

Published as:

Loran C¹, Munteanu C², Verburg PH^{1,3}, Schmatz DR¹, Bürgi M¹, Zimmermann NE¹ (2017) **Long-term change in drivers of forest cover expansion: an analysis for Switzerland (1850-2000).** *Regional Environmental Change*. doi:10.1007/s10113-017-1148-y

¹ WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

² SILVIS Lab, Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA

³ Environmental Geography Group, VU University Amsterdam, de Boelelaan 1087, 1081 HV Amsterdam, The Netherlands

This document is the accepted manuscript version of the following article:

Loran, C., Munteanu, C., Verburg, P. H., Schmatz, D. R., Bürgi, M., & Zimmermann, N. E. (2017). Long-term change in drivers of forest cover expansion: an analysis for Switzerland (1850–2000). *Regional Environmental Change*, 17(8), 2223–2235. <https://doi.org/10.1007/s10113-017-1148-y>

Abstract

The spatial distribution of forests in Europe represents the legacy of centuries of human land use decisions. Due to the limited availability of historical data, most studies on forest cover change focus only on analyzing recent decades, thereby overlooking the important long-term context. However, the latter is essential to improve our understanding of present landscape patterns. This study quantifies the spatio-temporal dynamics in drivers of forest gain in Switzerland. Specifically, we model forest gain in a long-term study covering 150 years (1850-2000) split into periods of similar length (~30 yrs). This makes it possible to identify non-linear dynamics and whether drivers have changed over time. The rates of forest change are quantified based on analyzing historical maps and contemporary forest inventory data. Generalized Additive Models (GAMs) are fitted to examine the variation in the relative importance of socioeconomic and biophysical explanatory variables. Our results suggest that both biophysical and socioeconomic variables co-drive forest gain. Biophysical variables (such as temperature and slope) were identified as the major drivers explaining variations in forest gain. The most important socioeconomic driver was the change in the percentage of people employed per economic sector, although its effect came with a substantial time lag. Changes in employment per sector for the periods 1920-1941 and 1941-1980 were relevant for forest gain between 1980 and 2000. The identified time-lag effect emphasizes the added value of long-term studies, since legacies may persist for decades, adding further complexity to contemporary land-change processes. These findings are relevant to many temperate ecosystems that are experiencing increases in forest cover. Such insights can improve both future forest change predictions as well as the development of policies for sustainable landscape management.

Keywords: long-term forest cover expansion, socioeconomic and biophysical drivers, Switzerland, time-lag effect, historical maps

Introduction

Human decisions and land management activities have changed and shaped our landscapes over centuries. A current example of human influence on land use and cover change (LUCC) is the abandonment of agricultural land due to decreasing economic income from and the importance of agriculture (Lambin & Meyfroidt 2011, Melendez-Pastor et al. 2014, Price et al. 2015), which has triggered forest regrowth in many regions around the globe in recent decades (e.g. Pazur et al. 2014; Jepsen et al. 2015; van Vliet et al. 2015). In particular, marginal areas in mountainous regions with less favorable growing conditions for agriculture have been abandoned due to a lack of profitability or because of new sources of income which have led to reduced economic dependence on agriculture (Mather & Fairbairn 2000; Verburg and Overmars 2009). Positive consequences of forest expansion include stabilization of soils, protection against landslides in mountainous areas (Tasser et al. 2013; Malek et al. 2015), and increased carbon sequestration (Leuschner et al. 2014; Wilkenskield et al. 2014). Besides these positive aspects, negative consequences include the loss of traditional forms of cultivation or the loss of species-rich habitats (Pellisier et al. 2013; van Strien et al. 2014).

Changes in forest cover are driven by of a complex interplay of various natural and anthropogenic processes operating at different temporal and spatial scales. These processes can be considered as underlying drivers, which in turn drive direct proximity causes that are defined as human activities or immediate actions that take place at a given location (Meyfroidt 2015; Plieninger et al. 2016). These drivers are generally categorized as socioeconomic, political, technological, cultural, or natural in origin (Bürgi et al. 2004; Hersperger and Bürgi 2009). Drivers can act remotely in space and time with regard to observed impacts (Serneels & Lambin 2001). Therefore, long-term studies across broad spatial scales are required in order to improve our understanding of recent changes and the emergence of current forest cover patterns as an outcome of past land use (Munteanu et al. 2015; Rhemtulla et al. 2009). Such information is essential for enhanced future landscape management (Antrop 2005; Swetnam et al. 1999).

Switzerland is a highly suitable case study area because it has undergone the two opposing trends of intensification of agricultural land use and increasing urbanization in the lowlands,

and the extensification and abandonment of marginal agricultural land in mountainous areas with subsequent forest regrowth. Without intervention to conserve mountain pasture this process of forest expansion is forecast to continue in many parts in Switzerland (Price et al. 2015). There is increasing concern about forest cover expansion in Switzerland, mostly because traditional agricultural management practice has preserved unique landscapes and habitats of high ecological value which are now threatened (Hunziker 1995). Therefore, forest regrowth is an important topic in current Swiss forest policy discussions (Hirschi et al. 2012), leading to recent changes in Swiss forest law to prevent further uncontrolled forest expansion (FOEN 2013). In order to adopt appropriate additional measures to prevent uncontrolled expansion, knowledge is required about legacy effects on current forest patterns (Levers et al. 2014; Munteanu et al. 2015).

Over the past 150 years, Switzerland has experienced an increase in forest cover. However, this increase has varied strongly through space and time (Loran et al. 2016), indicating that its drivers have likely varied accordingly. To date, these drivers have been studied only over rather short timescales (e.g. Gellrich et al. 2007a; Rutherford et al. 2008) or at rather small spatial scales for case study areas in Switzerland (e.g. Bürgi et al. 2015; Schneeberger et al. 2007). A clear drawback of such short-term studies is the resulting stationary view of drivers and the inability to account for potential time lags (Perz and Skole 2003, Gellrich et al. 2007b) between socioeconomic changes and the visible impact on forest cover. Consequently, temporal scales should be long enough to account for the temporal dynamics in drivers and their potential time lags.

The aim of this study is to quantify the spatio-temporal dynamics in drivers of forest gain in Switzerland between 1850 and 2000. Modelling forest gain by means of its drivers in a long-term study covering 150 years split into periods of change of similar length (~ 30 years) will allow for the identification of non-linear dynamics in which drivers have likely changed over time (Grêt-Regamey et al. 2013; Verburg et al. 2004). To account for regional differences, our analyses were performed for Switzerland at three spatial scales (national, alpine, and biogeographical) by focusing on the following three questions: (1) Does the relative importance of socioeconomic and biophysical drivers vary across Switzerland? (2) How

strongly did past socioeconomic changes influence forest gain? (3) What is the time lag between societal changes and changes in forest cover?

Material & Methods

Study area – forest gain and its potential drivers

Switzerland, located in Central Europe, is characterized by high variability in environmental and cultural conditions, with altitudes ranging from 196 to 4,634 m a.s.l. (SFSO 1997) and landscapes ranging from densely populated lowlands to remote areas in high mountains. This diversity is also expressed in the flora and fauna, which can be divided into six biogeographical regions (Gonseth et al. 2001) (Fig. 1). Forest cover expanded from 20% in 1850 up to 30% in 2000 at the national scale. This overall net gain of 10% over the past 150 years varies strongly across the country (Fig. 1). The most rapid forest gain took place in the decades after 1940. Overall, the highest increase in forest cover occurred in the Southern Alps with 26%.

