RESEARCH ARTICLE

Soil carbon pools in Swiss forests show legacy effects from historic forest litter raking

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Abstract Globally, forest soils contain twice as much carbon as forest vegetation. Consequently, natural and anthropogenic disturbances affecting carbon accumulation in forest soils can alter regional to global carbon balance. In this study, we evaluate the effects of historic litter raking on soil carbon stocks, a former forest use which used to be widespread throughout Europe for centuries. We estimate, for Switzerland, the carbon sink potential in current forest soils due to recovery from past litter raking ('legacy effect'). The year 1650 was chosen as starting year for litter raking, with three different end years (1875/1925/1960) implemented for this forest use in the

biogeochemical model LPJ-GUESS. The model was run for different agricultural and climatic zones separately. Number of cattle, grain production and the area of wet meadow have an impact on the specific demand for forest litter. The demand was consequently calculated based on historical statistical data on these factors. The results show soil carbon pools to be reduced by an average of 17 % after 310 years of litter raking and legacy effects were still visible 130 years after abandonment of this forest use (2 % average reduction). We estimate the remaining carbon sink potential in Swiss forest due to legacy effects from past litter raking to amount to 158,000 tC. Integrating historical data into biogeochemical models provides insight into the relevance of past land-use practices. Our study underlines the importance of considering potentially long-lasting effects of such land use practices for carbon accounting.

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Research Unit Soil Sciences, Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland **Keywords** Historical ecology · Land-use legacy · Soil carbon pool · Biogeochemical modeling · Recovery time · Switzerland

Introduction

Soils play an important role in the global carbon cycle. The majority of carbon in terrestrial ecosystems is stored in soil organic matter and most thereof in forest soils (Dixon et al. 1994; Janzen 2004). Focusing on



temperate forest ecosystems, the carbon pool in forest soils is approximately twice as large as the pool in forest vegetation (Malhi et al. 1999). Forest soil carbon pools are characterized by slow accumulation rates but fast losses, which makes them susceptible to natural and anthropogenic disturbances, and consequently recovery from such disturbances is a very long lasting process (e.g., Smith et al. 1997; Thürig et al. 2005; Jandl et al. 2007). Recent studies identified European forests as large sinks for atmospheric CO₂ (Ciais et al. 2008). Important factors for this sink are the increase of standing timber volume in consequence of modern management systems, enhanced tree growth due to CO2 and N fertilization, and forest expansion after land-use abandonment on marginal agricultural land (Alberti et al. 2008; Luyssaert et al. 2010). In a recent modeling study Bellassen et al. (2011) found a large relative contribution of CO₂ fertilization compared to effects by changes in climate and forest age structure for European forests. Other processes such as the contribution of forest ecosystem recovery from historic forest uses are still largely unknown but considered to have important effects (Ciais et al. 2008; Luyssaert et al. 2010).

Forest litter raking used to be a common traditional non-timber forest use historical widespread in Central European forests (Bürgi and Gimmi 2007). The leaves and needles removed from the forest floor were mainly used as a substitute for straw to bind the cattle's manure in the barn (Gimmi and Bürgi 2007). With the rise of modern forestry in the nineteenth century traditional forms of forest use came into conflict with the aim to maximize timber production. The practice was so prevalent that concerns about reduced soil fertility and consequences for tree growth and hindered regeneration due to litter raking became an almost standard issue in forest management plans of this period (Bürgi 1999; Gimmi and Bürgi 2007). In some remote regions, such as in inner-alpine valleys, litter raking was practiced until 50 years ago (Gimmi et al. 2008). In a pioneer study, Ebermayer (1876) explored the negative effects of continuous litter removal on nutrient cycling, tree recruitment and tree growth. More recent studies experimentally proved that nutrients (mainly nitrogen and phosphorous) were depleted as a consequence of repeated litter removal (Glatzel 1990; Glatzel 1991; Dzwonko and Gawronski 2002) and detected long recovery times after abandonment of the practice (Hüttl and Schaaf 1995). Current tree species composition is also considered to be largely shaped by the legacies of past litter removal, even decades after abandonment of the practices (Gimmi et al. 2010).

