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**The use of land-use statistics to investigate large-scale successional processes**

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Presented by  
GILLIAN NICOLE RUTHERFORD

Master of Science, Auckland University, New Zealand

Born 06.12.1973

Citizen of New Zealand

accepted on the recommendation of

Professor Peter J Edwards, examiner  
Dr. Niklaus E Zimmermann, co-examiner  
Dr. Peter Bebi, co-examiner  
Associate Professor Antoine Guisan, co-examiner

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‘A good scientist has freed herself of concepts  
and keeps her mind open to what is’

*Tao Te Ching*

*- Lao Tzu*



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## **Summary**

Land-use and land cover change are two of the most important components of global change. As such, considerable questions about their causes and consequences have been raised. One of the marked changes occurring throughout Europe today is the giving up of the agricultural use of land, particularly in the mountainous regions such as the Alps. Switzerland is no exception showing gains in forest area of approximately 30-50% of its territory since the mid 19<sup>th</sup> century, much of which is a direct consequence of land abandonment. These changes are commonly attributed to changing socio-economic circumstances under which it may no longer be considered profitable to maintain agricultural use. Whatever the causes, underlying or proximate, the act of abandonment initiates a change in the land cover – here, vegetation - which acts as a signature of the process of change in space and time. When the spatial and temporal patterns of the consequent vegetation change show particular characteristics, it is useful to describe and quantify these characteristics to 1. Understand the process; 2. Predict the process. Addressing such questions at the landscape scale requires the availability of large volumes of data of sufficient quality to arrive at the answers sought. Not only must the data be of good quality but methods appropriate to answering the questions at hand must be selected.

To this end the aims of this thesis were firstly to determine whether or not the Swiss land-use statistics, as a large spatially explicit landscape scale statistical dataset, could be used to investigate ecological processes such as semi-natural secondary forest succession that are normally studied at a smaller spatial scale. The second aim was to then use the data to understand and predict the spatial and temporal patterns of forest development in Switzerland at larger spatial scales.

The relevant classes of the Swiss land-use statistics from the periods 1979/85 and 1992/97 were aggregated to form five new land-use and land cover classes representing stages between agricultural use and forest cover: (1) intensively used agricultural land, (2) extensively used agricultural land, (3) areas overgrown with shrubs and small trees, (4) open canopy forest, (5) closed canopy forest. The land cover change data was then used in the calibration and evaluation of spatially explicit statistical models with a view to explaining and understanding the observed changes and to ascertain the ability of the resulting models to predict future changes. In order to

do this, different forms of logistic regression were employed: binomial for changes between two land cover classes, and ordinal and multinomial for grouped changes from one land cover class to multiple outcomes.

Spatial and temporal patterns of land abandonment and subsequent forest regeneration are evident in Switzerland. Factors consistently identified as valuable in the prediction of land cover change post-abandonment can be broadly summarised into the composition of the surrounding neighbourhood and environment. The rate of forest succession and hence land cover change varies considerably at the regional scale in Switzerland, and is dependent on local factors such as propagule availability as well as larger scale climatic factors such as continentality. It is important to take into consideration that the choice of sampling regime and statistical modelling method implemented can influence the results yielded. When considered appropriately the different logistic regression techniques prove valuable tools in the investigation of land cover change presented here. In conclusion, the analysis of large landscape scale statistical datasets such as the Swiss land-use statistics which measure land cover change offers a promising way to investigate ecological processes such as forest succession at a large spatial scale.

## **Zusammenfassung**

Veränderungen der Bodennutzung und der Bodenbedeckung gehören zu den wichtigsten Indikatoren globaler Veränderungen. Aus diesem Grunde werden ihre Ursachen und Folgen seit längerem diskutiert. Die Aufgabe von landwirtschaftlicher Bodennutzung, insbesondere in Bergregionen wie den Alpen, ist eine der markantesten Änderungen, die heute in Europa beobachtet werden. Die Schweiz ist dabei keine Ausnahme. Schätzungen zufolge nahm die schweizerische Waldfläche seit Mitte des 19. Jahrhunderts um ca. 30-50% zu, was direkt auf die Landaufgabe zurückgeführt werden kann. Solche Entwicklungen lassen sich in der Regel mit Veränderungen der sozioökonomischen Umstände erklären, unter denen sich die weitere Bewirtschaftung nicht mehr rentiert. Unabhängig davon, ob die Ursachen direkt oder indirekt sind, hat die Nutzungsaufgabe eine Veränderung in der Bodenbedeckung und der Vegetation zur Folge; ein charakteristisches Beispiel eines räumlichen und zeitlichen Veränderungsprozesses. Wenn die räumlichen und zeitlichen Abfolgen der resultierenden Vegetationsveränderungen typische Muster aufweisen, ist es wertvoll, diese Muster zu beschreiben und die Zusammenhänge zu quantifizieren, um: 1. Diesen Prozess zu verstehen; 2. Solche Prozesse vorherzusagen. Für die Beantwortung dieser Fragen auf der Regionalen Ebene, sind grosse Datensätze mit ausreichender Qualität erforderlich. Neben der Datenqualität ist zudem die Auswahl von geeigneten Methoden wichtig.

Zwei Hauptziele wurden daher für die vorliegende Dissertation formuliert. Erstens soll abgeklärt werden, ob sich die Daten der Schweizer Arealstatistik als grosser räumlich-statistischer Datensatz auf Landschaftsebene zur Beschreibung von ökologischen Prozessen wie sekundärer Waldsukzession verwenden lassen. Dies erschien wichtig, weil solche Prozesse normalerweise nur auf kleineren räumlichen Skalen untersucht werden. Zweitens sollen die Daten dazu verwendet werden, um die räumliche und zeitliche Muster der Waldsukzession besser zu verstehen und auf grossräumiger Skala vorhersagen zu können.

Die für die Fragestellung relevanten Klassen der Schweizer Arealstatistik von 1979/85 und 1992/97 wurden zu fünf neuen Bodennutzungs- und Bodenbedeckungsklassen zusammengefasst, welche den Sukzessionsstadien zwischen landwirtschaftlicher Nutzung und Wald entsprechen: (1) intensiv genutzte Landwirtschaft, (2) extensiv genutzte Landwirtschaft, (3) überwachsene

Flächen mit Gebüsch und Strauchvegetation, (4) offener Wald und (5) geschlossener Wald. Anhand dieser Daten wurden räumlich-explicite statistische Modelle kalibriert und evaluiert, um die beobachteten Veränderungen zu verstehen und zu erklären, und um die Eignung der Modelle für die Vorhersage künftiger Veränderungen zu testen. Hierzu wurden verschiedene Formen von logistischen Regression eingesetzt: Binomiale Modelle für Veränderungen zwischen zwei Bodenbedeckungsklassen, sowie ordinale und multinomiale Modelle für gruppierte Übergänge von einer Klasse zu mehrere anderen Klassen.

Räumliche und zeitliche Muster der Landaufgabe und der nachfolgenden Wiederbewaldung konnten für die Schweiz identifiziert werden. Die Faktoren, welche die Vorhersage von Veränderungen in der Bodenbedeckung erklären, können allgemein zusammengefasst werden zu Struktur der Nachbarschaft und Umweltbedingungen. Die Intensität der Waldsukzession und der Veränderung der Landschaft variiert in der Schweiz regional erheblich und ist sowohl abhängig von lokalen Faktoren (z.B. Samenverfügbarkeit) als auch von grossräumigen klimatischen Faktoren (z.B. Kontinentalität). Das Design der Stichprobeverfahren und die Wahl der statistischen Modelle haben grossen Einfluss auf die Ergebnisse. Wird dies entsprechendberücksichtigt, bewähren sich die verschiedenen logistischen Regressionsmodelle für die hier präsentierte Untersuchung der Veränderungen der Bodenbedeckung. Zusammenfassend kann gesagt werden, dass die Analyse grosser statistischer Datensätze auf Landschaftsebene, wie zum Beispiel der Schweizer Arealstatistik, somit eine viel versprechende Möglichkeit bietet, um ökologische Prozesse wie Waldsukzession und Landschaftsveränderung grosser Regionen zu untersuchen.

## **1. General Introduction:**

### ***1.1. Land-use and land cover change***

There is increasing concern about the impact of the various forms of global change upon ecosystems and ecosystem services (Foley *et al.* 2005). Land-use change and its consequences for land cover are components of these global phenomena (Vitousek 1994; Fukami & Wardle 2005) and are driven principally by global forces (Lambin *et al.* 2001). There is great complexity in how different aspects of global change interact and the feedback that occurs (Lambin *et al.* 2003); for example, a changing climate affects rates of land cover change and disturbance régimes. Likewise a changing climate potentially influences the decisions of land managers concerning the specific land-use of a parcel due to related changes in agricultural productivity and profitability (Dale 1997). And because changes in land-use and land cover affect ecosystem processes they in turn influence other forms of global change such as the distribution and abundance of species, biological invasions (Vitousek *et al.* 1997; Dukes & Mooney 1999), greenhouse gas emissions (Dale 1997), climate at local, regional and global scales (Foley *et al.* 2003) and ecosystems services (Schröter *et al.* 2005) such as carbon sequestration (Houghton *et al.* 1999).

The landscape of Europe is defined by a long history of human influence (Laiolo *et al.* 2004) dating back 6000 – 4500 years B.P (in Switzerland – Burga 1988). According to palynological studies there have been waves of intensive and widespread agricultural use and subsequent abandonment followed by an increase in forest area, steered at times by changing climate and at other times by changing technology (Tinner *et al.* 2003).

#### ***1.1.1 Land abandonment and forest regeneration***

Agriculture as an act is ‘fundamentally a social endeavour shaped by market forces, social and economic policy, and human values’ (Robertson & Swinton 2005). The use of ‘marginal’ land for agricultural purposes has historically taken place where the restricted options created by poverty have driven inappropriate land-use and consequently resulted in land degradation (Lambin *et al.* 2001). As a result of technological and economic developments, farming practices increasingly involve the more intensive use of suitable land, and the need to farm marginal land has been considerably reduced (Mather & Fairbairn 2000). Agriculture in these areas may either be extensified or abandoned completely; and where the land is not used for

some other purpose (e.g. urbanisation) forest vegetation (depending on site conditions) usually establishes (Turner & Meyer 1994). It has been estimated that since 1850 a total of 1.5 million km<sup>2</sup> out of the 6 million km<sup>2</sup> land that was originally cleared for agriculture has been abandoned (Ramankutty & Foley 1999).

Many examples of land abandonment and subsequent vegetation development have been documented from Europe and Eastern North America, dating back to the early 20th century (e.g. Brenchley & Adam 1915; Bazzazz 1968; MacDonald *et al.* 2000; Höchtl *et al.* 2005). These processes have been prevalent in Eastern Asian countries such as China, which have a long history of agricultural and forestry practices (Fang *et al.* 2001), and have also been documented in the Neotropics (Rudel *et al.* 2000; Myster 2004). In 2005 Rejmánek and Van Katwyk released a bibliography of 1511 references published prior to 1991 in which old-field succession and related topics worldwide were addressed. Since 1991 much has been written concerning land abandonment and subsequent vegetation succession and articles can be found in a range of journals, grey literature and online documentation. This is particularly true of the mountainous regions of Western Europe (such as the Pyrenees and the European Alps) of which Switzerland is a part (e.g. Burel & Baudry 1995; Tasser *et al.* 1999a; MacDonald *et al.* 2000; Dullinger *et al.* 2003; Laiolo *et al.* 2004; Vicente-Serrano *et al.* 2005; Gellrich *et al.* in review; Mottet *et al.* 2006).

## **1.2. Background to this doctoral thesis**

### **1.2.1 Study area**

Switzerland is a topographically and climatically diverse country with a long history of human exploitation, which has transformed a previously forested landscape (during interglacial periods) into a mosaic of landscape elements shaped by human activities (Wachter 2002). The wide range of topography and climate has produced diverse agricultural practices in different areas. Alpine agriculture consists largely of pasture and hay meadows, although up until as recently as the 1940's, the higher altitude valley areas were also used for cropland. Extensively used meadows and pastures, both fertilised and unfertilised, have characterised much of the land-use in mountain regions but in recent decades have progressively been abandoned (Zoller *et al.* 1984).

### **1.2.2 Driving forces & proximate causes**

It is generally accepted that land-use change is driven by socio-economic forces (MacDonald *et al* 2000). More specifically, socio-economic drivers of land-use change such as land abandonment was suggested by Lambin *et al* (2001) to be a product of ‘people’s responses to economic opportunities’. Land abandonment is often explained by the process whereby the cost of maintained use outweighs the potential yield, although other theories to do with depopulation, technological advances and willingness to innovate have been suggested and to some extent tested (Walther 1986). Current research in Switzerland confirms that land abandonment is the expression in the landscape of a profound social and economic change, with evidence implying that the process will continue despite agricultural policies designed to hinder it (Baur 2006).

Following abandonment, ecological and environmental factors determine the rate and nature of change in vegetation cover (Turner & Meyer 1994), as does the management history of the site (Hill 1992). Thus the type of vegetation that develops (e.g. which species dominate) reflects historical, environmental and ecological factors. Such effects can be observed in the vegetation long after abandonment has occurred (Zoller *et al.* 1984). This type of ripple effect can act as a signature (c.f. crop signature: Myster 2004) of both past and present forces acting upon an ecosystem.