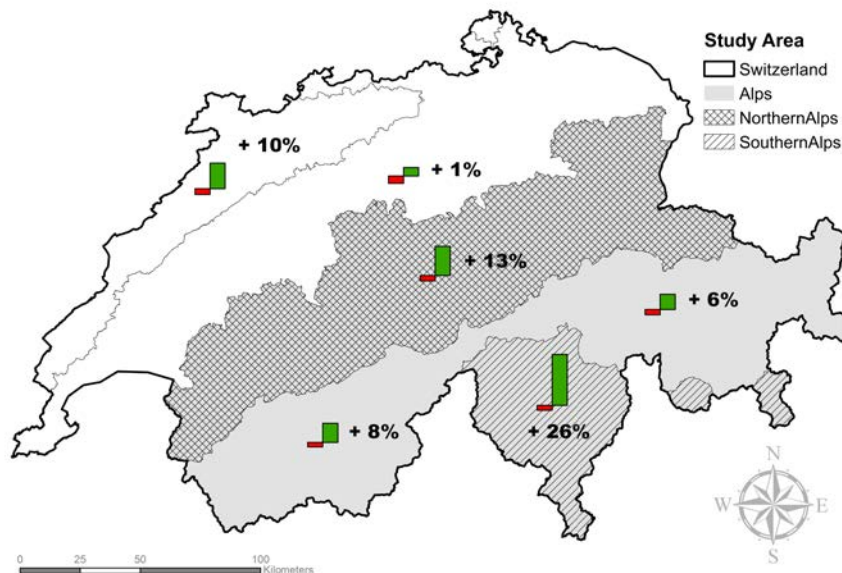
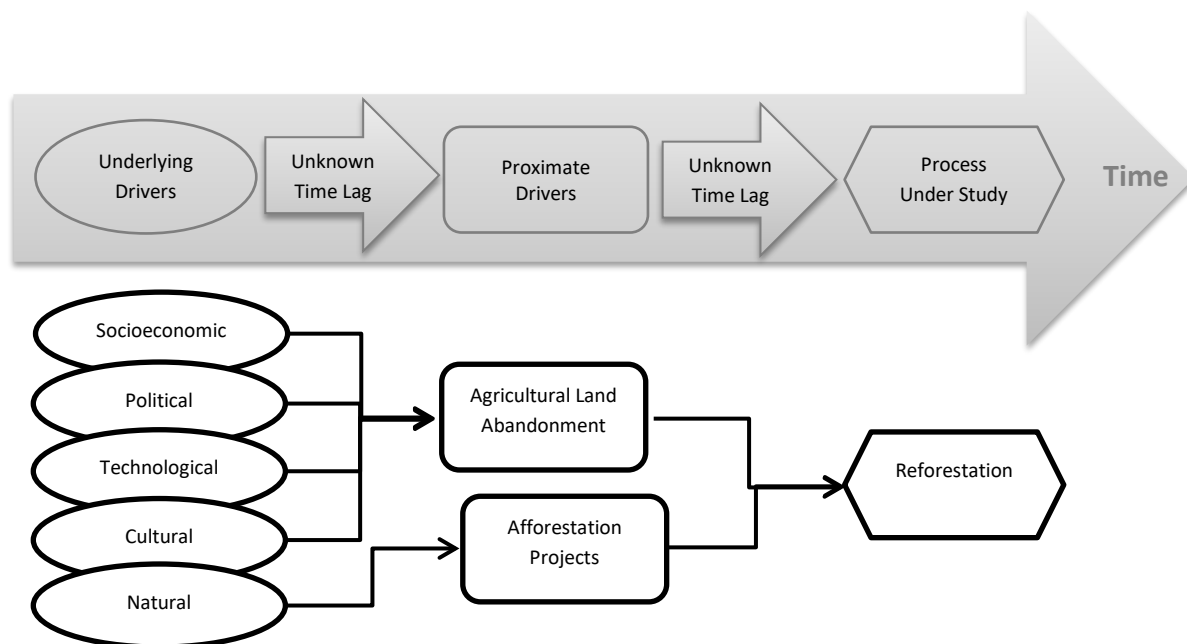


Fig. 1: Switzerland and its six biogeographical regions (*Jura Mountains, Central Plateau, Northern Alps, Eastern Alps, Western Alps and Southern Alps*). Analyses are performed for a) Switzerland, including all biogeographical regions; b) the Alps as a whole (shaded), including all four alpine sub-regions (*Northern Alps, Eastern Alps, Western Alps, Southern Alps*); c) the *Northern Alps* and d) the *Southern Alps* individually. The

bars show the gross forest cover change and the numbers the net forest cover change for each biogeographical region.

Forest cover expansion has at least two main proximate drivers in Switzerland (Fig. 2). On the one hand, afforestation projects took place mainly between 1880 and 1920 in the Jura Mountains and Northern Alps in order to protect the population from further floods (Brändli



2010). On the other hand, natural forest cover gain took place on abandoned agricultural land.

Fig. 2: The underlying and proximate drivers of reforestation in Switzerland, and the potential time lag.

In a Europe-wide analysis by van Vliet et al. (2015), the most relevant underlying drivers (Fig. 2) of land abandonment were identified as being demographic (e.g. population density, migration), economic (e.g. globalization, off-farm employment, urbanization) and institutional (e.g. land consolidation, subsidies, tenure security). In addition, biophysical factors (e.g. accessibility, climate, topography) and farm(er) characteristics (e.g. attitude, age, farming motivation) were also considered important. Of less importance in this European study were sociocultural (e.g. recreation and tourism, societal demand for ecosystem services) and technological drivers (e.g. land improvements, mechanization).

As it is impossible to comprehend all aspects influencing land abandonment and subsequent forest cover expansion in a statistical model, some simplifications are required. We therefore selected a set of predictor variables found to be important in earlier Swiss forest cover change studies from Gellrich and Zimmermann (2007) and Rutherford et al. (2008). Their studies covered the periods 1979-1985 and 1992-1997 and discovered that forest regrowth occurred where cultivation costs were high and yield potential low. Our empirical models will focus on agricultural land abandonment as proximate driver given that we do not have spatially explicit data regarding afforestation projects.

Temporal and spatial scale of statistical models

The temporal scale of this study covering 150 years (1850-2000) is dependent on the availability of historical maps on forest cover at the national scale (Loran et al. 2016). To identify the non-linear behavior of drivers of forest gain, five time periods of similar length were selected (1850-1880, 1880-1910, 1910-1940, 1940-1980, 1980-2000). The spatial extent of the statistical models refer to three scales, namely Switzerland as a whole, the Swiss Alps as a whole, and two of the individual alpine sub-regions—Northern and Southern Alps—where most of the changes occurred. The unit of analysis in the statistical models is the municipality ($n = 2,802$), which was the smallest available unit for socioeconomic variables. Biophysical variables were aggregated from the plot to the municipality level (Tab. 1) in spite of the fact that the strong variability of biophysical variables within municipalities would be lost. This is owing to the fact that running analyses at finer spatial scales would not result in useful information due to the lack of socioeconomic data at that level.

Derivation of the response variable: forest gain (%)

In order to quantify the proportion of forest cover in Switzerland per municipality, we reconstructed forest cover for the past 150 years based on a time series of historical maps (1850 Dufour Original Survey Map, 1880-1940 Siegfried Map series) and contemporary forest data (1980-2000 National Forest Inventory, NFI). The required maps and forest inventory

data are available at the Swiss Federal Institute of Forest, Snow and Landscape Research (WSL) and most of the map series can be viewed online (Swisstopo 2015).

In order to incorporate forest information from the historical maps into statistical models, both point sampling and wall-to-wall mapping are common methods (Kaim et al. 2016). Due to the large spatial extent (all of Switzerland) and the long time span (150 years, represented by six time ranges), point sampling was chosen for this analysis to keep data quantities manageable (Ginzler et al. 2011). The locations of the 20,618 sample plots across Switzerland correspond to the sampling scheme of the official Swiss NFI with a lattice of 1.4 x 1.4 km. Based on this sampling scheme, the forest area is reported from the NFI surveys—which have been conducted approximately every ten years since 1983—and is considered a good statistical approximation of forest area (Brändli 2010). The NFI collects data on trees, stands, and sample plots to record the state of, as well as changes in, forest area based on field surveys and aerial photograph interpretation. As the NFI sample plots comprise only areas covered by forest, we extended the lattice to non-forest areas to cover the whole country. In this study a forest/non-forest classification was generated for each of the 20,618 lattice points and for six points in time (1850, 1880, 1910, 1940, 1980, 2000), which allowed us to determine the gross forest gain and loss in forest cover for five consecutive time periods (Loran et al. 2016). Since, overall, the gross loss is minor compared to the gain, only the gross forest gain was modeled in this study.

Derivation of explanatory variables: potential drivers of forest gain

The basic assumption behind this study is that forest gain is mostly the result of land abandonment (proximate driver), which occurs when the opportunity costs (the value of alternative use) of farm labor are too high. This is often the case in mountainous areas, where cultivation costs are high due to topographic and climatic factors. In order to calibrate models for forest gain, we evaluated explanatory variables that fulfill the following criteria: (a) relevant in earlier Swiss forest studies (Baur et al. 2006; Gellrich et al. 2007b; Rutherford et al. 2008), (b) available in a spatially explicit form for all of Switzerland, (c) available from at least 1940 onwards in order to capture the possible time-lag effect. In the following sections,

we identify the final set of selected biophysical and socioeconomic variables, and explain their hypothesized effect on forest gain.

Biophysical variables

Forest cover per municipality (%): Densely forested neighborhoods or large forest patches increase the diaspora pressure on extensively used or abandoned agricultural fields (Chételat et al. 2013) and, consequently, favor forest expansion. The amount of forest cover per municipality was used as a replacement for the variable “distance to forest”, which was found to be significant in predicting forest gain in the Swiss Alps according to Gellrich et al. (2007a,b) and Bolliger et al. (2017). This substitution was based on the fact that in our point sample of forest cover we did not have information regarding forest borders. A positive relationship between the forest gain and its proportion per municipality is expected.