Experimental and local case studies help to understand the mechanism behind the effects of past litter raking activities on biogeochemical cycling. However, to assess the broader scale impacts these findings need to be integrated in ecosystem models that enable to upscale the effects (Kaplan et al. 2012). For example, Perruchoud et al. (1999) included time series of litter removal in a model for the twentieth century carbon budget of forest soils in the Swiss Alps. However, the authors qualified their assessment of litter removal as too simplistic due to a lack of reliable quantitative data on historical litter harvesting. Our study aims to overcoming these limitations by quantifying the effects of traditional litter removal on carbon pools in forest soils across Switzerland by combining detailed historical information on traditional forest litter raking with ecological modeling techniques.

Specifically our research goals are to:

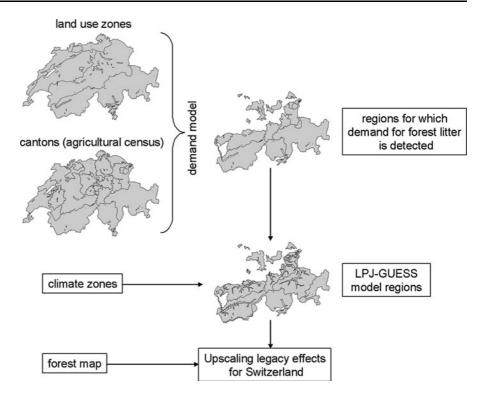
- (a) Estimate the demand for forest litter across Switzerland for 1850, 1900 and 1950
- (b) Construct historic litter raking scenarios.
- (c) Evaluate the effects of historic litter raking scenarios on the forest soil carbon budget.
- (d) Estimate the carbon sink potential in current forest soils due to recovery from past litter raking for entire Switzerland.

Data and methods

Our approach to estimate the carbon sink potential in Swiss forest soils due to past litter raking is split into three steps (Fig. 1). The first step includes a model to estimate the local demand for forest litter over time and is based on information on historic distribution of typical land use zones across Switzerland and historical agricultural census data. Based on the results we extracted those regions for which we detected demand for forest litter. In the next step we run a biogeochemical model (LPJ-GUESS) for different climate zones and vegetation types to assess the impact of long-term litter removal on the forest soil carbon budget. In the final step, we upscaled the model results to the entire



Fig. 1 Conceptual diagram illustrating the procedure to estimate the carbon sink potential in Swiss forest soils due to recovery from past litter raking



Swiss forest area formerly affected by litter raking. The procedure is described in full detail in the following sections.

Estimate local litter demand over time

The two basic factors determining the demand for forest litter are (a) the number of animals (mainly cattle) that have to be supplied with bedding material and (b) the availability of substitute products (straw from crop production and litter from wet meadows) that alternatively could be used to replace forest litter (Gimmi et al. 2008). Consequently, the local demand for forest litter is strongly related to the regional agricultural system (i.e., area of grain production) and ecological setting (i.e., area of wet meadows). In order to achieve a realistic assessment on the spatiotemporal distribution of historic forest litter removal and to generate reliable estimates on the quantitative forest litter demand we need information about the contemporary agricultural system and its development over time. Agricultural zones were delineated based on Paravicini (1928) who described and mapped land-use systems existing in Switzerland in the late nineteenth century that have remained remarkably consistent. We aggregated the 23 land-use types into 8 generalized types and evaluated the relative importance of animal versus crop production for each type according to data available for selected municipalities in Paravicini's publication (Table 1). Numerical data for livestock (cattle only) and grain production area were derived from the Federal Agricultural Census (Ritzmann-Blickensdorfer 1996). These data were available on cantonal level (the Canton is the highest administrative unit in Switzerland) back to 1850. Cattle number and grain production area were allocated to the specific land-use types within the Cantons using spatial weighting and considering the importance of livestock versus crop for the specific land use type.