### **1.2.3 WaSAlp Project – Forest Expansion in the Swiss Alps**

This PhD thesis is part of a larger project that addressed the question: ‘How can we explain the pattern of land abandonment and forest expansion during the last decades with the help of newly available large quantitative datasets?’ (Bebi & Baur 2002). One component of the project sought to quantify and explain spatial patterns of land abandonment (Gellrich *et al.* in review; Gellrich & Zimmermann in review). The second component, presented here, used available data to investigate spatial and temporal patterns of forest regeneration following the giving up of agricultural use.

#### ***1.2.4 Aims of this doctoral thesis***

The main aims were: 1) to determine whether large landscape scale statistical datasets can be used to investigate ecological processes such as semi-natural secondary forest succession that are normally studied at a smaller spatial scale; and 2) to use these data to understand and predict spatial and temporal patterns of forest development.

#### ***1.2.5 Data***

##### ***1.2.5.1 Land cover data***

There are a number of spatially explicit data sources of land and forest cover for Switzerland: The Landscape at Risk inventory, the Swiss National Forest Inventory (NFI) and the Swiss Land-Use statistics (ASCH). The Landscape at Risk inventory is undertaken on a six year cycle (1972/83, 1978/89, 1984/95) to record significant changes in the Swiss landscape and to determine whether or not measures taken to protect landscape elements have been effective (Sigmaplan/Metron/Meteotest 2001). Data is collected from the regularly updated 1:25,000 land cover maps (which themselves are delineated from up-to-date aerial photograph sequences) by reviewing the map symbols (signatures) of eight landscape elements (including: forest; overgrown areas and extensively used agricultural land; ‘small structures’ such as hedges and groups of trees). A sample of 240 x 12km<sup>2</sup> units is surveyed and supplemented by other available statistical data relevant to the inventory, yielding information that is summarised for six Cantonal groups and four geographical regions (Metron/Sigmaplan 1991). This data is not available digitally and does not cover the whole of the Swiss territory and was therefore not appropriate as a source of land cover data for this study.

The NFI is a Swiss-wide, regularly spaced sample database of forest cover intended to provide reliable information about the current state and changes of Swiss forest at all its functional levels. It provides detailed data about forest structure and composition for 1983-85 and 1993-95 for the whole of Switzerland on a 1.4 km regular raster (1 km for the first) prepared from a combination of aerial photograph and field surveys (Brassel & Lischke 2001). It does not yield information about shrub vegetation, overgrown or

agricultural areas and was therefore not useful for this study. The third NFI which will be completed in 2007 does include some of this information.

The Swiss Land-Use statistics are derived from sequences of aerial photos on a one hectare raster (SFSO 2001), where one of 74 possible classes is assigned to each hectare based on the identification of the land-use/land cover at the lower left corner point of the hectare cell i.e. a lattice grid. Where the identification at the point is impeded (e.g. percentage forest canopy cover cannot be determined from point information), a reference area of 25m<sup>2</sup> around the point is used (Sager & Finger 1992). It is also a regularly spaced sample database that covers the whole territory of Switzerland. This data is available for the periods 1979/1985 (ASCH85) and 1992/1997 (ASCH97). After the ASCH97 was completed the ASCH85 was revised to improve its comparability with the latter e.g. by using the more up-to-date digital elevation model (DEM25) for Switzerland as an underlay, accounting for the new categories introduced in 1997, accounting for sample and interpretation error from the 1985 survey (see <http://www.bfs.admin.ch/> for more details (in German, French or Italian)). The 1972 Swiss Land-Use statistics were conducted (a) by assigning land-use and land cover to land cover maps rather than directly to aerial photographs; (b) over a greater time period than the ASCH85 and ASCH97 (1957 to 1971); (c) using a different classification system with 12 classes (and thus different definitions); (d) from data at varying resolutions (1:25,000 for the plateau; 1:50,000 for the mountain regions) and then a class assigned per hectare. The first three Swiss Land-Use statistics (1912, 1923/24, 1952), performed using the Siegfried land cover maps, were at the political municipality resolution and the results were incomplete. Direct comparisons between the latter two datasets (ASCH85 and ASCH97) and those previously undertaken are not recommended due to the possibility that observed land cover changes result only from methodological differences and not from actual change.

As a consequence of the potentials and limitations of the above discussed datasets, the Swiss Land-Use statistics (revised ASCH85 and original ASCH97) were used as the land cover data for the study presented here. This dataset covers the whole of Switzerland (c.f. the Landscape at Risk data) and yields better information than the NFI for the land-use

and land cover classes required to investigate the process of succession, which follows agricultural land abandonment, with forest cover as the probable end-point. Of the 74 possible land-use and land cover classes, 20 were aggregated into a further five to form the following categories used in all papers presented here: 1. Intensively used agricultural land (excluding crops, orchards and vineyards); 2. Extensively used agricultural land; 3. Areas overgrown with shrubs and small trees; 4. Open canopy forest; 5. Closed canopy forest (excluding afforested areas actively planted by people). A more detailed description of the aggregation and the criteria used to form it can be found in paper 1.

As with all remote sensing data there is a certain amount of error introduced when assigning land-use and land cover classes, especially for the less common classes and when changes in the classes are being investigated (as opposed to when a class remains the same over time) (BfS, 2006). We considered that it was still feasible to use the data to understand the observed changes for two reasons: 1. The use of a thematic aggregation of the categories reduces the incidence of error; 2. The large size of the dataset means that even weak trends may be detectable. It is nevertheless difficult to quantify how much noise is introduced into statistical models calibrated using this data, either by the classification system itself and/or the aggregation used here and we acknowledge this as a potential drawback in some of the results generated. Assuming that the errors are randomly distributed, we hypothesise that it will only weaken statistical models, rather than forcing wrong findings by emphasising explanations that are not real. The latter would only be the case if the errors are systematically allocated in the landscape and along gradients of predictors.

#### ***1.2.5.2 Explanatory data***

According to Baldock *et al.* (1996), the main environmental factors influencing the agricultural potential of an area - and thus also the likelihood of land abandonment - are: soil, climate, water supply, relief, altitude and pollution. And subsequent to land abandonment the path and rate of succession are influenced by both environmental and historical factors (Hill 1992; Turner & Meyer 1994) that can be global, regional or local

in nature. Therefore, to interpret the land cover changes represented by the Swiss Land-Use statistics, compatible spatial data concerning these factors are required.

Climate maps have been derived from the measurements of climate stations throughout Switzerland for the period 1961 to 1990 (Zimmermann & Kienast 1999) and provide 30-year normals of annual and monthly information about temperature, precipitation, potential evapotranspiration, and direct and diffuse solar radiation. Combined with topographical information, these data can provide measures of such factors as continentality (Gams index), site water balance and topographic position. Soil data were available as raster maps for six soil characteristics derived from the Swiss soil suitability map (BEK): soil depth, soil permeability, water-logging, nutrient-holding capacity, water-holding capacity and soil stoniness. Other data such as the composition of the neighbourhood (Brown *et al.* 2002), distance to forest edge (Duncan & Duncan 2000), distance to roads and distance to historical destructive avalanche sites were derived in a GIS. Further details are provided in Paper 1.

Data representing the historical management of each site were not available at the extent and resolution and in the specificity that would be useful for our purposes. In particular, it would have been useful to have information on fertiliser use, and mowing or grazing régimes, as these factors not only influence the rate of succession but also which species dominate at different stages (Zoller *et al.* 1984; Tasser *et al.* 1999b).

### ***1.2.6 Land-use and land cover change modelling***

There are a number of good reviews of land-use and land cover change models (Baker 1989; Verburg *et al.* 2004) that are readily built upon and updated as the field of landscape ecology and associated modelling advances. The questions that can be addressed by the use of statistical models have been summarised by Lambin (1997) and are particularly relevant for the analysis and understanding of spatial and temporal pattern. Specifically, they can be broken down into the following three: Why has a change occurred? When will it occur again? Where will it occur again? Likewise, Turner *et al.* (2001) suggest that spatially explicit models are a requisite tool in investigating processes or biotic interactions which generate pattern.

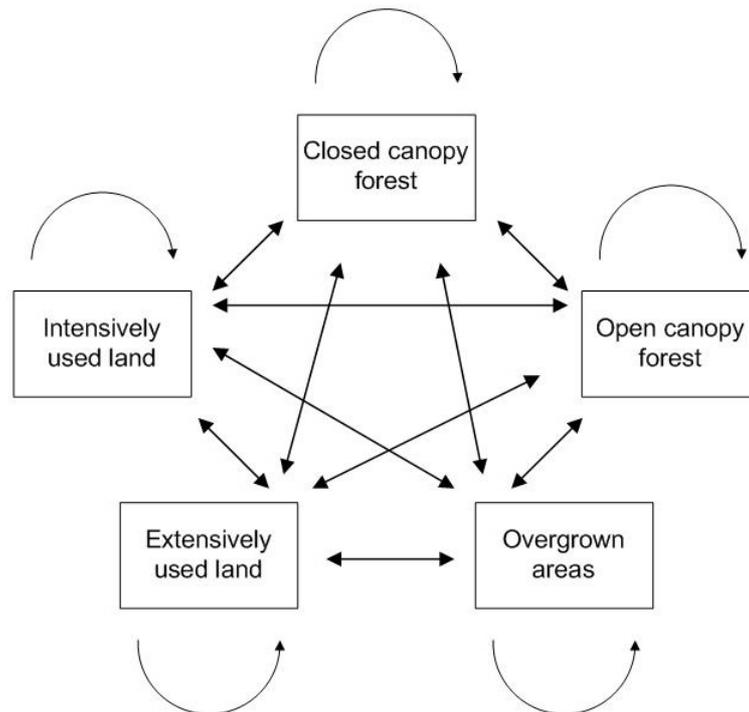
They are used both to explain past events (MacNally 2000) and to predict future events under various scenarios (Guisan & Zimmermann 2000; Clark *et al* 2001). There are various methods of generating spatially explicit statistical models of which some are used and presented in the following papers.

### ***1.3. Papers comprising this doctoral thesis***

The following is a short description giving a summary as to how each paper arose and the specific questions that were addressed.

#### ***1.3.1 Paper 1 - Assessing land-use statistics to model land cover change in a mountainous landscape. Rutherford, G. N., Zimmermann, N. E., Bebi, P., Edwards, P. J. Submission to *Ecological Modelling*.***

One of the first questions encountered in this study concerned which data to use in order to answer questions about ecological processes e.g. secondary succession. Given that the investigation of land cover change at a thematic resolution of ‘forest’/‘non-forest’ does not allow meaningful statements to be made about the vegetation dynamics of the stages in between, an aggregation of the Swiss land-use statistics that would allow this to be done was sought. The questions thus arose: Can we aggregate the available data to create land-use and land cover classes that are ecologically meaningful? Can we make inferences about ecological processes such as secondary succession from the aggregation? Thus a combination of binary logistic regression and generalized additive models (GAM’s) was used to develop spatially explicit models for each of the 25 land cover transitions between the five land-use and land cover classes that had been formed from the aggregation of the Swiss Land-Use statistics dataset (figure 1). The explanatory and predictive power of each of the models was examined.



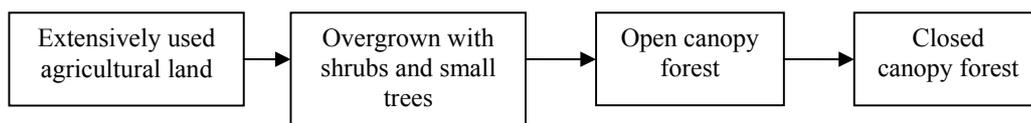
**Figure 1: Transition flow diagram, showing the 25 observed land cover/land-use transitions for which models were calibrated in this study using the Swiss land-use statistics from 1985 and 1997.**

**1.3.2 Paper 2 - Evaluating sampling strategies and logistic regression methods for modelling complex land cover changes. Rutherford, G. N., Guisan, A., Zimmermann, N. E. Submission to *Journal of Applied Ecology*.**

This paper was borne out of the following questions that were raised whilst conducting the analyses for papers 1 and 3: Which sampling method best represents the data? Which type of regression model best fits the data? Which measures should be used to test model accuracy? There are numerous sampling strategies that can be used in conducting statistical analyses, just as there are numerous modelling techniques that can be implemented. However, both choices can affect the results generated. To help determine which sampling and modelling strategies were preferable, three sampling régimes and two grouped discrete regression modelling techniques were tested. The results of the six trials were then compared with one another by comparing the variables retained after stepwise elimination and also comparing three different measures of predictive accuracy.

