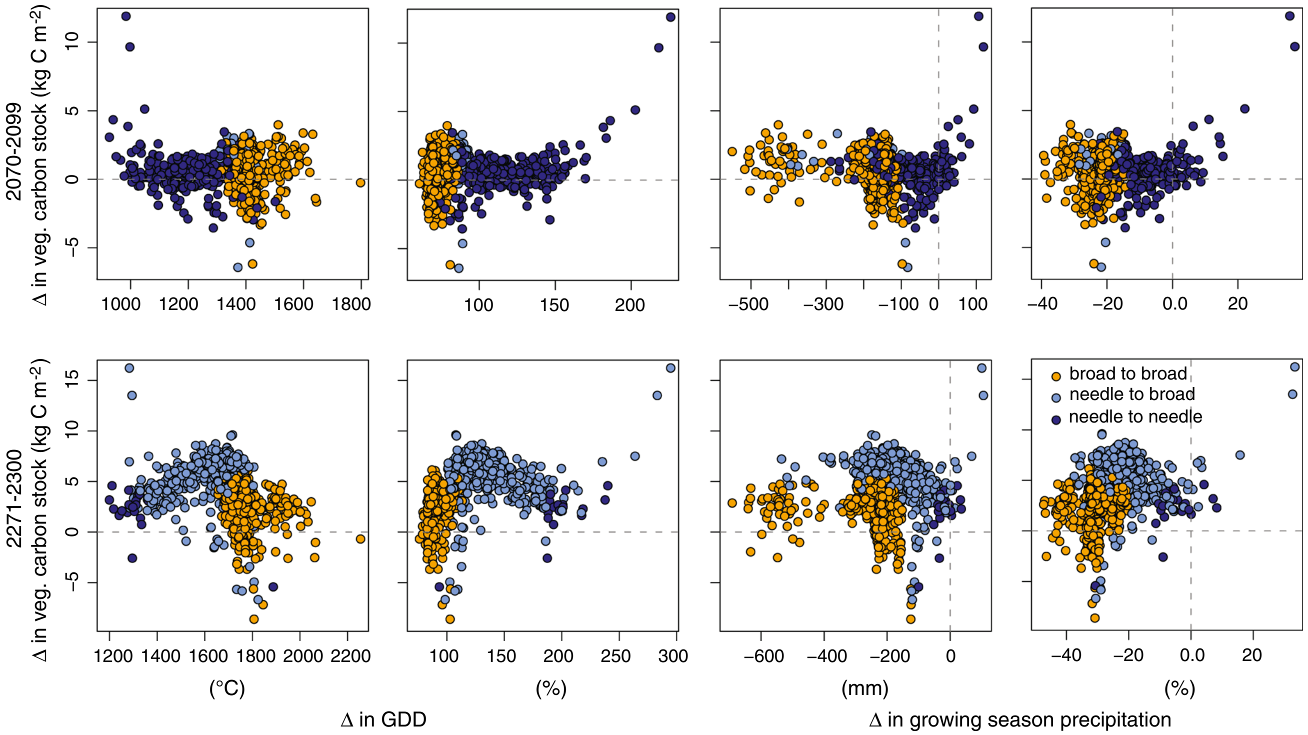


Fig. 5 Simulated mean change in vegetation carbon stocks (kg C m^{-2}) relative to 1980–2009 for the end of this century (upper panel) and the end of the simulation period (lower panel) versus absolute and relative differences in GDD and growing season precipitation using the most extreme scenario (A2 'Extreme'). Different colors indicate the simulated type of the dominant species (broadleaved or needle-leaved) in the reference period and the prospective dominant type for 2070–2099 and 2271–2300, respectively

Table 3 Simulated future carbon stock of vegetation (Veg) and soil (kg C m^{-2}) for all 915 sites based on the scenarios A2 'Extreme', CTR_CLIM, CTR_CO2 and CTR (see section "Simulation experiments") averaged for 50 year intervals

Period	A2 'Extreme'		CTR_CLIM		CTR_CO$_2$		CTR	
	Veg	Soil	Veg	Soil	Veg	Soil	Veg	Soil
2000–2050	12.4	17.2	12.1	17.1	12.7	18.1	12.4	17.9
2051–2100	12.5	15.4	10.4	14.2	13.6	20.1	12.3	18.4
2101–2150	13.2	12.7	8.9	10.3	13.8	22.7	12.2	18.4
2151–2200	14.8	12.1	9.7	8.9	13.7	23.9	12.3	18.5
2201–2250	15.3	12.4	10.2	8.8	13.4	24.2	12.2	18.5
2251–2300	15.4	12.7	10.4	9.0	13.6	24.3	12.2	18.5

additional climate change (Table 3). Thereafter, vegetation carbon stock increased further with climate change but was constant for CTR_CO2. In contrast, other studies suggested a prolonged fertilization with increasing CO$_2$ also when climate did not change (Cramer et al. 2001).