Based on previous evaluations of litter demand for livestock (Gimmi et al. 2008) we assumed the annual need for litter biomass to be 480 kg per head of cattle in the lowlands and 200 kg in alpine areas. The higher demand in the lowlands is because the animals were kept indoors during the entire year whereas in alpine areas the litter was mainly used during wintertime. From the resulting total regional litter demand we calculated the demand for forest litter by subtracting the amount of regionally available substitute products (straw and litter from wet meadows). For straw production we applied an average straw yield of three tons fresh biomass per hectare considering the main



Table 1 Relative importance of grassland versus crop economy for different land use systems based on information from Paravicini (1928)

Land use type	Relative area used for grassland farming	Relative area used for crops	Area (excluding large lakes)	
Improved three field system	0.75	0.25	2,157 km ² (5.2 % of Switzerland)	
Pure grassland farming	0.99	0.01	2,100 km ² (5.1 %)	
Grassland farming with crops	0.79	0.21	1,141 km ² (2.8 %)	
Grassland/Clover farming	0.77	0.23	7,655 km ² (18.5 %)	
Pasture farming in alpine areas	1	0	9,747 km ² (23.6 %)	
Agriculture of the Jura mountains	0.87	0.13	2,697 km ² (6.5 %)	
Agriculture of Alpine valleys	0.75	0.25	635 km ² (1.5 %)	
Alpine subsistence farming	0.93	0.07	13,829 km ² (33.5 %)	

grain types historically cultivated in Switzerland (data from Becker-Dillingen 1927). Further we assumed that only 50 % of locally produced straw was actually used as litter because straw was also used to feed animals in times of scarcity or was used as roofing material. We estimated regional total litter demand and straw production for 1850, 1900 and 1950. In addition, we used information on the historic extent and distribution of wet meadows from Früh and Schröter (1904) in order to quantify litter production from wetlands. The estimate for 1900 was directly adopted from a map published the Früh and Schröter showing the extent and spatial distribution of fens. Estimates for 1850 and 1950 have been interpolated by applying known historical trends in wetland cover changes for the Canton of Zurich (Gimmi et al. 2011). An average yield of 4.6 t biomass per hectare of fen has been applied according to information from historical data on litter yield from wet meadows (Statistische Mittheilungen betreffend den Kanton Zürich 1884–1910).

As a last assumption we included improved supraregional import possibilities for straw into our forest litter demand model. Over time, improved transport infrastructure and higher income level made less expensive straw imports affordable (Gimmi et al. 2008). For 1850 we considered for all regions only local production and no straw import. For the lowlands (see land use type 1–4 in Table 1) we assumed that in the twentieth century the entire demand for forest litter could be accommodated by straw imports from outside the regions. In the better accessible parts of the alpine area (land use types 5–7 in Table 1) we assessed a 50 % reduced demand in 1900 and a complete cover of the demand in 1950 due to straw

import. For the regions within the alpine subsistence farming zone (type 8) we reduced the demand by 25 % for 1900 and by 75 % for 1950 respectively.

Modeling the impact of litter removal on forest soil carbon pools

Information from historic sources (e.g. forest management plans) on where litter raking was practiced is generally limited in spatial accuracy (e.g. Gimmi and Bürgi 2007). There is circumstantial evidence that forest litter harvesting was practiced in specific regions or that litter was removed from specific forest stands, but it is not possible to identify the exact location of the past practice (Gimmi and Bürgi 2007). Consequently, it is not possible to measure the legacy effects due to past litter raking through direct measurements of soil carbon content. Alternatively, experimental approaches are only able to recreate the effects of litter raking over a few years duration (e.g., Dzwonko and Gawronski 2002) and do not allow for assessing long term carbon depletion or long term soil carbon recovery after the abandonment of raking. Due to these limitations we employed a biogeochemical ecosystem model to estimate carbon dynamics in forest soils disturbed by litter raking.