Slope: This serves as a proxy for accessibility and cultivation costs of agricultural fields, since steepness affects accessibility, whether using agricultural vehicles or travelling on foot (Gellrich et al. 2007a,b). This variable was obtained from the digital elevation model (DEM) with a 25-m resolution (<http://www.swisstopo.admin.ch>). The mean value per municipality was calculated using ArcGIS 10.2. The response variable is expected to increase as cultivation costs increases with the steepness of slopes.

Climatic conditions: Precipitation and temperature variables were used as proxy for yield potential of agricultural areas, which is generally greater in areas with higher precipitation and temperature. At the same time, both variables can be limiting factors if they fall below a certain threshold (e.g. tree line of forests in the mountains). In regions with high temperatures (indicating low elevations) the reforestation rate may be low as well due to competing land uses (i.e. agriculture, urban areas). Therefore, a non-linear response is expected, with low reforestation rates at both high and low temperatures and precipitation rates, respectively. At intermediate values, reforestation is expected to be at its highest.

We calculated long-term mean temperatures and precipitation sums to capture climate variation across our study region and climate change over the 150-year period. The gridded climate maps were produced using two different methods. The maps for the years 1931–2013 were developed by interpolating daily-measured data from weather stations (MeteoSwiss) over a 100-m DEM using Daymet (Thornton et al. 1997). For the years 1850–1930, we applied the change factor method (e.g. Anandhi et al. 2011) to downscale

reconstructed monthly temperature means (Luterbacher et al. 2004; Xoplaki et al. 2005) and seasonal precipitation sums (Pauling et al., 2006) from a resolution of 0.5° down to 100 m. The change factor method calculates anomalies relative to a baseline period. From the daily Daymet maps, long-term monthly means (temperature) and seasonal sums (precipitation) were aggregated for our 1961–1990 baseline period at high spatial resolution (100 m). The same long-term monthly means and seasonal sums of the reconstructed datasets were calculated to serve as the equivalent low-resolution (0.5°) baseline period. We expressed all monthly (and seasonal) values from the years 1850–1930 as anomalies relative to the baseline period. The resulting anomaly maps were bilinearly interpolated to the 100-m resolution and then added to the Daymet baseline maps to obtain high-resolution maps for the years 1850–1930. In order to correspond with the six historical and contemporary maps of forest information, we defined six periods: 1850–1865, 1866–1895, 1896–1925, 1926–1955, 1966–1990 and 1991–2013 for which we calculated temperature means and precipitation sums of the vegetation periods (March–August). These maps were subsequently aggregated to the municipality level by calculating mean values per municipality.

Socioeconomic variables

Based on the hypothesis that land abandonment is a proximate driver of forest gain in Switzerland, a set of variables (Tab. 1) was selected: changes in (1) population size, (2) the number of people employed per economic sector (derived from population censuses), (3) the number and size of farms (derived from farm censuses) and (4) the number of cattle (derived from livestock censuses). Assuming, therefore, that these variables are proximate drivers of land abandonment and, respectively, underlying drivers of forest gain, the percentage of change in these variables was calculated per municipality for the five time periods under study, and included in the models.

In order to make the data spatially explicit, a link to digital municipality coverage (available for the year 2000 with a total of 2,899 municipalities) was required. To achieve this, we harmonized census data with municipality boundaries for the year 2000 in cases where

administrative boundary changes occurred over the 150-year study period. To account for the unknown time lag between the socioeconomic determinants of land abandonment, effective land abandonment, and natural forest regrowth on abandoned land, only socioeconomic variables prior to the period of modeled forest gain were included in the model. For example, in order to model forest gain between 1910 and 1940, population change for the periods 1850-1880 and 1880-1910 were included in the model.

Table 1: Set of selected variables used to calibrate the predictive models explaining the gain or loss in forest cover (1850-2000). All variables were aggregated to the municipality scale, as this was the smallest available resolution for socioeconomic variables.

Variable	Unit (per municipality)	Original spatial resolution	Available time span	Source	Variables included in statistical model
Response variables					
Forest gain	%(gross change)	plot (25m x 25m)	1850 - 2000	1850: Dufour Original Survey Map	Yes
Forest loss				1880-1940: Siegfried Map 1980-2000: National Forest Inventory	Yes
Explanatory variables					
Biophysical					
Forest	%	plot (25m x 25m)	1850 - 2000	1850: Dufour Original Survey Map	Yes
Non-Forest				1880-1940: Siegfried Map 1980-2000: National Forest Inventory	No
Precipitation	mean mm growing season (March-August)	100m	1850 - 2000	1850-1930: Luterbacher et al., 1931-2010: Weatherstation MeteoSchweiz	Yes
Temperature	mean °C growing season (March-August)			1850-1930: Pauling et al., 1931-2010: Weatherstation MeteoSchweiz	Yes
Elevation	mean m	25m		DHM25	No
Slope	mean °				Yes
Socioeconomic					
Change in resident population			1850 - 2000	Population Census	Yes
Change in employees per industrial sector (S1, S2, S3)			1920 - 2000		Yes
Change in number of farms	%	Municipality	1939 - 2000	Farm Census	Yes
Change in size of farms					No
Change in number of cattle			1956 - 2000	Livestock Census	Yes

Modelling forest gain

Pre-evaluation of data / Preliminary statistical analysis

To prepare for statistical analyses, all response and explanatory variables (Tab. 1) used in this study were imported into R (R Development Core Team 3.2.2). The final set of explanatory variables for modelling was selected based on a three-step pre-evaluation: (1) based on reasonable grounds (literature review) regarding the relevance of the variable (potential driver), (2) the correlation between selected variables was not excessively high ($r < |0.8|$ to avoid multicollinearity) (Menard 2002), and (3) the explanatory power of the individual variables was measurable (non-random). To assess the explanatory power of each variable, we calculated separate generalized additive models (GAMs) for each individual potential explanatory variable against the response variable as a form of exploratory statistical analysis (Agresti 2002). A GAM is a non-parametric extension of a generalized linear model (GLM) (Hastie and Tibshirani 1990). The advantage of a GAM is its non-parametric, flexible response function that is used to describe the relationship between explanatory variables and the response variable, which maximizes the quality of prediction (Crawley 2007). Finally, among the highly correlated variables ($r > |0.8|$), only one variable was selected based on the deviance explained (D^2). Based on these three steps, the variables “elevation” and “size of farms” were excluded from the final models. A network-analysis map was created in R using the package “qgraph” (Epskamp 2012) to visualize the correlation structure among the final set of variables.

Model calibration

To model forest gain in Switzerland for the 150-year study period, a GAM was applied. GAM models were fitted in R version 3.2.2 using the package “mgcv” (Wood 2011). This GAM version runs an internal evaluation based on penalized regression, resulting in a computationally efficient estimation of the degree of smoothness in model components using generalized cross validation. With this approach, predictor variables are not tested for significance in predicting the response (and removed if insignificant). Rather, variables are downweighted statistically if found to have a lack of predictive power.

To assess and compare the overall goodness of model fit, we calculated the deviance explained. Predictive model accuracy was tested by means of a 10-fold cross-validation and used two measures to evaluate the predictive power of the models. The first measure used is the mean absolute error (MAE), which indicates the degree to which the model fails to represent the true value (irrespective of sign). The second measurement is the mean error (ME) (of signed values). Even if a model has errors at the level of individual municipalities regarding the predicted proportion of forest gain, we expect the model to show low ME, meaning that the (signed) errors should cancel each other out across all municipalities. The relative importance of each variable per model was calculated using the package “biomod2” (Thuiller 2016). Overall, we fitted 20 models (4 regions and 5 periods).

To investigate the contribution of biophysical and socioeconomic variables, we used the variation partitioning approach from Borcard et al. (1992) following Zimmermann et al. (2007) to partition out the individual and joint contribution of both predictor sets relative to the full model. To do so, we carried out the following analyses. First, we fitted (1) a full model using biophysical and socioeconomic variables as well as two partial models using (2) only the biophysical and (3) only the socioeconomic predictor variables to estimate the D^2 of each single model. Second, we subtracted the D^2 values of the biophysical model and the socioeconomic model from the D^2 of the full model, yielding the partial fractions of the full model not included in the socioeconomic and biophysical models, respectively. Third, from the sum of the two partial contributions we subtracted D^2 explained by the full model, which yielded the fraction of D^2 explained jointly by both predictor sets.