**1.3.3 Paper 3 - Analysing spatial and temporal patterns of forest succession on abandoned agricultural land using ordinal logistic regression. Rutherford, G. N., Edwards, P. J., Bebi, P., Zimmermann, N. E. Submission to *Journal of Vegetation Science*.**

The binomial logistic regression models calibrated as part of the analyses presented in paper 1 were shown with the use of diagnostic tests to be useful for explaining past occurrences and predicting future land cover changes. However it was notable that each transition probability yielded by a respective model was mutually exclusive of the other possible outcomes from the same starting state and that a grouped outcome model would yield transition probabilities of the outcomes in relation to each other. One group of transitions (i.e. from one starting state – extensively used agricultural land) was therefore selected because it best represented the ecological process of forest succession on abandoned agricultural land. Each individual land cover transition type also represented a rate of successional development (figure 2) which was of particular interest as one of the goals was to identify the ecological factors which distinguished the transition types (and thus rates of succession) from each other. Answers to the following questions were sought: Which environmental factors influence the rate of secondary forest succession on abandoned agricultural land? How do patterns of temporal change vary in space? Is ordinal logistic regression a suitable tool for the analysis of successional changes at the landscape scale?



**Figure 2: Conceptual model showing the ordered sequence of secondary forest succession on abandoned agricultural land.**

**1.4. Applications**

There are many examples of how predictive land cover change models can be used as bases for studies of what might happen under differing future scenarios. The following papers/PhD thesis chapter arose from the use of the binomial logistic regression transition models described in paper 1 and are as follows:

**1.4.1 Bolliger, J., Kienast, F., Soliva, R., Rutherford, G. N. Potential effects of agricultural change on species habitat distributions at the landscape scale – a scenario-based approach. Submission to *Landscape Ecology*.**

This paper presents predictions of the potential effects of land cover change on the spatial distribution of open land insect and bird species in Switzerland under various socio-economic based scenarios. The future scenarios are structured around different degrees of subsidisation of conservation, and agricultural liberalisation.

**1.4.2 Walz, A. Land use allocation modelling for Swiss alpine regions. *Land Use Modelling for an Integrated Approach to Regional Development in the Swiss Alps*. Unpublished PhD thesis, University of Zürich, Switzerland.**

The study presented in this thesis chapter used the binary logistic regression models described in paper 1 as a component of a larger modelling exercise to predict land use and land cover change under complex future scenarios for the region of Davos, Switzerland.

**1.4.3 Luetolf, M., Bolliger, J., Guisan, A., Kienast, F. Scenario-based assessment of future land-use change on butterfly species distributions. Submission to *Journal of Ecology*.**

This paper addresses the question of how two groups of butterfly species, inhabiting dry grasslands and wetlands, respectively, will cope with future land-use changes under four different scenarios based on agricultural liberalisation in Switzerland.

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## **2. Assessing land-use statistics to model land cover change in a mountainous landscape.**

Rutherford, G. N., Zimmermann, N. E., Bebi, P. & Edwards, P. J. Submission to *Ecological Modelling*.

**Abstract:** One of the predominant processes of land cover change in the European Alps over the last 150 years has been the abandonment of agricultural land and the subsequent regeneration of forest. Here, we employed two sequential datasets from Switzerland (for the periods 1979-85 and 1992-97) to show how land-use and land cover data can be used to investigate such large scale ecological and land cover change processes. We applied a combination of generalized additive and generalized linear modelling to develop spatially explicit statistical models for land cover transitions between any of the following types: intensively used agricultural land, extensively used agricultural land, overgrown areas, open canopy forest, closed canopy forest. Climate, soil, relief-related data, basic socio-economic variables and information about the composition of the surrounding neighbourhood of the samples were utilised as potential predictors of land cover change. The proportion of variance explained differed considerably between models but a consistently high AUC for both calibration and evaluation datasets was achieved for the majority of the 25, with resulting values ranging from 0.58 to 0.96. The model residuals showed some degree of spatial autocorrelation despite the use of a sparse sampling regime and the inclusion of neighbourhood variables. We conclude that the analysis of sequential land cover datasets using the kind of statistical models developed here offers a promising way to investigate ecological processes such as forest succession at a large spatial scale.

**Keywords:** land cover change; transition models; spatially explicit models; forest succession; generalized additive models; generalized linear models; land abandonment.

### **Introduction:**

Changing patterns of human settlement and economic activity lead directly or indirectly to changes in land cover; and while such changes have always occurred, the pace has increased dramatically in the past few decades. In areas where conditions are favourable for modern, high-input agriculture, there has been a strong trend towards intensifying production, with an associated loss of semi-natural elements in the landscape (Edwards *et al.* 1999). In contrast, in

more marginal areas - for example in mountainous regions - agriculture has tended to become more extensive or has even been abandoned altogether. Indeed, land abandonment followed by natural regeneration of forest has been widespread throughout Europe since the mid to late 20th century (Guidi & Piusi 1993; Girard *et al.* 1994; Baldock *et al.* 1996; Staaland *et al.* 1998; Tasser *et al.* 1998; MacDonald *et al.* 2000; Verburg *et al.* 2004), and the same phenomenon has been reported in the U.S. since the late 19<sup>th</sup> century (Keever 1950; Pickett & Cadenasso 2005). Factors that have led to the abandonment of agriculture in some areas include: (i) lack of profitability (Gellrich *et al.* in review); (ii) inefficiency resulting from a reluctance to change traditional farming practices (Walther 1986); (iii) new sources of income leading to reduced economic dependence on agriculture (Mather & Fairbairn 2000; Rudel *et al.* 2005).

As in other secondary successions, the development of forest on abandoned agricultural land commonly exhibits a predictable sequence of vegetation change, with different species or groups of species successively gaining and then losing predominance. Unlike in primary successions, where earlier appearing species may modify growth conditions and so permit the entry of later species (facilitation), most plant species in a secondary succession are either present at the outset or can colonise within a few years (Miles 1979). Thus, changes in the composition and appearance of the vegetation are largely caused by differences in growth and survival rates, competitive ability and longevity of the plant species present. For example, a few years after the abandonment of agriculture an open, shrub vegetation develops that includes both light demanding species as well as seedlings of more shade tolerant forest trees. With time, these trees can develop to form a closed canopy and the early successional species are gradually suppressed (Horn 1981).

There are important reasons for wanting to quantify and explain such changes in land cover. Not only can it help us to understand processes at the landscape level, but it can contribute to improved land management and better conservation practices (Rudel *et al.* 2005). However, understanding land cover change poses a considerable intellectual challenge because many different processes are at work, operating at different spatial scales. For example, the initial decision to abandon land is usually the result of socio-economic forces, while subsequent land cover changes are due to ecological processes which in turn are influenced by local environmental conditions and the history of the site (Hill 1992). And these various processes are investigated at different spatial scales: whereas ecological processes such as succession are

usually studied at a small spatial scale (field plot scale), land cover change is usually studied at a regional or even global scale using remotely sensed data.

To analyse the drivers of land cover change, spatially explicit models are increasingly used (Baker 1989; Turner *et al* 2001). These models - often in the form of generalised linear models - incorporate information about the surrounding landscape and the processes that influence it. They provide a tool to summarise data, taking into account both systematic effects and random variation (McCullagh & Nelder 1989). In the context of land cover change they have been used to address three key research questions: 1. where? - identifying areas affected by change and areas which are most likely to undergo some change in the future; 2. why? - linking potential causal factors with change; and 3. when? – measuring rates of change (Lambin 1997).

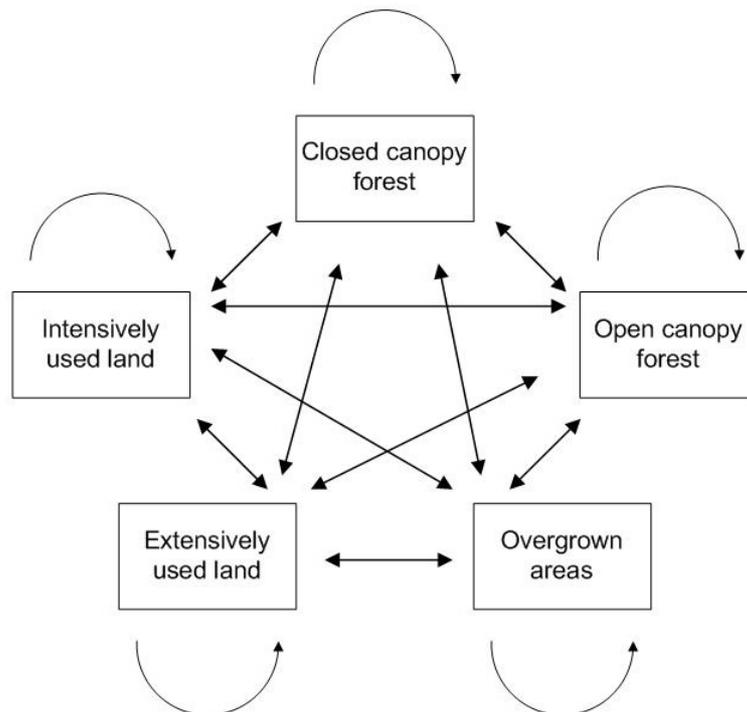
Several types of transition models have been used to investigate these questions and also to simulate future land cover change. Brown *et al* (2002) used GAMs and geostatistical methods to calculate transition probabilities, while other authors have used logistic regression (Wear & Bolstad 1998; Schneider & Pontius 2001; Aspinall 2004; Gellrich *et al.* in review) or discriminant analysis (Tasser *et al.* 1998). Canonical correspondence analysis (CCA) has also been used to distinguish land cover changes along different environmental gradients (Hietel *et al.* 2004). Skånes & Bunce (1997) used principal components analysis (PCA) to investigate changing relations between land cover/land-use changes.

Due to advances in remote sensing and Geographic Information System (GIS) technology, national (e.g. Swiss Land-Use Statistics) and international (e.g. Corine land cover inventory for Europe) spatially explicit land cover inventories are becoming standard tools. In this study we wanted to find out whether the land cover data contained in such inventories can be used as a source of ecological information, for example to study rates of forest succession following the abandonment of agriculture. In order to do so, we needed to answer two main questions. First, are the criteria used to define land-use and land cover classes adequate to make inferences about the type and status of vegetation and are the data of sufficient quality? For example, do the classes used in land cover inventories allow us to distinguish reliably between open and closed canopy forest? Second, is compatible ‘explanatory’ information available that can be used to interpret any patterns of vegetation change derived from the land-use statistics?

In this study we investigated these questions using the Swiss Land-Use Statistics. The specific aims of the work were:

1. To aggregate the agricultural and forest classes so as to be able to identify the intensity of land-use or, in areas not used for agriculture, the successional status of the vegetation;
2. To identify those pixels showing a change in either land-use intensity or successional status between two survey dates 12 years apart;
3. To develop spatially explicit statistical models in order to explain variation in land cover change during the 12 year study period.

Rather than estimating models for the broad land-use/cover changes of agriculture to forest and vice-versa, we sought to break down the changes into more specific categories of still-recognisable classes and calibrated transition models for the changes between these classes (Figure 1), directed toward explaining the observed changes and eventually predicting changes under comparable circumstances. It was not an investigation into driving forces per se, but rather an investigation into the changes themselves which result from the underlying and proximate sources of change (Turner & Meyer 1991).

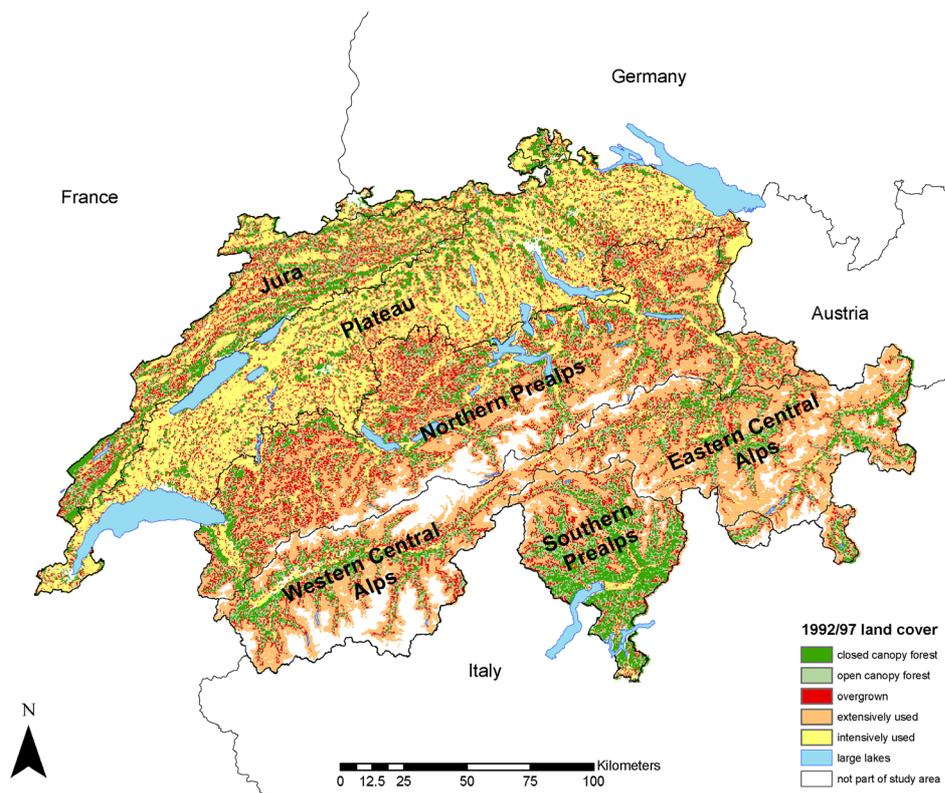


**Figure 1: Transition flow diagram, showing the 25 observed land cover/land-use transitions for which models were calibrated in this study using the Swiss land-use statistics from 1985 and 1997.**

## Methods:

### *Study Area and Data*

Switzerland (lat: 47°00'N; long: 8°00'E) is characterised by a diverse topography, ranging in altitude from 193m in the Ticino region (Southern Prealps) to 4634m in the Valais (Wachter 2002; Western Central Alps), including both high mountains and extensive lowland areas. Switzerland's diversity in climate can be attributed both to its location in the middle of Europe and the European Alps dissecting the country on a SW to NE axis. Its climate thus ranges from oceanic in the Northwest to continental in the Eastern Central Alps, with a more Mediterranean influence in the South (Wachter 2002). The forest area of Switzerland has increased by 30 - 50% in the last 150 years (Brändli 2000), with most of this increase occurring on former agricultural land. Our study area included all those agricultural land-use and forest cover classes of interest to this study, together representing  $3 \times 10^6$  out of a total area of  $4.1 \times 10^6$  hectares (Figure 2).