We assume that the current state of recovery of long-term raked forest soils varies with the time since abandonment of the practice. In accordance with findings from previous studies on litter harvesting practices in Switzerland (Bürgi 1999; Bürgi and Gimmi 2007; Gimmi et al. 2008) we fixed the starting year of simulated litter harvesting to 1650 and implemented three scenarios for the end year (1875/1925/1960). We restricted our simulation to those



Table 2 Climate regions used for modeling impact of litter removal

Climate region	Station (low elevation)	Altitude Station (high elevation) (masl)		Altitude (masl)
Jura east	Basel-Binningen (BAS)	316		_
Plateau northeast	Güttingen (GUT)	440		
Plateau central	Buchs Aarau (BUS)	387		
N-Alps east	Vaduz (VAD)	460	Elm (ELM)	965
N-Alps central	Altdorf (ALT)	449	Engelberg (ENG)	1,035
N-Alps west	Interlaken (INT)	580	Adelboden (ABO)	1,320
Grisons	Chur (CHU)	556	Davos (DAV)	1,590
Valais	Visp (VIS)	640	Montana (MVE)	1,508
Engadin			Scuol (SCU)	1,298
S-Alps			Piotta (PIO)	1,007

climate by forest type categories where we modeled a demand for forest litter (see Fig. 1). In total, four litter harvest scenarios (including a no-harvest scenario) for 15 different climatic regions across Switzerland (Table 2, based on the climate classification scheme developed by Schüepp and Gensler (1980)) were conducted.

To simulate the effect of historic litter harvesting we used the biogeochemical model LPJ-GUESS (Smith et al. 2001). LPJ-GUESS is a forest gap model that simulates the development of forest cohorts (groupings of trees by age) through production and intra- and inter-specific competition. The advantage of the LPJ-GUESS model is that the carbon uptake and forest dynamics can be represented at the species level, making it appropriate for local-scale studies. Photosynthesis is estimated on a daily time step using the biochemical model of Farquhar (Farquhar et al. 1980) that is coupled to soil-moisture stress via water demand (Monteith 1995). Each year, the turnover of dead biomass simulated for tree, grass, foliage and woody carbon pools first enters a litter carbon pool, from which 70 % of the foliage carbon is directly respired to the atmosphere and the remaining 30 % of biomass enters the soil carbon pool. Of this dead biomass entering the soil carbon pool, 98 % enters an intermediate soil carbon turnover pool and 2 % into a slow carbon turnover pool based on fixed fractions determined by Meentemeyer (1978). The carbon respired from the litter, intermediate and slow turnover pools (i.e., maximum turnover rate for heterotrophic respiration, set to 2.85, 33, and 1000 years, respectively) are adjusted by a modified-Arrhenius soil temperature response and soil moisture (Foley 1995).

We modified the aboveground litter biomass inputs to the soil litter pool of LPJ-GUESS (and hence the intermediate and slow turnover pools) to annually remove leaves and foliage off-site, thus simulating the effects of litter harvesting. This included removing leaf and grass biomass following natural senescence when deciduous trees lose their leaves in winter (or when a fixed proportion of evergreen leaves turnover each year), and also included the harvesting of biomass from seed and fruit reproduction (fixed 10 % of net primary production in LPJ-GUESS). The biomass from dead wood entering the litter pool was not harvested and entered the soil carbon and litter pools as described by Smith et al. (2001).