Results

The most important findings of our study are summarized in two steps. First, we present the results of the network analysis among all predictor variables. Second, the importance of potential drivers of forest gain resulting from the statistical models is presented for a) all study periods (1850-1880, 1880-1910, 1910-1940, 1940-1980, 1980-2000), with a limited set of variables which were available from 1850 onwards to assess the temporal and spatial variation in importance; and b) for the last part of the study period (1980-2000), with the full set of modelled variables to quantify the contribution of the biophysical and socioeconomic variables in explaining the forest gain.

Network analysis of potential drivers of forest gain (1980-2000)

The network analysis revealed strong correlations between biophysical variables and forest gain (yellow and green nodes in Fig. 3). The results of this network analysis indicate that the correlation is highest between forest gain and the amount of forest area, slope, temperature and precipitation. Forest gain is positively correlated (green arrows) with precipitation and slope, and negatively (red arrows) with temperature. The proximity of nodes to each other, as well as how dark the arrows are, indicate the strength of the correlations between variables (i.e. closer and darker = higher correlation). The correlation between forest gain and socioeconomic variables (orange nodes) is rather low. The same is true for forest loss, which obviously is not directly influenced by the selected biophysical side conditions, nor by socioeconomic changes in the municipalities in this study.

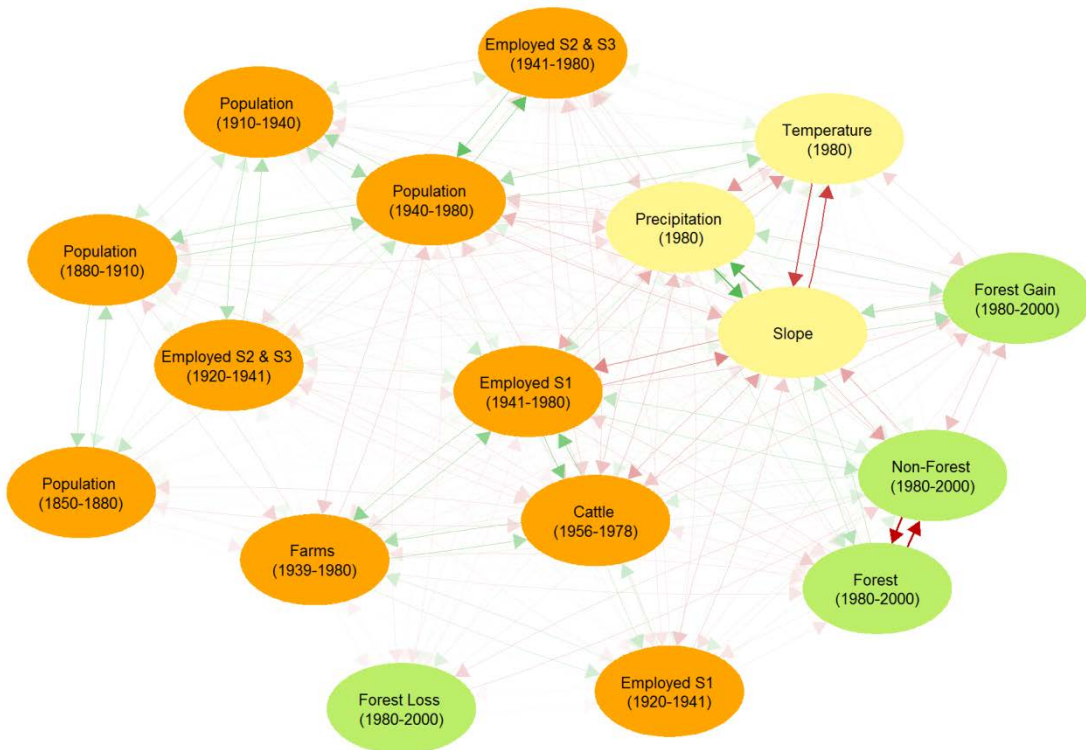


Fig. 3: Network visualization of potential drivers explaining differences in forest cover change (1980-2000) among Swiss municipalities. The map indicates positive (green arrows) and negative (red arrows) correlations among forest (green nodes), socioeconomic (orange nodes), and biophysical (yellow nodes) variables. The distances between nodes, as well as the visibility of the arrows illustrate the correlation intensity.

Variability in relative importance of drivers (1850-2000)

The models were fitted in order to investigate the spatial and temporal variation in importance of a set of eight selected variables (Fig. 4), which were available for the whole study period (150 years). The overall explanatory power (D^2) of the models varies between 0.087 and 0.408 (Tab. 2) over time and among the four modeled regions (Switzerland, Alps, Northern Alps, Southern Alps).

Tab. 2: Summary of forest model fit (D^2) and accuracy (ME, MAE). Accuracy measures were calculated based on the 10-fold cross-validated model results.

	Forest gain		
	D^2	ME	MAE
1850-1880			
Switzerland	0.208	0.007	0.090
Alps	0.307	0.007	0.097
Northern Alps	0.227	0.005	0.107
Southern Alps	0.251	-0.002	0.119
1880-1910			
Switzerland	0.087	-0.001	0.050
Alps	0.124	-0.003	0.059
Northern Alps	0.101	-0.004	0.060
Southern Alps	0.174	-0.004	0.080
1910-1940			
Switzerland	0.159	0.001	0.040
Alps	0.227	0.002	0.063
Northern Alps	0.180	0.004	0.049
Southern Alps	0.285	0.005	0.103
1940-1980			
Switzerland	0.352	-0.002	0.100
Alps	0.394	-0.012	0.163
Northern Alps	0.197	-0.003	0.111
Southern Alps	0.408	0.004	0.281
1980-2000			
Switzerland	0.299	0.001	0.050
Alps	0.310	0.001	0.101
Northern Alps	0.222	0.001	0.059
Southern Alps	0.354	0.010	0.204

The biophysical variables temperature and slope contribute significantly ($p < 0.05$) in most models towards explaining forest gain, except for the Southern Alps in the period 1880-1910, when forest gain was very low. Both variables show a non-linear relationship to the response variable. The probability of forest gain increases with increasing temperature and slope up to a certain value and decreases thereafter (temperature) or the increase fades away (slope) at higher temperatures, respectively, at steeper slopes. The relative importance of variables varies strongly between the regions and over time (Fig. 4). The relative importance of the proportion of forest cover is most relevant in the Southern Alps in two periods (1850-1880, 1910-1940). In these two periods, the proportion of forest cover and forest gain are

negatively correlated (i.e. the greater the proportion of forest cover per municipality, the harder it is to make significant gains in forest cover). Precipitation is not a significant predictor in most models. The only socioeconomic variable in these models, change in population, was relevant for forest gain only in the Northern Alps, where a decrease in population during the periods 1850-1880 and 1880-1910 influenced forest gain in 1910-1940. This delay in forest gain following changes in population confirms a time lag of one to two periods between societal changes and their effects on forest cover.

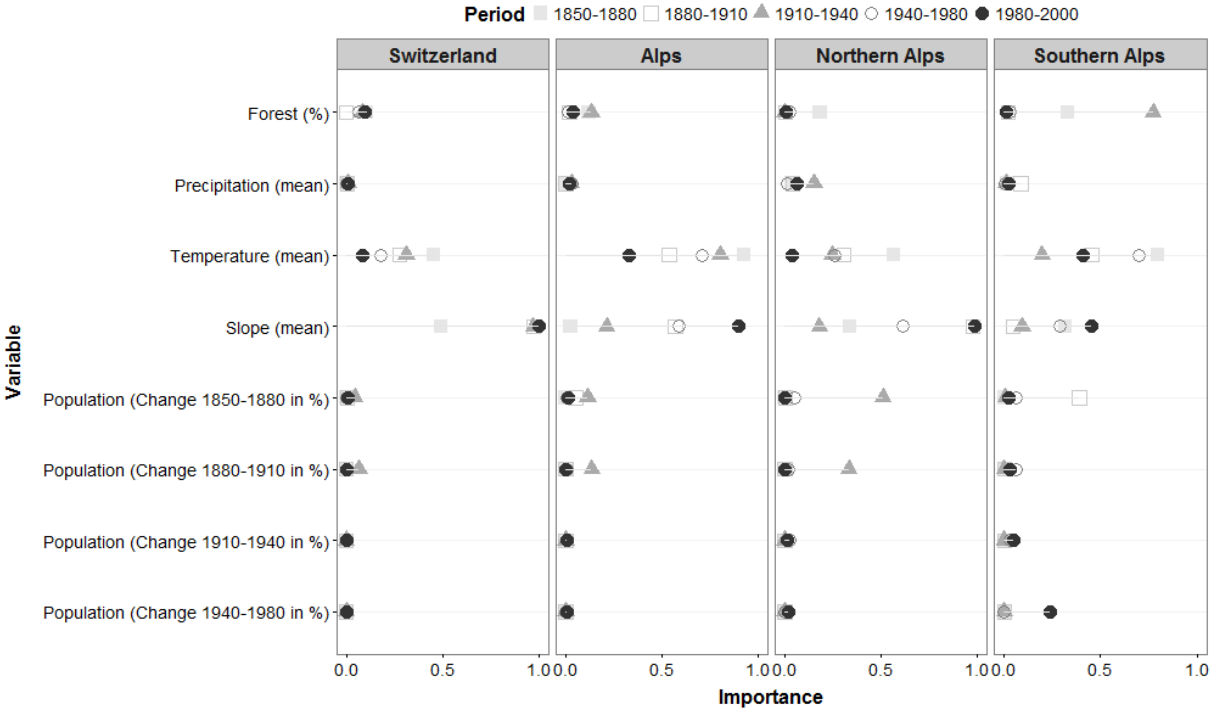


Fig. 4: The relative importance of variables for forest gain. The plot is divided into four parts representing the regions under study. The five periods under study are indicated by different shades of grey and shapes.