**Figure 2: The study area of Switzerland and the location of the aggregated land-use/land cover types under investigation. The broad biogeographical zones are labelled. White areas within Switzerland, not included in the study, consist largely of impermeable surfaces such as infrastructure, rock and snow/ice. The spatial resolution is 1 hectare.**

***Dependent variable(s)***

In order to investigate land cover change and its possible drivers in Switzerland we used the ‘Swiss Land Use Statistics’ produced by the Swiss Federal Department of Statistics (SFSD 2001). To produce this information, land cover data for the whole of Switzerland are derived from aerial photographs using a regular grid of sample points 100m apart (SFSD 1992). The land cover at each point is determined according to a system of 74 classes (see Sager & Finger (1992) for details), of which 20 were used in our study (Table 1). Most of the remaining 54 classes represent surfaces without vegetation such as glaciers, open water, urban environments or rock. Taking into account the normal sequence of vegetation succession following disturbance (Burroughs 1990; Begon *et al.* 1996), the 20 land cover classes were grouped into five classes representing varying degrees of land-use intensity and forest development as follows: intensive agricultural land-use, extensive agricultural land-use, overgrown areas, open canopy forest and closed canopy forest (Table 1).

Our aggregation of the Land-Use Statistics can be split into the 2 broad categories of land-use and land cover. The criteria for further dividing the land cover types into stages of forest succession was based on vegetation height, percentage cover density and the type of shrub/tree species present. ‘Hedges and groves’ were included in the closed canopy forest class according to our definitions, despite the fact that these are often linear elements in the landscape closely associated with intensive agricultural land-use. The reasons for attributing this cover type to the closed forest class were: a) no height restrictions are enforced for this type, and often it consists of mature trees, and b) no cover restriction is required for this type, and often it consists of closed canopies. Both allow this cover type to represent small patches in a landscape that have the characteristics of a closed canopy although the spatial dimension is restricted. The cover type was also retained here for calculating the neighbourhood variable of ‘number of surrounding closed canopy forest neighbours’ (see below); hedges and groves are as much a potential seed source as the other classes within the closed canopy forest category. As only spontaneous forest regeneration was of interest, forest plantation areas were excluded from the study. The open canopy forest category is a mix of land-use and cover, but due to the fluid nature of the classes within and the often resulting difficulty in distinguishing the 2 (Sager & Finger 1992), we chose to follow our cover based criteria nonetheless. The extensively and intensively used land-use classes were defined primarily by machine accessibility and whether use, irrespective of the

actual management practice, was year-round or not. Croplands, vineyards and orchards were not included in the study because very few, if any, had been subject to abandonment and subsequent spontaneous forest regeneration, and their seeds do not contribute to natural forest regeneration.

**Table 1: Aggregated classes from the Swiss land-use/land cover statistics (ASCH85 & ASCH97) used in this study. Numbers in parentheses represent the official ASCH classes (Sager & Finger 1992). The criteria used to aggregate the classes are listed.**

Aggregated class	Classes from Swiss land use statistics	Broad definition
Closed canopy forest	<ul style="list-style-type: none"> <li>• Other forest (10)</li> <li>• Normal forest (11)</li> <li>• Strips and blocks (14)</li> <li>• Bushes (15)</li> <li>• Groves &amp; hedges (17)</li> </ul>	Vegetation height > 3m, Cover density > 60%, Composed of tree species.
Open canopy forest	<ul style="list-style-type: none"> <li>• On non-agriculturally used land (12)</li> <li>• On agriculturally used land (13)</li> <li>• Groups of trees on agriculturally used land (18)</li> <li>• Other groves (19)</li> </ul>	Vegetation height > 3m, Cover density 20 - 60%, Composed of tree species.
Overgrown areas	<ul style="list-style-type: none"> <li>• Overgrown meadows (84)</li> <li>• Overgrown alpine pasture (86)</li> <li>• Shrubs and bushes (16)</li> </ul>	Vegetation height < 3m, Cover density > 50%.
Extensive land use	<ul style="list-style-type: none"> <li>• Pasture in the vicinity of settlements (83)</li> <li>• ‘Maiensässe’, hay alps, mountain meadows(85)</li> <li>• Sheep alps (87)</li> <li>• Favourable to pasturing (88)</li> <li>• Stony alpine pasture (89)</li> <li>• Grass and herb vegetation (97)</li> </ul>	Used for grazing, Use not year-round, Not machine-accessible.
Intensive land use	<ul style="list-style-type: none"> <li>• Machine accessible meadows (81)</li> <li>• Meadows with limited machine access (82)</li> </ul>	Year-round use In the vicinity of settlements, Mown.

Comparable land-use statistics are available for Switzerland for the periods 1979-85 and 1992-97 (referred to as AS85 and AS97 hereafter). Although these time bands are broad, the flight sequence for both periods was for the most part the same and thus the time difference for most pixels is approximately 12 years, with around 19% of pixels having a difference of 13 years (of which a considerable proportion consisted of land cover classes not used in our study). We used a GIS to reclassify both datasets into 5 aggregated classes and then calculated the transitions

that occurred among classes between the two periods. In this way we produced a grid with 25 possible classes, each representing a land cover transition type showing either intensification in use, dis-intensification in use (extensification), cessation of use (land abandonment), changes that represented progression in forest succession and changes that represented a decrease in woody vegetation cover. The 5 static states indicating ‘no change’ were also included (Figure 1). This yielded a classic Markov transition matrix (Usher 1981).

### ***Sample Design***

In order to maintain a systematic and consistent system of transition model estimation, the same numbers of sample points for the calibration datasets were selected for each transition, irrespective of its observed prevalence. In doing so we aimed to sample out the effect of persistence i.e. where samples are weighted heavily toward the ‘no change’ static state purely due to its dominance. It enabled us to also calibrate the ‘rare’ transitions, which was necessary as we wished to eventually determine the underlying and proximate causes for the various land cover changes. The sample size choice of 250 points per response was based on the least common transition type (249 points for overgrown to intensively used land). For the other transition types, sample points were randomly selected, without replacement, and each sample with the same original land cover state combined to give five calibration datasets of 1250 randomly selected points with the same starting state and equal proportions of the 5 possible end states. The same method was followed using another set of randomly selected points without replacement to generate the respective five evaluation datasets, to later test the forecasting power of the models (Rykiel 1996; Wear & Bolstad 1998).

### ***Independent Variables***

As described by Baker (1989) and further discussed by Brown *et al.* (2000), we extended the Markovian transition model by calibrating each transition as a function of exogenous and endogenous explanatory variables. These are useful in interpreting the transitions and can also serve as spatial predictors of land cover change. Endogenous explanatory variables are related, at least in part, to other variables or parameters within the model. Baker (1989) uses the example of factors relating to landscape composition and structure. In contrast, exogenous variables are determined by forces outside of the model such as climatic or socioeconomic factors. A large

pool of possible predictors was available from which a selection was made for inclusion in the stepwise model development procedure (Table 2). Potential explanatory variables were selected after consideration of which factors – for example climate, soil, topography and adjacent land cover (e.g. potential seed source or likely land use) – were expected to influence either land abandonment or subsequent plant growth. Although land-use history is also known to be a factor affecting the nature and speed of land cover change following abandonment (Bunce 1991; Hill 1992), there was no spatial dataset at the required resolution that we could use.

As with the response variables, all explanatory variables were used at a spatial resolution of 100 metres (1 hectare). Elevation was obtained directly from the Swiss Digital Elevation Model (DEM). The derivation of further explanatory variables was performed in a GIS using existing digital data of a partly finer grain. Slope and aspect were both derived from the DEM. Aspect was later converted to cosine of aspect and sine of aspect to give values relative to South and West respectively.

A set of climate variables had been generated previously from climate station data recorded throughout Switzerland and from digital elevation models (see Zimmermann & Kienast (1999)). The maps represent climate normals of the period 1961 to 1990. Soil variables were derived from the soil suitability map of Switzerland (SFSO 1992) and have been modelled over a DEM to include variations due to topographical aspects. Six different layers were available for use, each representing a soil characteristic, i.e. soil depth, permeability, nutrient-holding capacity, water-holding capacity, stoniness and water-logging. The soil suitability map lists minima and maxima for each soil layer. We used the pixel-wise varying topographic exposure within each soil type for spanning the values for each soil characteristic between minimum and maximum. For example, the most acute ridges would be assigned the minimum values for soil depth and water holding capacity per soil type, while the most distinct gullies and toe slopes would be assigned the maximum values per soil type.

The number of neighbours of any of the 5 different land cover types was calculated in a GIS using a 5 x 5 cell rectangular moving window, thus returning a value between 0 and 24 hectares. Distance to a particular land-cover type was calculated in a GIS using the straight line distance function. The variable ‘distance to roads’ was derived from the Swiss national Vector 25© map using the same function. Similarly, distance to settlements was derived from the ‘Settled Areas of Switzerland’ (SGCH) grid.

**Table 2: Independent variables used to calibrate the predictive models explaining the 25 land cover transitions between agricultural use and forest cover. All grids were available at 100m resolution.**

Variable	Unit	Proxy for	Source
<b>Climate-related variables</b>			
Continental index, Gams		Large scale weather pattern	CSD/DEM25
Moisture index	cm/100	Small-scale water availability	CSD/DEM25
Direct solar radiation	kJ/day	Energy input, drought stress	CSD/DEM25
Precipitation	(1/10mm)/month	Precip during growing season	CSD/DEM25
# summer precipitation days	number	Frequency of rainfall	CSD/DEM25
<b>Relief-related variables</b>			
Elevation	m	Potential evapotranspiration Growing degree days Monthly average temperature	DEM25
Slope	°	Diffuse solar radiation	DEM25
Topographic position	-∞ to +∞	Exposure of site, drought	DEM25
Topographic wetness index		Moisture accumulation	DEM25
Site water balance	(1/10mm)/year	Available soil moisture	CSD/DEM25
Sine of aspect		Aspect relative to south	DEM25
Cosine of aspect		Aspect relative to west	DEM25
<b>Soil-related variables</b>			
Soil depth	(cm)	Soil water & nutrient availability	BEK200/DEM25
Soil permeability	(cm/day)	Water infiltration, risk of drought	BEK200/DEM25
Soil stoniness	(%)	Water holding capacity	BEK200/DEM25
<b>Neighbourhood variables</b>			
# closed canopy forest neighbours	(number/25)	Woody species seed source	ASCH85
# open canopy forest neighbours	(number/25)	Woody species seed source	ASCH85
# overgrown neighbours	(number/25)	Woody species seed source Density of abandonment	ASCH85
# extensively used neighbours	(number/25)	Density of extensive use	ASCH85
# intensively used neighbours	(number/25)	Density of intense use	ASCH85
<b>Distance variables</b>			
Distance to roads	(m)	Accessibility	Vector25
Distance to settlements	(m)	Accessibility	SGCH
Distance to closed canopy forest	(m)	Likelihood of abandonment	ASCH85
Distance to open canopy forest	(m)	Likelihood of abandonment	ASCH85
Distance to overgrown areas	(m)	Likelihood of abandonment	ASCH85
Distance to extensively used	(m)	Likelihood of extensive use	ASCH85
Distance to intensively used	(m)	Likelihood of intensive use	ASCH85

CSD: Climate Station Data from the period 1961 – 1990. DEM25: Digital elevation model for Switzerland at 25m resolution from the Swiss Federal Office of Topography (SwissTopo). BEK200: Soil suitability map 1:200,000 (Bodeneignungskarte der Schweiz, SFSO, 1992). ASCH85: Swiss land-use statistics 1985 (SFSO, 2001). Vector25: Mapped street data, Vector 25 © 2006, Swiss Federal Office of Topography (DV033594). SGCH: Settled areas of Switzerland (Siedlungsgebiete der Schweiz, SFSO, 1992).

The randomly selected sample of the response variables was intersected with the associated 27 explanatory variable values (Table 2) to produce a database which was then imported into S-Plus (Insightful Corp. 2000) and R (R Development Core Team 2004) for the statistical analyses. The X and Y co-ordinates for each sample point were added before export, to ensure that the subsequent models would remain spatially explicit and to allow testing for spatial autocorrelation of the model residuals.