The model requires forcing data for temperature, precipitation, radiation, CO₂, soil texture, and species information for simulations. For the 15 sites in our study, we accessed daily climate data (1960–2009) from the MeteoSwiss database (CLIMAP) and aggregated these to monthly values. Monthly climate data at 0.5 degree spatial resolution, from 1901 to 2009, were also obtained from the Climatic Research Unit (CRU TS3.0) (New et al. 2000). Climate anomalies from CRU TS3.0 were added to the MeteoSwiss 1961–1990 climate baseline to generate a twentieth Century time series of monthly temperature and precipitation for each site. The observed mean monthly radiation data were simply recycled to extend before the observation period. The first 30 years (1901–1930) of climate data



were also recycled beginning in year 1501 to recreate historical conditions but with pre-industrial CO₂ levels (285 ppm). Species parameterization represented vegetation common to European forests (Hickler et al. 2012), and three sets of species mixes were simulated to evaluate different vegetation types within each climate zone (i.e., mixed forests, pure broadleaf, and pure evergreen phenology types). LPJ-GUESS was run in cohort mode, simulating stochastic establishment, mortality, and deterministic growth for 100 patches (1,000 m² in size). Following a 1000-year spin up to reach soil and vegetation equilibrium, and then transient simulations (1501–2005), the patch-level data were averaged at the end of the simulation to represent mean forest conditions.

Upscaling legacy effects for Switzerland

For upscaling the legacy effects for Switzerland, we extracted the proportion of conifer, mixed and deciduous forests for each region from country level land cover data (BFS Bundesamst für Statistik 2001). This procedure allowed for calculating the annual biomass of litterfall for the regions based on our biogeochemical model results, i.e., the amount of litter potentially available to be raked. We used this information in combination with our regional forest litter demand estimates to hindcast the forest area necessary to fulfill the demand for forest litter for all time steps (assuming that land cover was constant—see "Discussion and conclusion"). By summing up the differences between model results for non-raked stands (control scenarios) and the stands affected by litter raking, we evaluated the future carbon sink potential of contemporary forests.

Results

Changes in demand for forest litter and forest proportion affected

We estimated the annual demand for forest litter for entire Switzerland up to 82,300 tons of dry biomass around 1850, 48,000 tons in 1900, and still 10,600 tons in 1950 respectively. The highest absolute demand was calculated for the pasture farming areas especially in the Bernese Alps and the areas dominated by subsistence farming. In order to accommodate this demand (accounting for substitute products), we estimated that

about 93,000 ha had to be raked until 1850, reducing to 58,000 ha in 1900 and 12,000 ha in 1950. For the mid nineteenth century we estimated high pressure on the forest especially at the northern fringe of the Alps, where up to 55 % of the forest area below 1,800 m elevation had to be raked annually to fulfill the local demand for forest litter (Fig. 2). Medium pressure (30-40 % of the forest area affected) was found for lowland regions with pure grassland farming. Until 1900 we observed an almost constant demand in the alpine areas whereas litter raking completely disappeared from the lowland north of the Alps. In the inneralpine zones with subsistence farming we observed a relatively low but continuous pressure on the forests until the mid twentieth century. The high absolute demand for forest litter was partially absorbed by the large forest areas available in these regions. No litter harvest pressure was found over the entire period for large parts of the lowlands, the Jura region in the northwestern part of Switzerland and the valley bottoms in the Valais and the Ticino region because of the availability of substitute products and imports.

Modeled effects of litter raking scenarios on forest soils

The modeled impact of litter removal scenarios on the three different soil carbon pools distinguished by LPJ-GUESS (litter, intermediate and slow pool) is shown for the example under Davos climate (Grisons high elevation climate region in Table 2) in Fig. 3. The litter carbon pool features an immediate reaction at the onset of litter raking, levels off approximately 0.2 kg/m² lower after a few years and recovers rapidly after abandonment of raking. The intermediate carbon pool show largest absolute carbon depletion after long term litter raking (up to 0.82 kg/m²). The behavior of the slow carbon pool is characterized by a slow but steady response to litter removal and an even slower recovery. Absolute carbon depletion in the slow carbon pool is relatively low (maximum 0.06 kg/m²). The resulting maximum depletion of the total carbon pool adds up to 1.2 kg/m² after long term litter removal. Both depletion and recovery are clearly non-linear processes.