Biophysical vs. socioeconomic drivers (1980-2000)

To investigate the contribution of biophysical and socioeconomic variables (Fig. 5), as well as the joint contribution of both predictor sets relative to the full model, we applied the partitioning approach. These models contain the same four biophysical variables as in the 1850-2000 models, but include more socioeconomic variables (10 in total). We included variables related to employees, and farm and cattle only in the period 1980-2000 because

they were not available for the entire 150-year timeframe. Biophysical variables explained a higher proportion of D^2 than socioeconomic variables for all four modeled regions (Fig. 5).

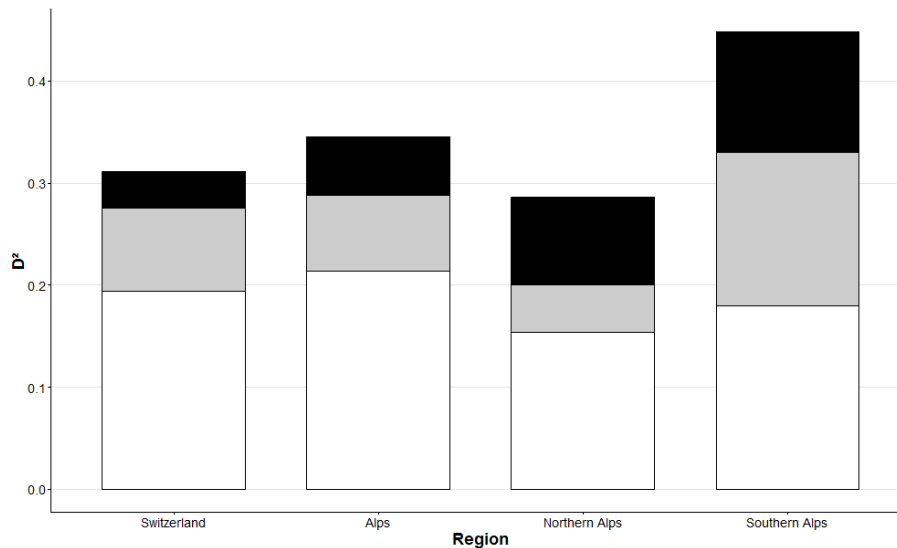


Fig. 5: Explained deviance (D^2) of forest cover gain models between 1980 and 2000 for the four regions under study. The D^2 explained by the socioeconomic model is indicated in black; the D^2 explained by the biophysical model is shown in white. The overlap (grey) indicates that the sum of D^2 explained by both partial models exceeds the D^2 explained by the full model based both on socioeconomic and biophysical factors.

In the Southern Alps, however, the deviance explained by socioeconomic variables is almost as high as that by biophysical variables. In the full model with all variables retained, slope was the most important variable followed by temperature (Fig. 6). The same was true for the biophysical model. In the socioeconomic model, the most important drivers were changes in the proportion of employees in farming (1st sector) and non-farming jobs (2nd and 3rd sector). The gain in forest cover between 1980 and 2000 was mainly affected by a decrease in the proportion of people working in agriculture and more people working outside of agriculture between 1920 and 1980. At the national scale, the decreasing population between 1940 and 1980 contributed to the increase in forest cover between 1980 and 2000. Overall, the time lag between socioeconomic changes and forest gain was measurable up to 60 years later.

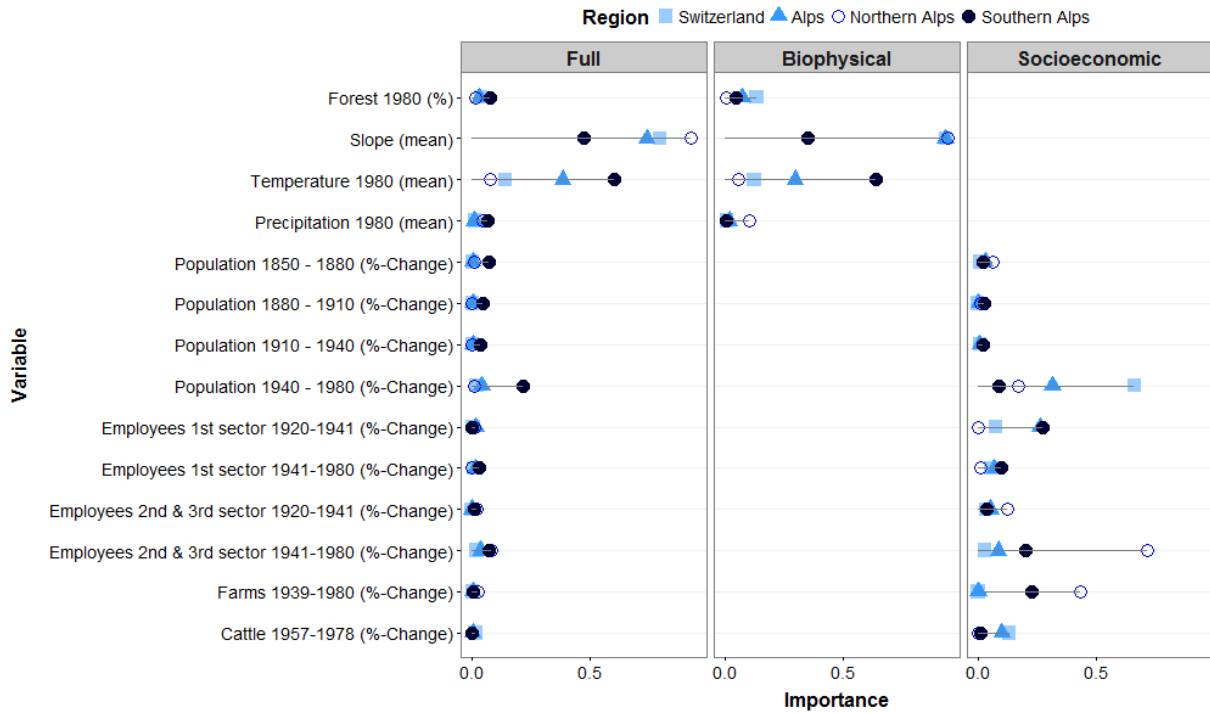


Fig. 6: The relative importance of variables for forest gain between 1980 and 2000. The plot is divided into three parts to represent the three models (full, biophysical, and socioeconomic) from the variance partitioning analysis. The colors and shapes indicate the four regions under study.

Discussion

In the present study, which examines the expansion in forest cover and its drivers in Switzerland over a period of 150 years between 1850 and 2000, we have (1) quantified the spatio-temporal variation in importance of socioeconomic and biophysical drivers, (2) identified the influence of past socioeconomic changes on forest gain and (3) measured the time lag between these societal changes and gain in forest cover. In the following sections, we discuss the importance of potential drivers and the discovered time lags between changes in land-use and effective expansion in forest cover. Secondly, we discuss the limitations of our study in the light of the availability of data sources and the selected modelling approach. Finally, we illustrate the wider implications of this study and conclude with recommendations for further research.