### ***Statistical Analyses***

We combined Generalised Additive Modelling (GAM) and Generalised Linear Modelling (GLM) to estimate transition probabilities for each of 3.1 million hectares based on endogenous and exogenous factors.

First we calculated GAMs for each individual potential explanatory variable against each response as a form of exploratory statistical analysis (Agresti 2002). The deviance explained ( $D^2$ ) by each model was then used to select the explanatory variables that were most significant statistically. The loess smoothed GAM functions were plotted to ascertain whether the dependent variable showed a linear or non-linear response to the explanatory variables, and thus to determine whether polynomial terms should be used in the formulation of the GLM models (Guisan & Zimmermann 2000).

We then used scatterplots and Spearman rank correlation coefficients to determine whether explanatory variables were correlated. We used a cut-off level of 0.8 as recommended by Menard (2002). Groups of highly correlated variables were thus identified and one variable from each group selected for the multivariate modelling process. Menard (2002) warns of the risk of the omission of correlated variables from models but also highlights the fact that their retention causes the calculated coefficients to have large standard errors, thus decreasing the accuracy of the coefficient estimates. We therefore chose to retain one proxy for the correlated variables.

The final transition models were generated by calibrating GLMs (McCullagh & Nelder 1989) to estimate the coefficients of the multiple model parameters. In this study, each statistical model has a binary response, where the probability of a success (a particular land cover transition occurring) is calculated, a so-called failure thus being when the respective event (transition) does not occur (Agresti 2002). The appropriate statistical modelling method is therefore logistic regression (Menard 2002). The models were first fitted using those variables shown from the

GAMs as having significant explanatory power, that were not correlated with other explanatory variables. Where the single-variable relationship was shown from the GAM plots to be non-linear, polynomial terms up to the 4<sup>th</sup> degree, when necessary, were used. A bidirectional automated stepwise regression starting from a full model was then performed to eliminate variables which did not serve to increase the explanatory power of the models. The stepwise regression used Akaike's information criterion (AIC) to select the model of best fit (Bozdogan 1987).

Residual analysis was performed to investigate whether or not the assumptions of the models were violated, and to explore the adequacy of the models with regards to the variance and link functions, and the terms in the linear predictor (McCullagh & Nelder 1989). We tested for spatial autocorrelation of the model residuals using empirical variograms and correlograms.

Various measures can be used to test the accuracy of calibrated models. First, the correct classification rate (CCR) uses a 2 x 2 confusion matrix to calculate the proportion of correctly classified values predicted by the fitted model. The CCR, however, is not always an appropriate measure of accuracy as it is heavily influenced by the prevalence of the presence/absence events. Another approach is the kappa statistic (Cohen 1960); this statistic provides a measure of agreement between datasets but is sensitive to sample size and may therefore not be an appropriate measure of accuracy, especially as it is unreliable if one class dominates (Fielding & Bell 1997; Fielding 1999). We used the area under the Receiver Operating Characteristic (ROC) curve (AUC), which returns a single value that can be used as a measure of model accuracy and predictive power. Unlike other accuracy measures, it is independent of the observed prevalence of the event (Metz 1978) if the values are neither very high nor very low (McPherson *et al* 2004) and it is independent of a threshold to discriminate between binary responses (Fielding & Bell 1997). It is thus a useful tool in the evaluation of statistical models such as those describing land cover changes (Pontius & Schneider 2001). For each of the calculated logistic regressions the AUC was calculated. The models were tested using the evaluation dataset. An accuracy measure of 1.0 characterises perfect model fit. A value of 0.5 represents agreement by chance and values below 0.5 indicate systematic errors. We also calculated the deviance explained by each model ( $D^2$ ).

**Results:**

***Spatially Aggregated Transition Probabilities***

The transition matrix (Table 3) shows that the land cover of most pixels did not change during the period investigated. However, there were some important transitions in land cover, the most notable being the shifts from overgrown areas to closed forest (8.71% of initially overgrown areas), and from open to closed canopy forest (7.58%). Overall extensive forest establishment and succession occurred over a total of 45,417 hectares (Table 4), while 16,639 hectares showed an opposite trend, becoming less densely covered by woody species and/or more intensively used. These numbers constitute 1.1% and 0.4% of the Swiss territory, respectively.

**Table 3: Transition probabilities calculated from the observed changes between land cover types between 1985 and 1997 for Switzerland, using the aggregated ASCH datasets. “No change” transition types are bold.**

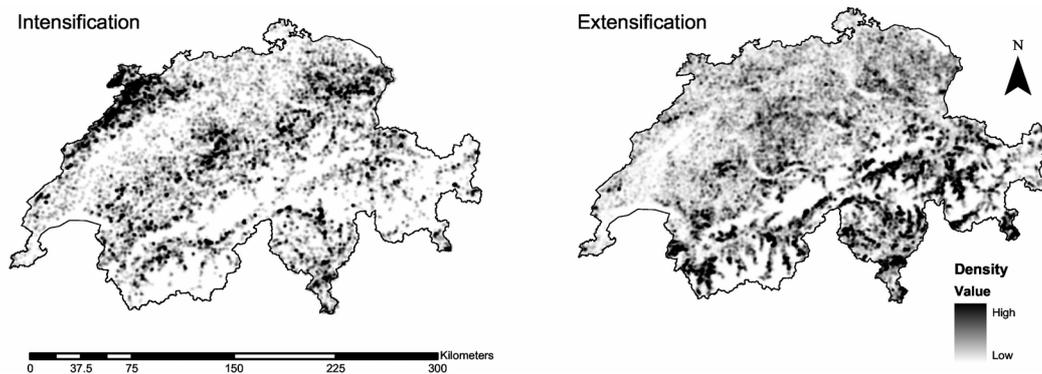
		Land cover in 1997 (ha)					Totals
		Closed canopy forest (1,116,690)	Open canopy forest (149,246)	Overgrown (110,693)	Extensive land-use (761,972)	Intensive land-use (822,682)	
<b>Land cover in 1985 (ha)</b>	Closed canopy forest (1,097,373 )	<b>0.9956</b>	0.0020	0.0005	0.0010	0.0009	1.00
	Open canopy forest (151,476)	0.0758	<b>0.8949</b>	0.0031	0.0155	0.0107	1.00
	Overgrown (112,200)	0.0871	0.0392	<b>0.8629</b>	0.0086	0.0022	1.00
	Extensive land-use (762,289)	0.0027	0.0063	0.0157	<b>0.9675</b>	0.0078	1.00
	Intensive land-use (837,945)	0.0013	0.0025	0.0011	0.0237	<b>0.9714</b>	1.00

Figure 3 shows the spatial distribution of various land cover changes in Switzerland during the 12 year study period. The process of intensification tended to be focused in certain regions, notably in the Jura Region in the North-West of Switzerland, in the Entlebuch area of the Northern Prealps, and in the North East (area of Appenzell). Intensification can also be detected on valley floors in other areas, particularly in the South-West of the Central Alps (Rhône Valley) and in the Southern Prealps (Ticino and Brenno valleys). In contrast, pixels showing extensification were more evenly distributed, though particularly high densities occurred in the alpine region, especially in the Central Alps and the Southern Prealps.

**Table 4: Model quality and goodness of fit for the 25 calibrated models and the subsequent evaluation datasets. The occurrence of each observed land cover transition between 1985 and 1997, from the Swiss land-use statistics (ASCH), is shown.**

Change in land cover (1985 to 1997)	Observed occurrence (ha)	Explanatory power ( $D^2$ ) of model	Goodness of fit calibration data (AUC)	Goodness of fit evaluation data (AUC)
Closed canopy to closed canopy forest	1092296	0.21	0.79	0.79
Closed canopy to open canopy forest	2389	0.09	0.71	0.69
Closed canopy to overgrown	551	0.22	0.81	0.76
Closed canopy to extensively used agr.	1257	0.09	0.70	0.68
Closed canopy to intensively used agr.	880	0.40	0.90	0.90
Open canopy to closed canopy forest	11482	0.12	0.74	0.73
Open canopy to open canopy forest	135560	0.16	0.76	0.69
Open canopy to overgrown	457	0.10	0.72	0.70
Open canopy to extensively used agr.	2352	0.18	0.79	0.80
Open canopy to intensively used agr.	1625	0.51	0.94	0.92
Overgrown to closed canopy forest	9772	0.13	0.75	0.75
Overgrown to open canopy forest	4398	0.23	0.81	0.74
Overgrown to overgrown	96820	0.33	0.87	0.83
Overgrown to extensively used agr.	961	0.20	0.79	0.76
Overgrown to intensively used agr.	249	0.13	0.75	§
Extensively used to closed canopy forest	2064	0.21	0.81	0.79
Extensively used to open canopy forest	4836	0.21	0.81	0.78
Extensively used agric. to overgrown	11930	0.22	0.81	0.79
Extensively used to extensively used agr.	737541	0.31	0.84	0.84
Extensively used to intensively used agr.	5918	0.60	0.96	0.96
Intensively used to closed canopy forest	1076	0.02	0.60	0.58
Intensively used to open canopy forest	2063	0.08	0.70	0.70
Intensively used to overgrown	935	0.21	0.81	0.83
Intensively used to extensively used agr.	19861	0.21	0.82	0.79
Intensively used to intensively used agr.	814010	0.22	0.81	0.80

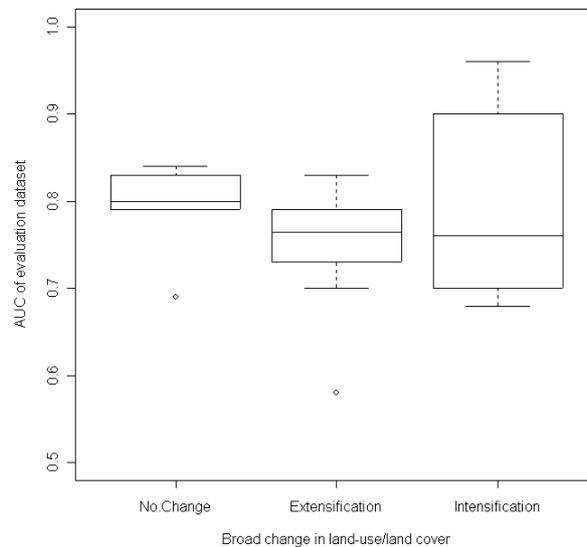
§ as all 249 observations were used in the estimation of this model, no validation was undertaken



**Figure 3: Spatial pattern of land-use/cover extensification and intensification in Switzerland between 1979/85 and 1992/97 based on the density of observed occurrences from the Swiss land use statistics.**

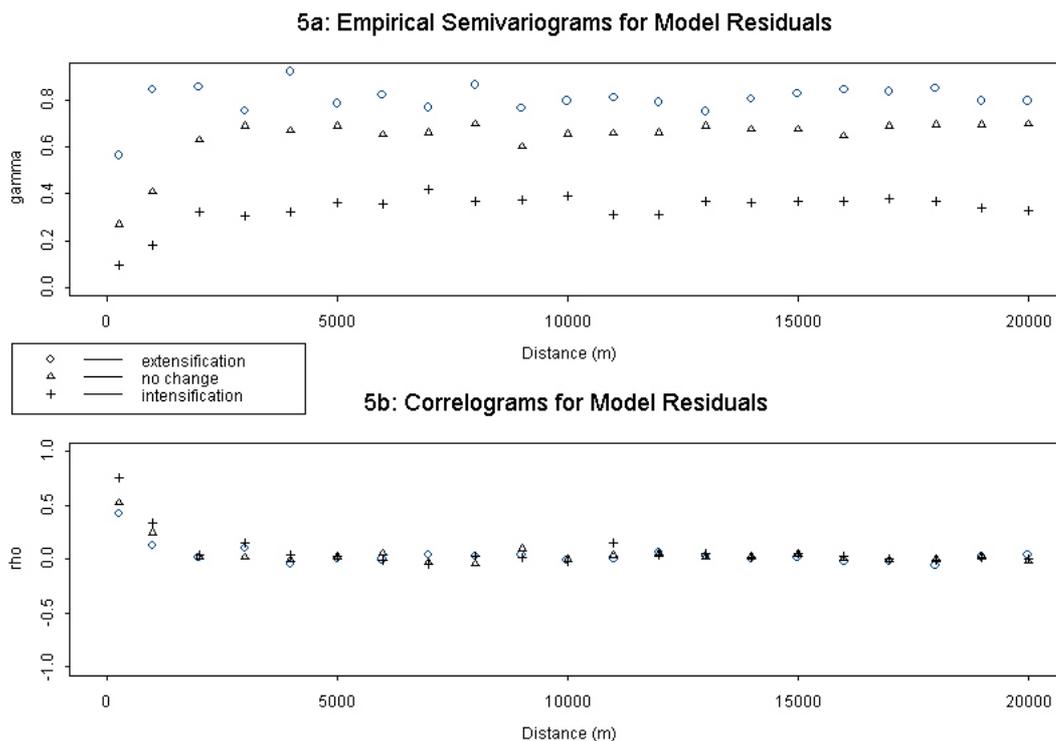
### ***Spatially Explicit Transition Models***

The proportion of deviance explained ( $D^2$ ) varied greatly among the 25 models (Table 4), the lowest proportion being 0.02 (intensively used agricultural land becoming closed canopy forest) and the highest being 0.60 (extensively used agricultural land becoming intensively used). However, for several of the models a similar proportion of deviance (approximately 20%) was explained. With the exception of the model for intensively used land becoming closed canopy forest, the AUC values for most models were ‘useful’ to ‘high in accuracy’ (Swets, 1988), for both the calibration (range: 0.70 to 0.96) and evaluation (range: from 0.69 to 0.96) datasets, indicating that a consistent level of model accuracy was achieved. AUC values for the evaluation data were almost always slightly lower than those of the calibration data but were generally similar indicating the absence of sampling bias and little overfitting of the calibration data. Overall, the models explaining intensification had the widest range in accuracy, yielding both the least and most accurate models (with the exception of one outlying model for extensification); those explaining no change in current land-use were the most consistent, with one outlier (open canopy forest remaining the same) (Figure 4). The models explaining extensification revealed intermediate accuracy and consistency, with the exception of the weakest outlier (intensively used agricultural land becoming closed canopy forest).