Across all vegetation types and climate zones, soil carbon pools display a mean reduction of 17.4 % after long term (310 years from 1650 to 1960) simulated litter removal. Carbon depletion was significantly



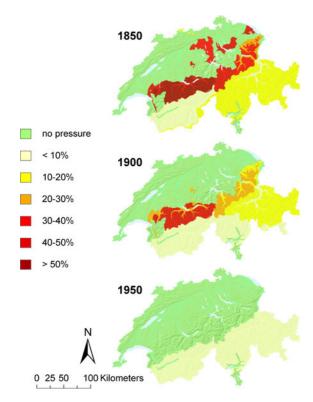


Fig. 2 Proportion of forests below 1,800 masl to be raked in order to accommodate the local demand for forest litter in 1850, 1900 and 1950

lower in conifer stands (13 %) than in deciduous (19.5 %) and mixed stands (18.2 %) (Fig. 4). Less productive stands at higher altitudes tended to display higher relative depletion than more productive sites. However, the relationship between productivity, altitude and carbon depletion did not turn out to be statistically significant, probably due to our low sample size. Soil carbon pools were able to recover considerably within a few decades after abandonment of litter raking (Fig. 4). However, legacy effects from litter harvest were still observed after 130 years of soil carbon recovery (Fig. 5), with recovery rates largely determined by the rates of litter input (not shown).

Legacy effects and carbon sink potential in Swiss forests due to past litter raking

We estimate today's carbon sink potential in Swiss forest soils due to legacy effects from past litter raking to amount to 158,000 tC. We found the highest legacy effects in regions affected by litter raking until 1960 (Fig. 6) and at the sites with lower aboveground

productivity. Some of the stands display a relatively large sink potential of more than 4 tC per hectare. Overall, formerly raked stands across the entire alpine region of the country typically show a carbon sink potential between one and four tons per hectare (about 70–280 % of current net annual increment of Swiss mountain forests (Brändli 2010)). But also forests in the lowlands where litter raking has been abandoned since 130 years still show a small soil carbon sink potential compared to control simulations.

Discussion and conclusion

Our study is relevant for carbon accounting, as forest soils in stands historically affected by long-term litter raking still show reduced carbon pools up to more than a century after abandonment of this practice. This underlines that considering the long-lasting effects of historical land-use practices is not only important for biodiversity and forest stand composition (Dambrine et al. 2007; Chauchard et al. 2007; Gimmi et al. 2010), but is also relevant for biogeochemical cycling. This confirms the limited ability of forest soils to recover from anthropogenic disturbances within short periods (Dupouey et al. 2002). Our results add to recent efforts aiming at quantifying the relative contribution of different factors to carbon sink effects in European forests (Luyssaert et al. 2010; Bellassen et al. 2011). The total carbon sink potential in Swiss forest soils due to effects from past litter raking is estimated to amount to 158,000 tC, which means that Swiss forest soils could potentially sequester additional 580,000 tons of atmospheric CO₂ due to this legacy effect (where 1 t C is equal to 3.67 t CO_2). This is about 6.5 times theannual Swiss Land Use Land Cover Change (LULCC) emissions (United Nations Framework Convention on Climate Change (UNFCCC): National Inventory Submissions 2011). However, it remains unclear the timeframe (i.e., decades to centuries) within which soil carbon pools could fully recover and reach equilibrium. Typical annual C-accumulation in Swiss forests soils is about 0.11–0.58 Mt (Perruchoud et al. 2000), but non-linear accumulation of carbon as demonstrated in our study (see Fig. 3) makes estimating recovery speed difficult. Generally, it appears challenging to model accurately the time-lag of recovery after abandonment of historic forest management activities (Weber et al. 2008).