Drivers of forest gain

The results of the forest gain models confirm that the importance of drivers varies in a non-linear fashion at temporal and spatial scales. The steepness of slopes, which affects accessibility by agricultural machinery—a good proxy for land abandonment—was identified as very important driver. The positive linear relationship between slope and forest gain supports the finding of earlier studies conducted in Switzerland (Baur et al. 2006; Gellrich et al. 2007b; Rutherford et al. 2008) that more recent forest expansion has occurred mainly in the Swiss mountain areas. Similar observations exist for other European countries as well (Corbelle-Rico et al. 2012; Fjellstad and Dramstad 1999; Kozak et al. 2007; MacDonald et al. 2000; Mottet et al. 2006; Regos 2015). However, within the Swiss mountain areas, temperature was more important than slope over many periods. Areas with very low temperatures are simply unsuitable for forest growth (Rickebusch et al. 2007), while increasing temperatures enhances growing conditions only up to a certain point. In this study, however, the probability of forest gain decreases above a certain temperature threshold, suggesting that these areas are occupied by other land uses (e.g. agriculture or urban area). Precipitation and the proportion of forest cover per municipality were less important in our study compared to temperature and slope. We interpret this to mean that abandoned and overgrown land has sufficient precipitation to enable forest regrowth. Regarding the proportion of forest cover per municipality, we conclude that it is not a suitable variable to replace the distance to forest, which was significant in the study of Bolliger et al. (2017). In municipalities with forest gain, we observed a decrease in the proportion of employees in farming (1st sector) while the proportion of non-farming jobs (2nd & 3rd sector) increased concurrently. This indicates that farmers likely changed to off-farm jobs and continued living in their municipalities. The low importance of population change as a predictor of forest gain supports this assumption and enables the exclusion of a major effect due to migratory movements, which is in line with the findings from Gellrich et al. (2007a). However, this is in contrast to other mountainous areas in Europe, where rural depopulation is a prominent process leading to forest gain (MacDonald et al. 2000). According to our model results, forest expansion was influenced significantly by both socioeconomic and biophysical variables, although biophysical site conditions had a stronger

impact on forest gain than socioeconomic variables. In fact, forest expansion as a result of agricultural land abandonment is generally triggered by farmers' economic considerations, which in turn are influenced by strongly heterogeneous biophysical conditions (van Vliet et al. 2015). Consequently, it is essential to include both biophysical and socioeconomic variables in the model. This is especially true considering the fact that a time lag of up to 60 years was found between socioeconomic changes and forest gain.

The highest importance of socioeconomic drivers for forest gain was observed in the Southern Alps (Fig. 5). This region experienced a drastic socioeconomic change towards a more service-oriented economy where off-farm employment caused land abandonment or at least decreased the intensity of land management in many municipalities (Conedera 2009). Furthermore, this observed strength of importance in the Southern Alps compared to the other regions may originate from delayed land consolidation, which took more than 30 years (from the 1960s to the 1990s) until the processes of readjustment and rearrangement of land parcels and their ownership were completed (Gellrich 2006). Many landowners decided to abandon their land at that time due to insecurity and structural obstacles to intensification (Baur et al. 2006). This was because producers had to cope with competition from other production regions that had a comparative advantage due to better biophysical conditions (Verburg and Overmars 2009). This process is generally a consequence of globalization.

Statistical modelling and its limitations

The mostly non-linear relationships between our response and explanatory variables were fitted by GAM models because this statistical approach provides a better model fit than GLMs. Models were originally fitted both at the municipality and plot levels (only municipality-level results are presented here). The different resolutions had a significant impact on overall model fit. The models at municipality level had a much better fit than those fitted at the plot level. On the one hand, our municipality models neglect the strong variation in biophysical site conditions by using a mean value. On the other hand, the available data was not suitable for models at the plot level, as socioeconomic variables were available only at the municipality level. Furthermore, the biophysical conditions of neighboring parcels are

also decisive for land cover change. Even though we are convinced that the municipality level is best suited to our analysis, it was not possible to account for the spatial variability within municipalities. In order to avoid multicollinearity between explanatory variables in the model, it was impossible to include the range or standard deviation of a predictor variable as well. In summary, in testing several approaches, we found that the municipality is a good compromise between units that are too small—with a high degree of random variation and lower predictive power—and units that are too large—with smooth but rather trivial trends.

The municipality is a political unit in Switzerland at which many decisions are taken that affect land use change. Nevertheless, we expect that model fit could be improved by agricultural and socioeconomic data at the farm level, as this would enable a more precise modelling of land cover changes and facilitate capturing the diversity between different farms that is a determinant of farm management and the possible abandonment of plots. The remaining unexplained deviance in the models (Tab. 2) suggests that possibly not all relevant drivers of forest gain were accounted for. It is also possible that the whole process of forest gain might be highly stochastic, even at the municipality level. In addition, besides factors that are relevant at macro scales, there are likely many local characteristics that can influence micro scale changes (e.g. farmers' decisions as mentioned above), which explain why forest expansion took place in one location but not in another under otherwise comparable conditions (Bezák and Mitchley 2014; van Vliet et al. 2015).

Overall, this long trend of expanding forest cover due to the forest law of 1876, which prohibited deforestation and encouraged reforestation (Bertogliati 2016) and the process of land abandonment in Swiss mountainous regions is predicted to continue over the next decades (Price et al. 2015), and will result in significant biodiversity losses in many grassland ecosystems (Colombaroli et al. 2013). In order to prevent further forest expansion, the Swiss forest law has recently been revised. The consequences of this revision will only become visible in several decades, since socioeconomic decisions have been shown to take many decades to be effective at the national scale.

Conclusion

The results of our study emphasize the importance of historical analyses given that recent changes are driven significantly by past processes (Foster et al. 2003, Munteanu et al. 2016; Rhemtulla and Mladenoff 2007; Perring et al. 2016). This is important because it shows that current land management decisions will likely also affect forest change for hundreds of years to come (Dearing et al. 2010). Our study has shown that the importance of drivers can vary over space and time. This finding is particularly relevant to land-use modelling approaches predicting future changes, which often assume drivers to remain constant over time (e.g. Price et al. 2016). Therefore, our findings are relevant to many temperate ecosystems across the globe, which are currently experiencing similar changes in forest cover (Eastern US, Europe, China). These regions share a long history of human land use, which has been thoroughly documented in land surveys in the US (e.g. Liu et al. 2011; Schulte and Mladenoff 2001) and military maps in Europe (Fuchs et al. 2015; Kaim et al. 2016). Understanding the importance of drivers of change and how they play out differently across space and over time is thus possible over large regions, and could support both future forest change predictions as well as target policies to manage our landscapes in a sustainable manner.

Acknowledgments

We gratefully acknowledge support by the Swiss National Science Foundation (SNSF) in the project Forest dynamics in Switzerland (FORDYNCH)—pattern, driving forces, and ecological implications (Grant No. 200021-143242), the National Aeronautic Space Administration (NASA) and the NASA Earth System Science Fellowship Program. Thanks to Curtis Gautschi who kindly improved the English. N.E.Z. additionally acknowledges support from the Swiss National Science Foundation (grant 40FA40_158395).

References

- Agresti A (2002) *Categorical Data Analysis*. Wiley, New Jersey
- Anandhi A, Frei A, Pierson DC, Schneiderman EM, Zion MS, Lounsbury D, Matonse AH (2011) Examination of change factor methodologies for climate change impact assessment. *Water Resour Res* 47(3). doi:10.1029/2010WR009104
- Antrop M (2005) Why landscapes of the past are important for the future. *Landsc Urban Plan* 70:21-34. doi:10.1016/j.landurbplan.2003.10.002
- Baur P, Bebi P, Gellrich M, Rutherford GN (2006) *WaSAp - Waldausdehnung im Schweizer Alpenraum. Eine quantitative Analyse naturräumlicher und sozio-ökonomischer Ursachen unter besonderer Berücksichtigung des Agrarstrukturwandels*. Swiss Federal Research Institute WSL, Birmensdorf
- Bertogliati M (2016) Agrarintensivierung – aus Wald wird Feld und Wiese. In: Mathieu J, Backhaus N, Hürlimann K, Bürgi M (ed) *Geschichte der Landschaft in der Schweiz*. Orell Füssli, Zürich
- Bezák P, Mitchley J (2014) Drivers of change in mountain farming in Slovakia: from socialist collectivisation to the Common Agricultural Policy. *Reg Environ Change* 14:1343-1356. doi:10.1007/s10113-013-0580-x
- Bolliger J, Schmatz D, Pazúr R, Ostapowicz K, Psomas A (2017) Reconstructing forest-cover change in the Swiss Alps between 1880 and 2010 using ensemble modelling *Regional Environmental Change*:1-13 doi:10.1007/s10113-016-1090-4
- Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055
- Brändli U-BR (2010) *Schweizerisches Landesforstinventar. Ergebnisse der dritten Erhebung 2004-2006*. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf. Bundesamt für Umwelt BAFU, Bern
- Bürgi M, Hersperger AM, Schneeberger N (2004) Driving forces of landscape change - current and new directions. *Landsc Ecol* 19:857-868. doi:10.1007/s10980-004-0245-8
- Bürgi M, Salzmann D, Gimmi U (2015) 264 years of change and persistence in an agrarian landscape: a case study from the Swiss lowlands. *Landsc Ecol* 30:1321-1333. doi:10.1007/s10980-015-0189-1
- Colombaroli D, Beckmann M, van der Knaap WO, Curdy P, Tinner W (2013) Changes in biodiversity and vegetation composition in the central Swiss Alps during the transition from pristine forest to first farming. *Divers and Distrib* 19:157-170. doi:10.1111/j.1472-4642.2012.00930.x