Most vegetation models do not consider that CO$_2$ fertilization may accelerate ecosystem carbon release due to faster life cycles (Bigler and Veblen 2009; Bugmann and Bigler 2011). In contrast, we simulated tree mortality to be size- instead of age-dependent, and thus allowed for the acceleration of tree life cycles (Manusch et al. 2012); as a consequence, in the long-term total vegetation, carbon was lower under the CTR_CO2 scenario than under projected climate change (A2 'Extreme,' Table 3). Furthermore, it is important to take into account that climate change may counteract a possible CO$_2$ fertilization due to impairing climatic conditions, e.g., droughts that are projected to occur more frequently and to be longer in many regions worldwide (IPCC 2007), thus suppressing tree growth and increasing mortality rates (Allen et al. 2010).

According to Norby et al. (2010), the CO$_2$ fertilization effect may also be limited in the long term by decreasing nitrogen (N) availability due to higher growth rates and larger vegetation carbon stocks. LPJ-GUESS does not feature an explicit N cycle and always assumes optimal N availability (Haxeltine and Prentice 1996), hence such N limitation is not reflected in the simulation results. However, anthropogenic N deposition is quite high in Swiss forests today (BUWAL and WSL 2005). It is likely to stay high in the future, and thus, it appears justified to assume that N limitation will be negligible for the future of Swiss forests. Accordingly, leaf nitrogen concentrations were shown to decrease only slightly under elevated CO$_2$ in mature trees at a Swiss study site (Körner et al. 2005).

Although mean vegetation carbon stocks for Switzerland were simulated to increase, this did not hold true for all sites and species (Fig. 5). Importantly, the number of sites dominated by needle-leaved species (particularly *Picea abies*) was projected to decrease, and broadleaved species became dominant (typically *Fagus sylvatica* and *Quercus spp*., cf. Figs. 4, 5). This shift was caused by the parameterized climatic constraints for the establishment of boreal species, i.e., the requirement of low winter temperatures, which is used to describe current species distribution patterns (Dahl 2007). In combination with the CO$_2$ fertilization effect described above and less competition by needle-leaved trees, this led to strong increases in the carbon stocks of the broadleaved species. Thus, this phenomenon may not occur under managed conditions that favored needle-leaved trees for centuries. Additionally, this counteraction to the negative effects of impairing climatic conditions for the extant species requires that new species have enough time to grow and mature. Nevertheless, this shift from needle-leaved to broadleaved species is in line with other studies from the montane to the subalpine zone in Switzerland (cf. Theurillat and Guisan 2001).

This has still implications for forest management. Today, Swiss policy favors natural regeneration (WaG 1991, 2008); during the last four decades, plantations were diminished from ca. 15 M trees in 1975 to 1.2 M in 2011 (BAFU 2012). This policy may meet its limitations in the coming decades whether the climatic margins of the distribution of some tree species are approached. For example, Castro et al. (2004) showed that natural seed dispersal had low establishment success at the margins of the range of a species and therefore was unable to counteract the high seedling mortality rates. Thus, to avoid enhanced future carbon losses, a rethinking of management practices may be required. Without planting species that are adapted to future climatic conditions and promoting high species diversity, the environmental and economic consequences may be disastrous (Millar et al. 2007; Thomas Ledig and Kitzmiller 1992).

Soil carbon stocks were simulated to decrease or increase only slightly toward the end of the simulation period (Tables 2, 3), as found in previous studies with the related model LPJ (Zaehle et al. 2007). However, other dynamic vegetation models showed an increase in global soil carbon stocks under climate change (Sitch et al. 2008). Indeed, the quantification of the impact of elevated temperature on decomposition rates is still subject to discussion (Davidson and Janssens 2006; Hakkenberg et al. 2008). Consequently, soil carbon turnover and its dependency on temperature continue to be modeled differently with different vegetation models (Portner et al. 2009), leading to quantitative and qualitative differences in simulation results, thus indicating considerable uncertainty due to methodological difficulties.

In LPJ and LPJ-GUESS, decomposition rates depend on temperature using a general empirical relationship (Zaehle et al. 2007). Its effects are clearly visible when comparing

CTR_CLIM and CTR_CO2 (Table 3): when CO_2 did not increase, but climate changed, i.e., temperatures increased, decomposition rates were highest, thus leading to minimum soil carbon. An increase in CO_2, but constant temperature and precipitation patterns, resulted in increasing soil carbon stock due higher litter production rates. Besides rising temperatures, other factors such as management or land use changes may augment the decrease in soil carbon stocks (Heikkinen et al. 2013), but these were not considered in our study.