Fig. 3 Development of different soil carbon pools (litter/intermediate/slow and total pool) in LPJ for three different land use scenarios in conifer forests under Davos climate (see Table 2). Start of litter raking for all scenarios in 1650. The black lines indicate abandonment in 1875, red 1925, and green 1960. Values are given as difference (kg/m²) to control scenario without litter raking (dashed line). Note the different scales on y-axis

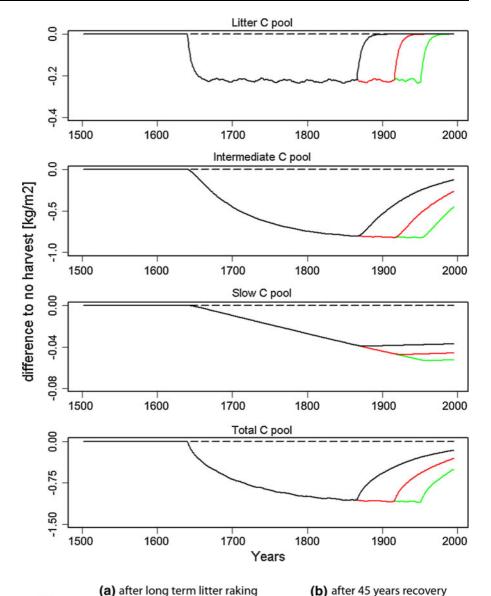
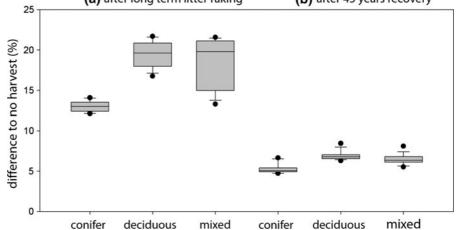


Fig. 4 Soil carbon depletion (a) after long term (1650–1960) litter raking and (b) followed by 45 years recovery after abandonment of litter raking. Comparison between conifer, deciduous, and mixed forests. Values are given as relative difference to control scenarios without litter raking





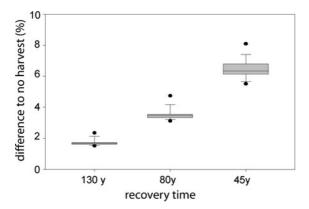


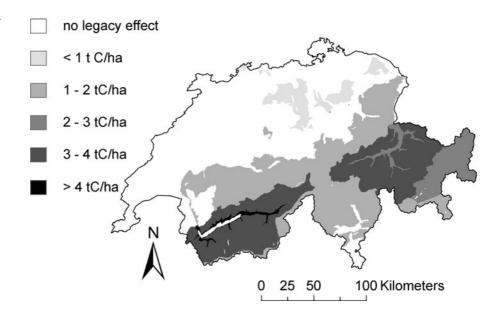
Fig. 5 Soil carbon depletion in mixed forest stands after long term litter raking and for different timeframes of recovery (130, 80 and 45 after abandonment of litter raking). Values are given as relative difference to control scenarios without litter raking

Our results include various uncertainties deriving either from assumptions made for the assessment of historical forest litter demand or constraints inherent in the biogeochemical model for litter production and soil carbon dynamics. However, we designed the study in a way that both the results for historic forest litter demand and the model estimates for carbon depletion are conservative, i.e., they tend to underestimate the forest area affected by historic litter raking and the amount of carbon depletion, respectively. Consequently, our final estimates for the future carbon sink potential due to recovery from past litter raking represents rather a minimum estimate. For example

we did not include the use of dry leaves to stuff mattresses, blankets, and pillows, despite this practice was common in some regions (Roth and Bürgi 2006) and our estimates for litter demand per head of cattle (480 kg in the lowlands and 200 kg in alpine areas) are at the lower end of the demand estimates (Gimmi et al. 2008). Further, we included the full amount of litter potentially available from wet meadows to the model although it's very likely that some fens were not suitable for litter production or have not been managed for this purpose. The pressure on the forests would have been higher in case of a lower litter contribution from wet meadows. In contrast, the decision for not including the full amount of straw is justified because straw has been used also for other purposes than for litter. However, this assumption was not very relevant for the demand model because most regions where we detected a demand for forest litter displayed very low grain production anyway. Also we did not consider short term fluctuations in the litter demand such as the enhanced pressure on the forest due to reduced straw imports during World War I and II (see Perruchoud et al. 1999) because we assume that such short term litter raking had no relevant impact on the carbon balance of forest soils.