- Conedera M (2009) Implementing fire history and fire ecology in fire risk assessment: the study case of Canton Ticino (southern Switzerland). Dissertation, University of Karlsruhe
- Corbelle-Rico E, Crecente-Maseda R, Santé-Riveira I (2012) Multi-scale assessment and spatial modelling of agricultural land abandonment in a European peripheral region: Galicia (Spain), 1956–2004. *Land Use Policy* 29:493-501. doi:10.1016/j.landusepol.2011.08.008
- Crawley MJ (2007) *The R Book*. Wiley, Chichester
- Dearing JA, Braimoh AK, Reenberg A, Turner BL, van der Leeuw S (2010) Complex land systems: The need for long time perspectives to assess their future. *Ecol Soc* 15(4):21. [online] URL: <http://www.ecologyandsociety.org/vol15/iss4/art21/> Accessed 7 June 2016.
- Epskamp S, Cramer AOJ, Waldorp LJ, Schmittmann VD, Borsboom D (2012) qgraph: Network Visualizations of Relationships in Psychometric Data. *Journal Stat Softw*, 48(4):1-18. [online] URL: <http://www.jstatsoft.org/v48/i04/>. Accessed 6 June 2016
- Fjellstad WJ, Dramstad WE (1999) Patterns of change in two contrasting Norwegian agricultural landscapes. *Landsc Urban Plan* 45:177-191. doi:[http://dx.doi.org/10.1016/S0169-2046\(99\)00055-9](http://dx.doi.org/10.1016/S0169-2046(99)00055-9)
- FOEN, Swiss Federal Office for the Environment (2013) Federal Act on Forest. [online] URL: <http://www.bafu.admin.ch/wald/11352/14350/index.html?lang=en>. Accessed 7 June 2016
- Foster DR, Swanson FJ, Aber J, Burke I, Brokaw N, Tilman D, Knapp A (2003) The importance of land-use legacies to ecology and conservation. *Bioscience* 53:77–88. doi: 10.1641/0006-3568(2003)053[0077:TIOULU]2.0.CO;2
- Fuchs R, Verburg PH, Clevers JGPW, Herold M (2015) The potential of old maps and encyclopaedias for reconstructing historic European land cover/use change. *Appl Geogr* 59:43-55. doi:10.1016/j.apgeog.2015.02.013
- Gellrich M (2006) Natural forest re-growth on abandoned agricultural land in the Swiss mountains. An economic analysis of patterns and causes using spatial statistical models and interviews. Dissertation, Albert-Ludwigs-University
- Gellrich M, Baur P, Koch B, Zimmermann NE (2007a) Agricultural land abandonment and natural forest re-growth in the Swiss mountains: A spatially explicit economic analysis. *Agric Ecosyst Environ* 118:93-108. doi:10.1016/j.agee.2006.05.001
- Gellrich M, Baur P, Zimmermann NE (2007b) Natural forest regrowth as a proxy variable for agricultural land abandonment in the Swiss mountains: a spatial statistical model based on geophysical and socio-economic variables. *Environ Model Assess* 12:269-278. doi:10.1007/s10666-006-9062-6
- Gellrich M, Zimmermann NE (2007) Investigating the regional-scale pattern of agricultural land abandonment in the Swiss mountains: A spatial statistical modelling approach *Landsc Urban Plan* 79:65-76 doi:10.1016/j.landurbplan.2006.03.004
- Ginzler C, Brändli U-B, Hägeli M (2011) Waldflächenentwicklung der letzten 120 Jahre in der Schweiz. *Z Forstwes* 162:337-343. doi:10.3188/szf.2011.0337
- Gonseth Y, Wohlgemuth T, Sansonnens B, Buttler A (2001) Die biogeographischen Regionen der Schweiz. Erläuterungen und Einteilungsstandard. *Umwelt Materialien Nr. 137* Bundesamt für Umwelt, Wald und Landschaft Bern. 48p.

- Grêt-Regamey A, Rabe S-E, Crespo R, Lautenbach S, Ryffel A, Schlup B (2013) On the importance of non-linear relationships between landscape patterns and the sustainable provision of ecosystem services. *Landsc Ecol* 29:201-212. doi:10.1007/s10980-013-9957-y
- Hastie T, Tibshirani R (1990) *Generalized additive models*. Chapman and Hall, London
- Hersperger AM, Bürgi M (2009) Going beyond landscape change description: Quantifying the importance of driving forces of landscape change in a Central Europe case study. *Land Use Policy* 26:640-648. doi:10.1016/j.landusepol.2008.08.015
- Hunziker M (1995) The spontaneous reforestation in abandoned agricultural lands: perception and aesthetic assessment by locals and tourists *Landsc Urban Plan* 31:399-410 doi:http://dx.doi.org/10.1016/0169-2046(95)93251-J
- Jepsen MR et al. (2015) Transitions in European land-management regimes between 1800 and 2010 *Land Use Policy* 49:53-64 doi:10.1016/j.landusepol.2015.07.003
- Lambin EF, Meyfroidt P (2011) Global land use change, economic globalization, and the looming land scarcity *Proceedings of the National Academy of Sciences of the United States of America* 108:3465-3472 doi:10.1073/pnas.1100480108
- Leuschner C, Wulf M, Bäuchler P, Hertel D (2014) Forest Continuity as a Key Determinant of Soil Carbon and Nutrient Storage in Beech Forests on Sandy Soils in Northern Germany *Ecosystems* 17:497-511 doi:10.1007/s10021-013-9738-
- Kaim D, Kozak J, Kolecka N, Ziółkowska E, Ostafin K, Ostapowicz K, Gimmi U, Munteanu C, Radeloff VC (2016) Broad scale forest cover reconstruction from historical topographic maps. *Appl Geogr* 67:39-48. doi:http://dx.doi.org/10.1016/j.apgeog.2015.12.003
- Kozak J, Estreguil C, Troll M (2007) Forest cover changes in the northern Carpathians in the 20th century: a slow transition. *J Land Use Sci* 2:127-146. doi:10.1080/17474230701218244
- Levers C, Verkerk PJ, Müller D, Verburg PH, Butsic V, Leitão PJ, Lindner M, Kuemmerle T (2014) Drivers of forest harvesting intensity patterns in Europe. *For Ecol Manage* 315:160-172. doi:10.1016/j.foreco.2013.12.030
- Liu F, Mladenoff DJ, Keuler NS, Schulte Moore L (2011) BROADSCALE variability in tree data of the historical Public Land Survey and its consequences for ecological studies. *Ecol Monogr* 81:259-275. doi:10.1890/10-0232.1
- Loran C, Ginzler C, Bürgi M (2016) Evaluating forest transition based on a multi-scale approach: forest area dynamics in Switzerland 1850–2000. *Reg Environ Change*. doi:10.1007/s10113-015-0911-1
- Luterbacher J, Dietrich D, Xoplaki E, Grosjean M, Wanner H (2004) European seasonal and annual temperature variability, trends, and extremes since 1500. *Science* 303(5663):1499-1503. doi:10.1126/science.1093877
- MacDonald D, Crabtree JR, Wiesinger G, Dax T, Stamou N, Fleury P, Gutierrez Lazpita J, Gibon A (2000) Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. *J Environ Manage* 59:47-69. doi:10.1006/jema.1999.0335
- Malek Ž, Boerboom L, Glade T (2015) Future Forest Cover Change Scenarios with Implications for Landslide Risk: An Example from Buzau Subcarpathians, Romania *Environmental management* 56:1228-1243 doi:10.1007/s00267-015-0577-y