**Figure 4: Boxplot of accuracies achieved by models explaining extensification, intensification and no change (remain).**

The examination of model residuals revealed that up to a distance of at least 1000m there was spatial autocorrelation, which varied in degree depending on the model (Figure 5). It was highest for the process of intensification and lowest for the process of extensification as shown by the initial spatial covariance values (Figure 5b). The extensification model had the smallest range and the highest nugget. The ‘no change’ model had the highest range and the second highest nugget, with intensification having the lowest nugget (Figure 5a).



extensification = extensively used land in 1985 becoming overgrown by 1997; no change = extensively used land in 1985 remaining extensively used in 1997; intensification = extensively used land in 1985 becoming intensively used by 1997.

**Figure 5: Empirical semivariograms and correlograms depicting presence of spatial autocorrelation in model residuals for extensification (extensively used land becoming overgrown with shrubs), intensification (extensively used land becoming more intensively used) and no change (extensively used land remaining so). Gamma = semivariance estimate (5a). Rho = a standardised measure of spatial covariance (5b).**

### Aggregation of the Swiss Land-Use Statistics

A breakdown of our aggregation of the Swiss Land-Use Statistics into their original classes gives insight into the transition types (see supplementary data). Most transitions represent a plausible change in land cover within a 12 year period. However, some transition types stand out as

unusual: of the 880 hectares of closed canopy forest becoming intensively used, 408 hectares were ‘hedges and groves’ becoming ‘meadows with limited machine accessibility’. More than 77% of the 1625 hectares of open canopy forest that became intensively used were ‘groups of trees on agriculturally used land’ becoming ‘meadows with limited machine accessibility’. Of the 2352 hectares of open canopy forest which became extensively used, 891 hectares were ‘groups of trees on agriculturally used land’ which became ‘land favourable to pasturing’. Likewise, the changes from intensively used land to either open or closed canopy forest were dominated by the opposite classifications: 623 hectares of ‘meadows with limited machine accessibility’ became ‘hedges and groves’, while 1671 hectares became ‘groups of trees on agriculturally used land’.

### **Discussion:**

The analysis of changes between agricultural land-use and forest cover in Switzerland between 1985 and 1997 revealed that both extensification and intensification occurred during this period, though extensification was three times more frequent. Hypothesis testing of whether the observed transition types were statistically significant would theoretically be of interest but not necessarily yield the information sought due to the potential presence of spatial autocorrelation in the data as well as the data format (grid cells in a GIS) not having the appropriate degrees of freedom (Pontius *et al* 2004). The same authors also make the important point that ‘statistical significance does not necessarily indicate practical importance’.

Overall, our aggregation of the Swiss Land-Use Statistics appears both ecologically sensible and useful for further analyses. There are however a number of anomalies, reflected in the poor explanatory power of some of the resulting models and when one closely considers the plausibility of some of the transition types. We consider that within a 12 year period, the possibility of intensively used land becoming covered in closed canopy forest is unlikely, especially given the fact that with our data we do not know at which point in the period under investigation that land abandonment occurred. This may equally be the case with the change from intensively used land to open canopy forest. We attribute the ‘observations’ of these two transition types to our inclusion of ‘hedges and groves’ in the closed canopy forest class and to the fact that ‘groups of trees on agriculturally used land’ in the open canopy forest class, are often directly associated with intensively used meadows, when observed in the vicinity of intensively used land and are areas of land that are still being used for agricultural purposes (Sager & Finger

1992). These associations may lead to error in the classes if the sample point in the two time periods was not in the exact same position. Indeed, of the intensively used land which became open canopy forest, a large percentage were ‘meadows with limited machine access’ becoming ‘groups of trees on agriculturally used land’. The relatively high proportion of the change to closed canopy forest consisting of ‘meadows with limited machine access’ becoming ‘hedges and groves’, further supports this point, although it is certainly possible that farmers actively planted hedges in this time and such management decisions and actions are not represented by any measure in our data. The reverse occurrences of closed and open canopy forest becoming intensively used could be similarly explained, although both models do have high explanatory and predictive power. The fact that the changes between the previously described classes appear to be either erroneous or represent changes which we can not measure with our data indicates that these particular models may not be suitable for use in further investigating ecological processes of land cover change. However, given that the changes between the classes appear to be confined only to those classes in question, we conclude that we can still have confidence in the remaining aggregation and the remaining models.

Some models were poor in explanatory power despite the presence of all variables which would be expected to influence and drive plant growth and forest regeneration e.g. the models estimating the transitions from both overgrown areas and open canopy forest to closed canopy forest. Yet, most of the resulting models still have strong predictive power (reflected by the AUC values) as is often the case (Venables & Ripley 2002). It seems to be more reliable in general to calibrate ( $D^2$ ) and explain (AUC) extensification and the static states than intensification with the predictors we used. This may indicate that environmental predictors are better able to explain extensification than intensification. The principal reasons for the act of land abandonment, the maintenance of agricultural management where the environmental conditions would permit forest regeneration and any intensification in management within the period investigated are socio-economic in nature (Gellrich *et al.* in review; Gellrich & Zimmermann in review) and therefore not explained explicitly by our models. Improving the explanatory power of these models would therefore require more specific socio-economic predictors.

Spatial autocorrelation is to some degree present in the models despite the inclusion of neighbourhood variables representing the nature of the surrounding landscape and distance to other land cover classes (Brown *et al.* 2002). In fact these variables are often the most important

in explaining the variation of whether a particular land cover transition occurs or not. Our sparse sampling regime also did not eliminate spatial autocorrelation from our models as may have been expected (Fortin *et al.* 1989). Spatial autocorrelation characterises important processes within the landscape (seed dispersal, land-use history etc.) and its presence in the models highlights the dynamism of land cover change. The nugget values in the variograms represent the variation in a model which is either not autocorrelated or is autocorrelated at a finer scale than represented by the model. This is shown by our results to be highest for the model representing extensification, which also exhibits the least spatial autocorrelation with a range of 997m (after which no autocorrelation is shown to occur) and low spatial covariance values. Conversely the model representing intensification shows the highest levels of spatial autocorrelation and the lowest level of variation which is either not autocorrelated or autocorrelated at a finer scale than represented by the model. We attribute the higher level of spatial autocorrelation exhibited in the intensification model to the fact that an active decision is required on the part of a land manager to intensify land-use and that this is much more likely to affect clusters of land units (Gellrich *et al.* in review). On the other hand land abandonment and subsequent spontaneous forest succession is likely to occur in a much more random fashion.

Two very different types of factors determine the land cover transitions observed in our data. The initial abandonment of agricultural land (or its intensification) is most likely determined by socio-economic factors. However, once the event of abandonment has occurred, ecological processes involving vegetation succession and ecosystem development become important, and these are influenced by factors such as radiation, temperature (represented here by elevation), soil quality, the composition of the surrounding landscape and the previous management regime (Hill 1992).

We fulfilled our aim of calibrating multivariate statistical land transition models in a spatially explicit manner at a high thematic resolution. The main advantage of using the data at this resolution over such a large area is that we can analyse ecological processes such as forest succession on a larger scale. The main disadvantage is that intuitively the greater the number of categories in a classification system, the more detailed and accurate the classification criteria are required to be, thus introducing a greater potential for error. However, the fact that ecologically sensible, statistically robust models resulted from our analyses shows that we can have confidence in the classes at this thematic resolution as well as in the models themselves.

### **Conclusion**

We conclude that it is feasible to model land cover change at the thematic resolution that we have presented here, and that this approach is a promising way of further investigating large-scale land cover change and the associated ecological process of forest succession in a spatially explicit manner with local driving forces. Specifically, such models can be used to address two key research questions concerning land cover change posed by Lambin (1997). Firstly, ‘what are the proximate causes of the observed land cover changes?’, and secondly ‘what distinguishes one type of land cover change from another with the same initial state, within the same time period, where foreseeably the same ecological process is underway i.e. forest succession?’ We believe that our approach is a sound step forward in answering such questions with regards to the changes between agricultural land-use and forest cover in a Central European landscape.

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## 2.1 Supplementary Data

### Breakdown of the transition types showing closed canopy forest that became another land cover class from 1985 to 1997.

closed canopy forest to other		closed canopy forest to other		closed canopy forest to other	
transition type	points	transition type	points	transition type	points
1010	1065	1413	51	1587	3
1011	383	1414	41506	1588	65
1012	44	1415	8	1589	3
1013	4	1416	52	1597	39
1014	2	1417	143	1711	260
1015	7	1418	137	1712	25
1016	1	1419	153	1713	62
1018	1	1481	34	1714	379
1019	2	1482	72	1715	4
1086	3	1483	55	1716	48
1110	12965	1484	6	1717	32904
1111	943412	1485	5	1718	185
1112	714	1486	5	1719	61
1113	324	1487	1	1781	173
1114	445	1488	99	1782	408
1115	49	1489	2	1783	141
1116	256	1497	27	1784	3
1117	124	1510	4	1785	7
1118	163	1511	1078	1786	5
1119	321	1512	49	1788	136
1181	36	1513	8	1797	17
1182	153	1514	36		
1183	116	1515	55740		
1184	13	1516	81		
1185	20	1517	6		
1186	30	1518	13		
1188	228	1519	29		
1197	287	1582	4		
1410	181	1583	4		
1411	1595	1585	2		
1412	43	1586	48		

The first two digits for each transition type represent the ASCH class in 1985. The second two digits are those of the ASCH in 1997. Both refer to the number assigned by the Swiss land-use statistics (Sager & Finger 1992). See Table 1 for the description and definition of each class.

**Breakdown of the transition types showing open canopy forest that became another land cover class from 1985 to 1997.**

open canopy forest to other		open canopy forest to other		open canopy forest to other	
transition type	points	transition type	points	transition type	points
1210	475	1382	63	1914	448
1211	5104	1383	58	1915	96
1212	47764	1384	13	1916	144
1213	8	1385	10	1917	89
1214	25	1386	28	1918	56
1215	34	1388	277	1919	30884
1216	57	1389	6	1981	21
1217	5	1397	15	1982	75
1218	6	1811	669	1983	38
1219	91	1812	218	1984	2
1281	2	1813	930	1985	7
1282	7	1814	484	1986	13
1283	5	1815	20	1987	4
1284	2	1816	114	1988	81
1285	3	1817	316	1989	4
1286	2	1818	31929	1997	142
1287	1	1819	473		
1288	18	1881	192		
1289	2	1882	1256		
1297	96	1883	568		
1310	158	1884	33		
1311	2234	1885	93		
1312	572	1886	38		
1313	21253	1887	1		
1314	106	1888	891		
1315	6	1889	8		
1316	11	1897	24		
1317	24	1910	1		
1318	240	1911	1188		
1319	21	1912	1082		
1381	9	1913	33		

The first two digits for each transition type represent the ASCH class in 1985. The second two digits are those of the ASCH in 1997. Both refer to the number assigned by the Swiss land-use statistics (Sager & Finger 1992). See Table 1 for the description and definition of each class.

**Breakdown of the transition types showing overgrown areas (left and middle) and intensively used agricultural land (right) that became another land cover class from 1985 to 1997.**

overgrown area to other		overgrown area to other		intensively used areas to other	
transition type	points	transition type	points	transition type	points
1610	1	8483	60	8111	4
1611	4015	8484	681	8114	4
1612	1185	8488	2	8116	27
1613	110	8497	12	8117	162
1614	666	8610	1	8118	57
1615	2739	8611	688	8119	10
1616	56234	8612	249	8181	533718
1617	491	8613	407	8182	4146
1618	158	8614	96	8183	6605
1619	1235	8615	730	8184	26
1681	34	8616	5890	8188	218
1682	100	8617	30	8197	15
1683	37	8618	554	8211	181
1684	11	8619	284	8212	43
1685	19	8681	3	8213	143
1686	46	8682	4	8214	88
1687	2	8683	1	8215	14
1688	135	8685	33	8216	373
1689	4	8686	33735	8217	623
1697	76	8687	1	8218	1671
8411	196	8688	441	8219	139
8412	16	8689	30	8281	6235
8413	52	8697	108	8282	269911
8414	60			8283	12147
8415	28			8284	502
8416	223			8285	1
8417	31			8286	7
8418	97			8288	747
8419	51			8297	128
8481	12				
8482	96				

The first two digits for each transition type represent the ASCH class in 1985. The second two digits are those of the ASCH in 1997. Both refer to the number assigned by the Swiss land-use statistics (Sager & Finger 1992). See Table 1 for the description and definition of each class.