At sites that are exposed to climatic limitations already under the current climate, i.e., at warm-dry sites or near upper treeline, forests showed the highest susceptibility to climate change, confirming the findings by Elkin et al. (2013). For the Rhone valley, the Engadin, Basel, and Schaffhausen, losses in vegetation carbon were simulated for all 'extreme' scenarios (Figs. 2, 3). Drought-induced growth reductions and increases in mortality for Scots pine in the Swiss Rhone valley and a shift toward the more drought-tolerant pubescent oak forests were reported in several studies (e.g., Bigler et al. 2006; Dobbertin et al. 2007; Rebetez and Dobbertin 2004; Rigling et al. 2013). In contrast, regions close to the current treeline were simulated to experience a strong increase in vegetation carbon stocks (Fig. 5). Indeed, growing conditions at current upper treeline in the European Alps have improved already, leading to ingrowth as well as upward shifts of forests near the current treeline—though not only due to climate but also due to land use changes (Gehrig-Fasel et al. 2007; Bolli et al. 2007).

Earlier simulation studies have shown that simulated carbon stocks depend on the underlying climate scenarios (Berthelot et al. 2005; Schaphoff et al. 2006; Scholze et al. 2006). Due to the breadth of climate scenarios employed here, we were able to identify that only simulations using the 'moderate' and 'medium' variants of the scenarios A1B and A2 show an increase in vegetation carbon at currently dry sites toward the end of this century and in the twenty-third century (Figs. 2, 3), whereas all other scenarios resulted in decreasing vegetation carbon. The increases were caused by shifts from needle- to broadleaved species that were accelerated when climate exceeded the tolerances of the needle-leaved species. The resulting high mortality improved establishment and growing conditions for new, more warmth- and/or drought-adapted species. However, this does not necessarily imply that under such climate conditions, ecosystem services from forests would generally be safe. As Elkin et al. (2013) pointed out, some ecosystem services such as protection against rockfall or avalanches depend on particular tree species mixtures. Furthermore, extensive losses of Norway spruce, 'the major commercial tree species in Europe,' would be likely to reduce strongly the economic value of forest stands in Switzerland (Hanewinkel et al. 2013).

Interestingly, for the scenario with the weakest climate change signal (RCP3PD, Table 1), some areas showed an increase but others an decrease in vegetation carbon stocks under all variants, while the more severe scenarios tended to show an increase in carbon stocks. Koca et al. (2006) also found a higher carbon storage capacity with a higher CO_2 emission scenario compared to an 'environment oriented' scenario; the authors argued that higher CO_2 concentrations allowed for a higher fertilization effect. However, we showed that the effect is higher in the long term under climate change than without, which means that rising CO_2 is not the sole driver.

Finally, it is noteworthy that climatic growing conditions in the RCP3PD scenario were worse than before climate change, but not sufficiently poor (as in A1B and A2) to allow for adaptation such as species shifts that then would have been able to compensate carbon losses. Still, even under the smallest amount of climate change, some species shifts take place, although much more slowly, as indicated by the slight increase in vegetation carbon in the RCP3PD scenario by the end of the simulations in 2300.

Conclusion

This study provides a national overview of climate change impacts on potential carbon storage in Switzerland based on three novel climate scenarios, each featuring a quantification of the inherent uncertainty. As management was not included here, we recommend disentangling its effect in a follow-up study to provide recommendations for actions that support policy makers directly.

We demonstrated that species shifts maintain the current capacity of forests to act as a carbon sink over the coming decades and centuries even when management is excluded. Although growing conditions for current species in many areas of Switzerland are deteriorating due to higher temperatures and lower growing season precipitation, increasing CO_2 concentrations and particularly shifts to climatically better adapted species may lead to the maintenance of a carbon sink.

The magnitude and rate of change of carbon storage and tree species composition at the sub-national scale depend on the initial climatic conditions, the severity of the climate scenario as well as its uncertainty; for example, the more extreme scenarios such as A1B and A2 induce strong species shifts and thus allow for a faster adaptation of the ecosystem to the new conditions, including higher future vegetation carbon storage than under the smallest climate change (RCP3PD).

The uncertainties inherent in the climate scenarios lead to a high uncertainty in the simulation results; for example, sites that are prone to heat waves and droughts under current climatic conditions will experience losses in carbon stocks under the most 'extreme' assumptions in all scenarios but not necessarily under 'moderate' or 'medium' conditions. This suggests that while the national signal (i.e., continued carbon sink capacity) is relatively robust, the sub-national (regional) signal may be much less trustworthy. This uncertainty needs to be taken into account in ecosystem management strategies, as they are typically developed at spatial scales much below the national scale.

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