- Mather AS, Fairbairn J (2000) From Floods to Reforestation: The Forest Transition in Switzerland. *Environ Hist* 6(4):399-421. doi:10.3197/096734000129342352
- Menard S (2002) *Applied Logistic Regression Analysis*. Sage Publications, Thousand Oaks, 111 pp.
- Meyfroidt P (2015) Approaches and terminology for causal analysis in land systems science. *J Land Use Sci*:1-27. doi:10.1080/1747423x.2015.1117530
- Mottet A, Ladet S, Coqué N, Gibon A (2006) Agricultural land-use change and its drivers in mountain landscapes: A case study in the Pyrenees. *Agric Ecosyst Environ* 114:296-310. doi:10.1016/j.agee.2005.11.017
- Munteanu C, Kuemmerle T, Keuler NS, Müller D, Balázs P, Dobosz M, Griffiths P, Halada L, Kaim D, Király G, Konkoly-Gyuró É, Kozak J, Lieskovsky J, Ostafin K, Ostapowicz K, Shandra O, Radeloff VC (2015) Legacies of 19th century land use shape contemporary forest cover. *Glob Environ Chang* 34:83-94. doi:10.1016/j.gloenvcha.2015.06.015
- Munteanu C, Nita MD, Abrudan IV, Radeloff VC (2016) Historical forest management in Romania is imposing strong legacies on contemporary forests and their management. *For Ecol Manage* 361:179-193. doi:10.1016/j.foreco.2015.11.023
- Pauling AJ, Luterbacher C, Casty H, Wanner H (2006) Five hundred years of gridded high-resolution precipitation reconstructions over Europe and the connection to large-scale circulation. *Clim Dyn* 26(4):387-405. doi:10.1007/s00382-005-0090-8
- Pazúr R, Lieskovský J, Feranec J, Oťaheľ J (2014) Spatial determinants of abandonment of large-scale arable lands and managed grasslands in Slovakia during the periods of post-socialist transition and European Union accession *Applied Geography* 54:118-128 doi:10.1016/j.apgeog.2014.07.014
- Pellissier L, Anzini M, Maiorano L, Dubuis A, Pottier J, Vittoz P, Guisan A (2013) Spatial predictions of land-use transitions and associated threats to biodiversity: the case of forest regrowth in mountain grasslands. *Appl Veg Sci* 16:227-236. doi:10.1111/j.1654-109X.2012.01215.x
- Perring MP, De Frenne P, Baeten L, Maes SL, Depauw L, Blondeel H, Caron MM, Verheyen K (2016) Global environmental change effects on ecosystems: the importance of land-use legacies. *Glob Chang Biol* 22:1361-1371. doi:10.1111/gcb.13146
- Perz SG, Skole DL (2003) Secondary Forest Expansion in the Brazilian Amazon and the Refinement of Forest Transition Theory *Soc Natur Resour* 16:277-294 doi:10.1080/08941920390178856
- Plieninger T, Draux H, Fagerholm N, Bieling C, Bürgi M, Kizos T, Kuemmerle T, Primdahl J, Verburg PH (2016) The driving forces of landscape change in Europe: A systematic review of the evidence. *Land Use Policy* 57:204-214. doi:10.1016/j.landusepol.2016.04.040
- Price B, Kaim D, Szwagrzyk M, Ostapowicz K, Kolecka N, Schmatz DR, Wypych A, Kozak J (2016) Legacies, socio-economic and biophysical processes and drivers: the case of future forest cover expansion in the Polish Carpathians and Swiss Alps *Regional Environmental Change*:1-13 doi:10.1007/s10113-016-1079-z
- Price B, Kienast F, Seidl I, Ginzler C, Verburg PH, Bolliger J (2015) Future landscapes of Switzerland: Risk areas for urbanisation and land abandonment. *Appl Geogr* 57:32-41. doi:10.1016/j.apgeog.2014.12.009

- Pegos A, Ninyerola M, More G, Pons X (2015) Linking land cover dynamics with driving forces in mountain landscape of the Northwestern Iberian Peninsula. *Int J Appl Earth Obs Geoinf* 38:1-14. doi:10.1016/j.jag.2014.11.010
- Rhemtulla JM, Mladenoff DJ (2007) Why history matters in landscape ecology. *Landsc Ecol* 22:1-3. doi:10.1007/s10980-007-9163-x
- Rhemtulla JM, Mladenoff DJ, Clayton MK (2009) Legacies of historical land use on regional forest composition and structure in Wisconsin, USA (mid-1800s–1930s–2000s). *Ecol Appl* 19(4):1061–1078. doi:10.1890/08-1453.1
- Rickebusch S, Gellrich M, Lischke H, Guisan A, Zimmermann NE (2007) Combining probabilistic land-use change and tree population dynamics modelling to simulate responses in mountain forests *Ecological Modelling* 209:157-168
doi:http://dx.doi.org/10.1016/j.ecolmodel.2007.06.027
- Rosa IM, Purves D, Carreiras JM, Ewers RM (2015) Modelling land cover change in the Brazilian Amazon: temporal changes in drivers and calibration issues. *Reg Environ Change* 15:123-137. doi:10.1007/s10113-014-0614-z
- Rutherford GN, Bebi P, Edwards PJ, Zimmermann NE (2008) Assessing land-use statistics to model land cover change in a mountainous landscape in the European Alps. *Ecol Model* 212:460-471. doi:10.1016/j.ecolmodel.2007.10.050
- Schneeberger N, Bürgi M, Hersperger AM, Ewald KC (2007) Driving forces and rates of landscape change as a promising combination for landscape change research—An application on the northern fringe of the Swiss Alps. *Land Use Policy* 24:349-361. doi:10.1016/j.landusepol.2006.04.003
- Schulte LA, Mladenoff DJ (2001) The Original US Public Land Survey Records. Their Use and Limitations in Reconstructing Presettlement Vegetation. *Journal of Forestry*. [online] URL: http://landscape.forest.wisc.edu/PDF/Schulte_Mladenoff2001_JoF.pdf Accessed 7 June 2016
- Serneels S, Lambin EF (2001) Proximate causes of land-use change in Narok District, Kenya: a spatial statistical model *Agriculture, Ecosystems & Environment* 85:65-81
doi:http://dx.doi.org/10.1016/S0167-8809(01)00188-8
- SFSO, Swiss Federal Statistical Office (1997) *Statistisches Jahrbuch der Schweiz*. Zürich: Verlag Neue Zürcher Zeitung
- Swetnam TW, Allen CD, Betancourt JL (1999) Applied historical ecology: Using the past to manage for the future. *Ecol Appl* 9:1189-1206. doi:10.1890/1051-0761(1999)009[1189:AHEUTP]2.0.CO;2
- Swisstopo (2015) Journey through time—maps. Federal office of topography. https://map.geo.admin.ch/?topic=swisstopo&X=190000.00&Y=660000.00&zoom=1&lang=en&bgLayer=ch.swisstopo.pixelkarte-farbe&catalogNodes=1392&layers=ch.swisstopo.zeitreihen&time=1864&layers_times_tamp=18641231. Accessed 17 May 2016
- Thornton PE, Running SW, White MA (1997) Generating surfaces of daily meteorological variables over large regions of complex terrain. *J Hydrol* 190:214-251. doi:10.1016/S0022-1694(96)03128-9
- Thuiller W, Georges D, Engler R, Breiner F (2016). biomod2: Ensemble Platform for Species Distribution Modeling. R package version 3.3-7. <https://CRAN.R-project.org/package=biomod2>

- van Vliet J, de Groot HLF, Rietveld P, Verburg PH (2015) Manifestations and underlying drivers of agricultural land use change in Europe. *Landsc Urban Plan* 133:24-36. doi:<http://dx.doi.org/10.1016/j.landurbplan.2014.09.001>
- Verburg PH, Overmars KP (2009) Combining top-down and bottom-up dynamics in land use modeling: exploring the future of abandoned farmlands in Europe with the Dyna-CLUE model. *Landsc Ecol* 24:1167-1181. doi:10.1007/s10980-009-9355-7
- Verburg PH, Schot PP, Dijst MJ, Veldkamp A (2004) Land use change modelling: current practice and research priorities. *GeoJournal* 61:309-324. doi:10.1007/s10708-004-4946-y
- Wilkenskjeld S, Kloster S, Pongratz J, Raddatz T, Reick CH (2014) Comparing the influence of net and gross anthropogenic land-use and land-cover changes on the carbon cycle in the MPI-ESM Biogeosciences 11:4817-4828 doi:10.5194/bg-11-4817-2014
- Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc (B)* 73(1):3-36. doi:10.1111/j.1467-9868.2010.00749.x
- Xoplaki E, Luterbacher J, Paeth H, Dietrich D, Steiner N, Grosjean M, Wanner H (2005) European spring and autumn temperature variability and change of extremes over the last half millennium. *Geophys Res Lett* 32(15). doi:10.1029/2005GL023424
- Zimmermann NE, Edwards TC, Moisen GG, Frescino TS, Blackard JA (2007) Remote sensing-based predictors improve distribution models of rare, early successional and broadleaf tree species in Utah. *J Appl Ecol* 44:1057-1067. doi:10.1111/j.1365-2664.2007.01348.x