**Breakdown of the transition types showing extensively used agricultural land that became another land cover class from 1985 to 1997.**

extensively used areas to other							
transition type	points						
8311	59	8588	647	8887	64	9782	49
8312	8	8589	7	8888	363276	9783	11
8313	76	8597	33	8889	499	9785	3
8314	34	8711	18	8897	523	9786	5
8315	9	8712	34	8911	11	9787	184
8316	166	8713	1	8912	21	9788	81
8317	140	8714	7	8913	35	9789	31
8318	410	8715	90	8914	2	9797	177733
8319	28	8716	785	8915	33		
8381	1044	8718	4	8916	564		
8382	2721	8719	80	8917	3		
8383	65052	8786	30	8918	89		
8384	359	8787	50757	8919	57		
8386	1	8788	71	8982	1		
8388	10	8789	8	8983	1		
8397	30	8797	513	8985	14		
8511	69	8811	235	8986	94		
8512	11	8812	75	8987	7		
8513	122	8813	474	8988	574		
8514	25	8814	65	8989	44954		
8515	36	8815	165	8997	349		
8516	240	8816	1294	9711	395		
8517	19	8817	101	9712	425		
8518	361	8818	1778	9713	4		
8519	28	8819	96	9714	46		
8581	6	8881	918	9715	477		
8582	101	8882	1054	9716	2856		
8583	11	8883	39	9717	25		
8585	31626	8884	2	9718	9		
8586	351	8885	430	9719	610		
8587	3	8886	5183	9781	24		

The first two digits for each transition type represent the ASCH class in 1985. The second two digits are those of the ASCH in 1997. Both refer to the number assigned by the Swiss land-use statistics (Sager & Finger 1992). See Table 1 for the description and definition of each class.

## **2.2 Additional results**

The additional results presented here constitute a tabular summary of the 25 binomial logistic regression models whose calibration and evaluation are described in paper 1. The predictor variables and their ecological interpretation for the individual models were neither presented nor discussed within the paper. Rather they were further utilised as a basis for the prediction of ‘what might happen...’ under different land-use and land cover change scenarios (see Applications - section 1.4).

**Predictor variables shown to be significant for the binomial logistic regression models for ‘CLOSED CANOPY FOREST in 1985’ to the respective five states listed below in 1997.**

<b>Predictor Variables</b>	<b>Intensive</b>	<b>Extensive</b>	<b>Overgrown</b>	<b>Open canopy</b>	<b>Closed canopy</b>
ELEVATION	x		x	x	
^2		x	x		
^3			x		
DIRECT SOLAR RADIATION - JUNE			x		
^2			x		
SLOPE		x		x	x
^2		x	x		
TOPOGRAPHIC POSITION			x		x
^2			x		x
^3					x
^4					x
SITE WATER BALANCE					
^2			x		
SOIL PERMEABILITY			x		
^2			x		
SOIL DEPTH		x			
^2		x			
#CLOSED CAN NEIGHBOURS	x			x	x
^2				x	
#OPEN CAN NEIGHBOURS				x	
#OVERGROWN NEIGHBOURS			x		
^2			x		x
#EXTEN NEIGHBOURS		x			x
#INTEN NEIGHBOURS	x			x	x
DIST OPEN CANOPY					x
DIST OVERGROWN			x	x	x
^2			x		x
DIST EXTENSIVE		x			
DIST INTENSIVE	x		x	x	
^2			x	x	
DIST SETTLEMENT					
^2			x		
^3			x		

**Predictor variables shown to be significant for the binomial logistic regression models for ‘OPEN CANOPY FOREST in 1985’ to the respective five states listed below in 1997.**

<b>Predictor Variables</b>	<b>Intensive</b>	<b>Extensive</b>	<b>Overgrown</b>	<b>Open canopy</b>	<b>Closed canopy</b>
ELEVATION	x	x	x	x	x
PRECIPITATION - MAY			x		
^2		x			
^3		x			
MOISTURE INDEX - MAY		x			
^2		x			
PRECIPITATION DAYS					
^2			x		
^3			x		
CONTINENTALITY					
^2			x		
^3			x		
SLOPE	x	x		x	
^2		x	x		
^3		x			
SITE WATER BALANCE				x	
^2			x	x	
^3				x	
SOIL PERMEABILITY		x	x		
^2			x		
^3			x		
SOIL DEPTH			x	x	x
^2				x	x
#CLOSED CAN NEIGHBOURS					x
^2					x
#OPEN CAN NEIGHBOURS				x	
#OVERGROWN NEIGHBOURS	x		x		
^2			x		
^3			x		
^4			x		
#EXTEN NEIGHBOURS	x	x			
#INTEN NEIGHBOURS	x		x		
DIST CLOSED CANOPY					x
^2					x
^3					x
DIST OVERGROWN		x		x	x
^2	x	x	x		x
^3			x		x
DIST EXTENSIVE		x			
DIST INTENSIVE	x				x
^2	x			x	x
^3					x
DIST SETTLEMENT				x	
^2					x
DIST ROADS				x	

**Predictor variables shown to be significant for the binomial logistic regression models for ‘OVERGROWN in 1985’ to the respective five states listed below in 1997.**

<b>Predictor Variables</b>	<b>Intensive</b>	<b>Extensive</b>	<b>Overgrown</b>	<b>Open canopy</b>	<b>Closed canopy</b>
ELEVATION		x	x		x
^2		x		x	x
^3		x			
PRECIPITATION - MAY		x		x	
^2	x	x		x	
^3	x			x	
MOISTURE INDEX - MAY	x		x	x	x
^2				x	
^3				x	
DIRECT SOLAR RADIATION - JUNE	x				x
PRECIPITATION DAYS	x		x		
SLOPE	x	x	x		x
^2		x			x
TOPOGRAPHIC POSITION		x			x
^2		x			
SITE WATER BALANCE					
^2	x	x			
^3	x	x			
TOTAL WETNESS INDEX	x				
SOIL PERMEABILITY				x	
^2					
^3		x			
SOIL STONINESS	x				x
^2	x		x	x	x
^3	x			x	x
^4	x				x
SOIL DEPTH		x		x	x
^2					x
^3					x
#CCA NEIGHBOURS	x		x		
^2	x				
#OCA NEIGHBOURS			x	x	
#OVG NEIGHBOURS	x				
#EXT NEIGHBOURS	x	x			x
#INT NEIGHBOURS	x	x	x	x	
^2	x	x			
DIST CLOSED CANOPY			x		x
^2				x	x
DIST OPEN CANOPY				x	
^2			x	x	
DIST EXTENSIVE	x	x	x		
^2	x				
^3	x				
DIST INTENSIVE	x		x	x	
DIST ROADS	x		x		

**Predictor variables shown to be significant for the binomial logistic regression models for ‘EXTENSIVELY USED AGRICULTURAL LAND in 1985’ to the respective five states listed below in 1997.**

<b>Predictor Variables</b>	<b>Intensive</b>	<b>Extensive</b>	<b>Overgrown</b>	<b>Open canopy</b>	<b>Closed canopy</b>
ELEVATION	x	x		x	x
^2			x		x
PRECIPITATION - MAY			x		
MOISTURE INDEX - MAY	x		x	x	
PRECIPITATION DAYS		x			
SLOPE	x			x	
^2				x	x
^3				x	
TOPOGRAPHIC POSITION	x				x
^2	x				
^3			x		
SITE WATER BALANCE					
^2		x			
TOTAL WETNESS INDEX		x			
SOIL PERMEABILITY			x		
^2			x		
^3			x		x
^4			x		
SOIL STONINESS		x			
^2		x			
SOIL DEPTH	x	x			x
^2					x
^3					x
#CLOSED CAN NEIGHBOURS			x	x	
^2			x		
^3			x		
#OPEN CAN NEIGHBOURS		x		x	
^2					x
#OVERGROWN NEIGHBOURS			x		x
^2			x		x
^3			x		
#EXTEN NEIGHBOURS		x	x	x	x
^2			x		
#INTEN NEIGHBOURS	x				x
^2		x			x
DIST CLOSED CANOPY			x		x
^2			x		
DIST OPEN CANOPY				x	
DIST OVERGROWN	x	x	x		
^2	x	x	x		x
^3		x			x
^4					x
DIST INTENSIVE	x		x		
^2			x		
^3			x		
DIST SETTLEMENTS		x	x		
^2					
^3			x		
DIST ROADS		x			

**Predictor variables shown to be significant for the binomial logistic regression models for ‘INTENSIVELY USED AGRICULTURAL LAND in 1985’ to the respective five states listed below in 1997.**

<b>Predictor Variables</b>	<b>Intensive</b>	<b>Extensive</b>	<b>Overgrown</b>	<b>Open canopy</b>	<b>Closed canopy</b>
ELEVATION			X		X
^2			X		
PRECIPITATION - MAY	X		X		
^2	X				
MOISTURE INDEX - MAY					X
^2					X
PRECIPITATION DAYS		X			
^2		X			
CONTINENTALITY	X			X	
^2	X			X	
^3				X	
SLOPE	X	X	X		
^2		X	X		
^3			X		
TOPOGRAPHIC POSITION					
^2		X			
^3			X		
^4			X		
SITE WATER BALANCE			X		
^2			X		
TOTAL WETNESS INDEX				X	X
SOIL PERMEABILITY		X			
^2			X		
^3			X		
SOIL STONINESS	X				
^2		X			
SOIL DEPTH	X			X	
^2				X	
^3		X			X
#CLOSED CAN NEIGHBOURS				X	
#OPEN CAN NEIGHBOURS			X	X	
^2		X		X	
#OVERGROWN NEIGHBOURS	X	X	X		
^2	X				
^3	X	X			
^4		X			
#INTENSIVE NEIGHBOURS	X		X	X	
DIST CLOSED CANOPY	X				
DIST OPEN CANOPY		X	X		
^2		X	X		
DIST OVERGROWN		X	X		
^2	X		X		
DIST EXTENSIVE		X			
^2		X			
^3		X			
DIST SETTLEMENTS	X				
DIST ROADS					
^2					X
^3					X



### **3. Evaluating sampling strategies and logistic regression methods for modelling complex land cover changes.**

Rutherford, G. N., Guisan, A., Zimmermann, N. E. Submission to *Journal of Applied Ecology*.

#### **Summary**

1. The role of land cover change as a significant component of global change has become increasingly recognised in recent decades. Large databases measuring land cover change and the data which can be potentially used to explain the observed changes are also becoming more commonly available. When developing statistical models to investigate observed changes, it is important to be aware that the chosen sampling strategy and modelling techniques can influence results.
2. We present a comparison of three sampling strategies and two forms of grouped logistic regression models (multinomial and ordinal) in the investigation of patterns of successional change after agricultural land abandonment in Switzerland.
3. Results indicated that both ordinal and nominal transitional change occurs in the landscape and that the use of different sampling regimes and modelling techniques as investigative tools yield different results.
4. ***Synthesis and applications:*** Our multimodel inference successfully identified a set of important and consistently selected drivers of land cover change, which can be used to predict further change. This allows for more reliable decision making and planning with respect to landscape management. Although both model approaches gave similar results, ordinal regression yielded more parsimonious models that identified the important drivers of land cover change more efficiently. Thus, this approach is favourable where land cover change pattern can be interpreted as an ordinal process. Otherwise, multinomial logistic regression is a viable alternative.

#### **Key words**

Land cover change; Model accuracy; Model selection; Multinomial regression; Ordinal regression.

## **Introduction**

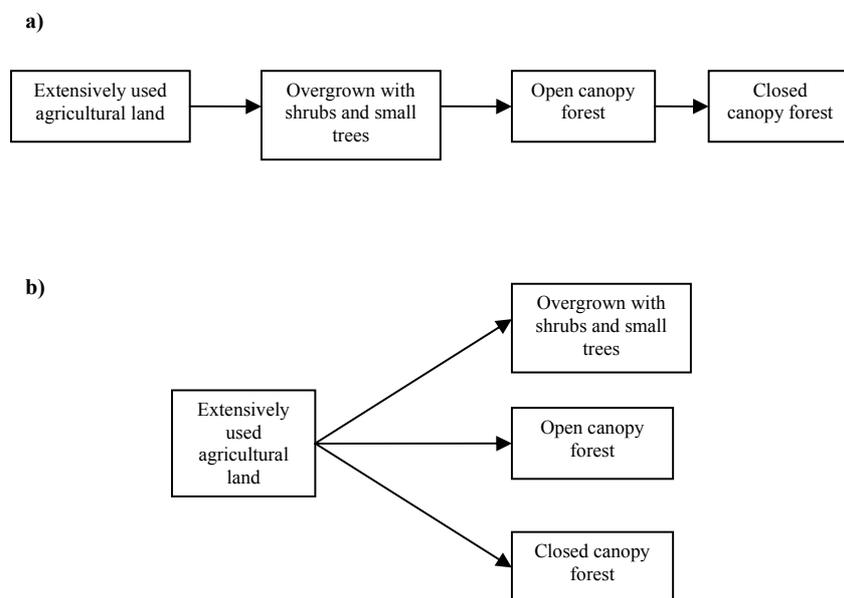
There is increasing concern within the scientific community about the effects of global changes on ecosystems and ecosystem services (Foley *et al* 2005). Along with climate change and biological invasions, land cover change is considered one of the most important components of these changes (Vitousek 1994; Fukami & Wardle 2005). Thus, understanding spatial and temporal patterns of land cover change and their resulting effects on ecosystems is one of the important challenges facing ecologists and managers worldwide. Two of the most profound land-use and land cover change processes in Europe today are urbanisation (Antrop 2004) and agricultural land abandonment (MacDonald *et al* 2000). This is particularly evident in Switzerland, where between 1985 and 1997 more than 45,500 hectares of agricultural land (1.1% of Swiss territory) was either converted to settled areas (in the lowlands: ca. 28,500 ha) or reverted to forest (mostly in steep mountainous areas on marginal land: >17,000 ha) (SFSO 2001). This represents the continuation of a process which has been underway for over 100 years (Mather & Fairbairn 2000).