A major limitation of the applied biogeochemical model is that it does not take into account soil-nutrient feedback processes between above and belowground processes. Soil-nutrient feedbacks have only recently been considered in biogeochemical models because of

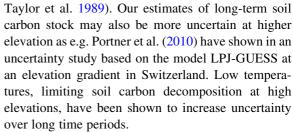
Fig. 6 Current reduction of carbon pools in forests soils for stands historically affected by litter raking





uncertainty in processes related to mineralization, nutrient uptake, and effects on productivity (Thornton et al. 2007). Consequently, the effects of soil nutrient depletion—through the removal of nutrient inputs from fresh grass and foliage litter—on productivity is not captured. It can be assumed that for aboveground growth, the depletion of C and at the same time lacking N input into the soil via litter is of minor influence as long as N is not strongly limited. Hence, we hypothesize that the influence of litter raking on the nutrient balance is playing a more decisive role at locations with higher soil C:N ratios, indicating nutrient limitation (Högberg et al. 2006). In Switzerland, this is particularly common at higher elevated forest sites where soil formation is more slowly due to lower temperatures and high precipitation and snow accumulation, respectively (Blaser et al. 2005). In this case, also originally productive sites may decrease in growth on the long-term and even may have a C sink potential not just below but also aboveground due to this legacy effects. In the model the biomass from dead wood entering the litter pool was not modified. Historically, in many forests, particularly in those near settlements, a large portion of the dead wood was removed and used for fire wood. This additional biomass removal would cause a stronger C depletion than modeled for litter collecting alone.

Turnover times of soil carbon pools and the fractionation of carbon between the pools represent an additional source of uncertainty as they may not be constant, but dependent on other factors such as climate or soil texture. As shown by Yurova et al. (2010) in a sensitivity analysis of the soil carbon dynamics of the LPJ DGVM (which has the same soil dynamics as LPJ GUESS), variations in the parameters of litter decomposition rate and the two fractionation parameters can result in high uncertainties upon estimation of soil carbon stocks. Because LPJ-GUESS does not differentiate between different litter qualities, the decomposition rates of LPJ-GUESS reflect more the decomposition rates of broadleaved litter, our estimates of soil carbon stocks therefore may be too low at higher elevations (or just at sites with needle leaved forest) as litter from different plant organs and different plant species is known to vary in its decomposition rate, needles and roots e.g. decompose slower than leaf litter (Gholz et al. 2000) and decomposition of woody litter depends on lignin concentrations (Melillo et al. 1984; Edmonds 1987;



We also assumed constant forest cover (current forest cover based on modern forest distribution map) for our estimates on the forest area historically affected by litter raking. There is strong evidence that the forest area was considerably lower in 1850 and gradually increased since then (Mather and Fairbairn 2000). This would increase the percentages of forest area affected (Fig. 2) but not have an influence on the total area affected and on the overall legacy effect (Fig. 6).

Numerous studies dealing with land-use change effects on terrestrial carbon balances have focused on effects from major land-use transition such as agricultural abandonment and forest re-growth (e.g., Smith et al. 1997; Post and Kwon 2000; Hurtt et al. 2006). We demonstrate with our study that land-use change that is not reflected in a change in land-cover, can cause long-lasting legacy effects in forested ecosystems. With our study we show that the integration of historical data into biogeochemical models is a useful way to gain important insights into the ecological relevance of past land-use practices.

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