Different methods of statistical modelling enable decision makers or land managers to answer different questions (Lambin 1997). One approach to assessing land cover change is to apply the kind of predictive statistical models widely used to predict the distribution of species or habitat types (Guisan & Zimmermann 2000). Many statistical modelling methods are currently being used to analyse, describe and understand spatial and temporal patterns of land cover change, of which binary logistic regression is amongst the most common (Aspinall 2004; Verburg *et al* 2004a; McDonald & Urban 2006). Ordinal and multinomial logistic regressions are both examples of discrete outcome modelling techniques, which allow outcomes with the same starting state to be modelled as a group, and are generalisations of the binomial model (Agresti 1996). Such models are appropriate where transitions starting from one cover type have different possible end states.

Ordinal regression assumes ordinality of the outcomes (Figure 1a), as its' name implies (McCullagh 1980; Guisan & Harrell 2000). It has been used in a few ecological studies that focussed on plant species distributions (Guisan & Harrell 2000; Dirnböck *et al* 2003), insect development (Manel & Debouzie 1997) and identifying the conservation values of sites (Spooner & Lunt 2004). Proportional odds regression is based on the cumulative odds of adjacent

outcomes and continuation ratio models, where latter outcomes have passed through the previous (Guisan & Harrell 2000).

Multinomial regression makes no assumptions concerning normality, linearity and homogeneity of variance for the independent variables (McCullagh & Nelder 1989). However, it assumes that the different outcome classes are nominal and that they are mutually exclusive (Figure 1b) (Agresti 1996; Augustin *et al* 2001). It is possible to model multinomial data in an ordinal way and *vice versa*, but if the wrong method is used this may introduce bias or loss of efficiency and information (Long 1997). Multinomial logistic regression is being increasingly used in studies of land cover change (Müller & Zeller 2002; Munroe *et al* 2004) and vegetation dynamics (Augustin *et al* 2001). Yet, where the possible new cover types following land abandonment can be distinguished along an axis of successional development (Fig. 1a), ordinal regression is conceptually valid as well. Thus, our first goal was to compare different statistical modelling techniques suitable for land cover change assessment and modelling. In trialling the two forms of grouped discrete outcome modelling techniques we aimed to test the hypotheses that the land cover transition types under investigation were better predicted by either ordinal or nominal regression models, in which cases we would respectively expect the ordinal or multinomial logistic regression model to fit the data best.



**Figure 1: Conceptual model of land cover change as an ordinal (a) or multinomial (b) process.**

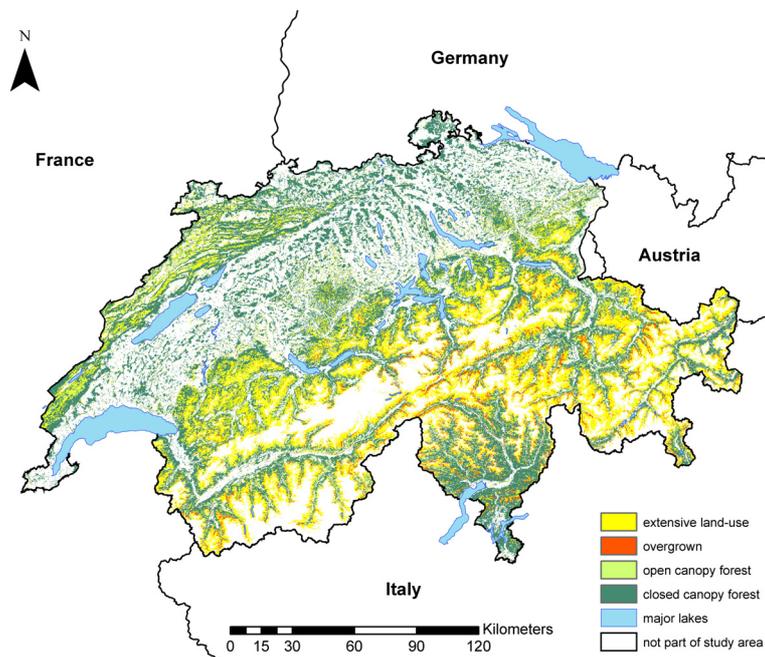
The choice of appropriate statistical models is important as it can affect the outcome and thus the interpretation of results (Olden & Jackson 2000; Guisan 2002). However, the design of the data collection is often of similar importance, since the performance of individual statistical methods is influenced by the nature and the design of the collected data (Edwards *et al* 2006; Guisan *et al* 2006). There are various sampling strategies, which can be used in ecological studies e.g. regularly spaced, random, bootstrap resampling of the entire dataset (Guisan & Zimmermann 2000). Resampling techniques allow the user to ‘obtain nearly unbiased estimates of model performance, without sacrificing sample size’ (Harrell 2001). However, when spatial data is being statistically analysed, using all the available data and resampling it will almost certainly introduce spatial autocorrelation into the models, thus violating assumptions of independence (Wagner & Fortin 2005). Dungan *et al* (2002) recommend determining the minimum distance needed between sampling points and then drawing either a regular or random sample to eliminate spatial autocorrelation. This method has been successfully implemented (Müller & Zeller 2002) but may lead to problems of small sample size, which is a recognised drawback of some singular empirical models for investigating land cover change (Verburg *et al* 2004b). A possible solution to this problem is multi-model inference and model averaging. Model averaging allows inferences to be made from several models, as opposed to fitting just one model to a particular dataset or testing one hypothesis (Burnham & Anderson 1998; Johnson & Omland 2004). The practice of using multiple models to investigate patterns in data is becoming more common in ecological studies (e.g. MacNally 2000; Aspinall 2004) and will likely continue to increase (Clark *et al* 2001). Thus the second goal of our study was to investigate whether different sampling strategies give rise to different model results and whether a particular sampling strategy appears to favour one modelling technique over the other.

In a continuously evolving landscape, tools that enable managers to monitor, understand and predict land cover changes and the forces behind the changes are invaluable. This is because a better understanding of the processes of land-use and land cover change allows more informed planning and management decisions to be made (Verburg *et al* 2004b). In this paper our aim was therefore to answer the following questions using the Swiss land-use statistics: 1. Which sampling strategy should be used to best represent our data? 2. Which modelling technique fits our data best? 3. From 1 and 2, can we infer transition modes (i.e. ordinal versus nominal) from spatial and temporal patterns of land cover change and their proximate causal factors?

## Materials and Methods

### *Study Area*

Switzerland (4.1 million ha) is a mountainous country located in the centre of Western Europe (lat: 47°00'N; long: 8°00'E) (Figure 2; Wachter 2002). The wide diversity of topography associated with altitudes ranging from 193m to 4634m a.s.l. contribute to great regional variation in climate. As with the rest of Europe, Switzerland has a long history of human habitation and its landscape is defined by this impact (Tinner *et al* 2003; Laiolo *et al* 2004).



**Figure 2: Map of the study area and the four aggregated land cover classes (state 1985). The surrounding countries are labelled.**

### *Data*

The response variable represented by land cover was prepared by using 18 out of the 74 Swiss land-use statistics classes (Sager & Finger 1992) and aggregating them into 4 classes: extensive agricultural land-use, overgrown, open canopy forest and closed canopy forest (Rutherford 2006). The land-use statistics of Switzerland was recorded for the periods 1979-1985 (ASCH85 hereafter) and 1992-1997 (ASCH97) by interpreting aerial photographs and allocating each lattice point in a 100m raster to one of 74 classes. The time span between the two assessments was 12 years for the vast majority of lattice points, but for a small proportion it was 13 years. We selected 18 original cover classes for our study and excluded the other (mostly urban) classes

from our analyses (Table 1). In investigating land cover changes, we were interested in the transitions observed from extensively used agricultural land in 1985 to one of three states in 1997: overgrown with trees and shrubs (11,930 ha), open canopy forest (4,836 ha) or closed canopy forest (2,064 ha). These new states represent three different rates of successional development (Rutherford 2006).

**Table 1: Aggregated classes from the Swiss land-use/land cover statistics (ASCH85 & ASCH97) used in this study. Numbers in parentheses represent the original class codes (Sager & Finger 1992). The criteria used to aggregate the classes are listed.**

Aggregated class	Classes from Swiss land use statistics	Broad definition
Closed canopy forest	<ul style="list-style-type: none"> <li>• Other forest (10)</li> <li>• Normal forest (11)</li> <li>• Strips and blocks (14)</li> <li>• Bushes (15)</li> <li>• Groves &amp; hedges (17)</li> </ul>	Vegetation height > 3m, Crown cover density > 60%, Composed of tree species.
Open canopy forest	<ul style="list-style-type: none"> <li>• On non-agriculturally used land (12)</li> <li>• On agriculturally used land (13)</li> <li>• Groups of trees on agriculturally used land (18)</li> <li>• Other groves (19)</li> </ul>	Vegetation height > 3m, Crown cover density 20 - 60%, Composed of tree species.
Overgrown areas	<ul style="list-style-type: none"> <li>• Overgrown meadows (84)</li> <li>• Overgrown alpine pasture (86)</li> <li>• Shrubs and bushes (16)</li> </ul>	Vegetation height < 3m, Crown cover density > 50%.
Extensive land use	<ul style="list-style-type: none"> <li>• Pasture in the vicinity of settlements (83)</li> <li>• ‘Maiensässe’, hay alps, mountain meadows (85)</li> <li>• Sheep alps (87)</li> <li>• Favourable to pasturing (88)</li> <li>• Stony alpine pasture (89)</li> <li>• Grass and herb vegetation (97)</li> </ul>	Used for grazing, Use not necessarily year-round, Not machine-accessible.

A pool of potential predictor variables was selected according to factors identified in previous studies and the ecological literature as influencing land cover change and forest succession (Myster & Pickett 1994; Rutherford 2006). These ecologically meaningful factors are mostly biogeophysical and can be broadly summarised into climatic, neighbourhood, soil and distance variables (Table 2). A description of how the climatic variables were derived can be found in Zimmermann & Kienast (1999) and the remaining explanatory variables in Rutherford (2006). All predictor variables were available as 100m grids matching the ASCH85 and ASCH97 lattice.

**Table 2: Independent variables used to calibrate the predictive models explaining the 3 land cover transitions between grassland and forest. All grids were available at 100m spatial resolution.**

Variable	Abbreviation	Unit	Proxy for	Source
<b>Climate-related variables</b>				
May moisture index	MIND5	cm/100	Small-scale water availability	CSD/DEM25
Yearly direct solar radiation	SDIRy	kJ/day	Energy input, drought stress	CSD/DEM25
June direct solar radiation	SDIR6	kJ/day	Energy input, drought stress	CSD/DEM25
Annual average temperature	TAVEy	°/year	Potential evapotranspiration Growing degree days, Elevation	CSD/DEM25
Continental index	CIND		Large scale weather pattern	CSD/DEM25
Annual average precipitation	PRCPy	(1/10mm)/year	Total water input to system	CSD/DEM25
# summer precipitation days	PDAY	number	Frequency of rainfall	CSD/DEM25
May average precipitation	PRCP5	(1/10mm)/month	Precipitation during growing season	CSD/DEM25
<b>Relief-related variables</b>				
Slope	SLOPE	°	Diffuse solar radiation	DEM25
Topographic position	TOPOS	-∞ to +∞	Exposure of site, drought	DEM25
Topographic wetness index	TWI		Moisture accumulation	DEM25
Site water balance	SWB	(1/10mm)/year	Available soil moisture	CSD/DEM25
<b>Soil-related variables</b>				
Soil depth	SDEP	cm	Soil water & nutrient availability	BEK200/DEM25
Soil permeability	SPRM	cm/day	Water infiltration, risk of drought	BEK200/DEM25
Soil stoniness	SSTO	%	Water holding capacity	BEK200/DEM25
<b>Neighbourhood variables</b>				
# closed canopy neighbours	#CCAN	number/25	Woody species seed source	ASCH85
# open canopy neighbours	#OCAN	number/25	Woody species seed source	ASCH85
# overgrown neighbours	#OVGN	number/25	Woody species seed source Density of abandonment	ASCH85
# extensively used neighbours	#EXTN	number/25	Density of extensive use	ASCH85
# intensively used neighbours	#INTN	number/25	Density of intense use	ASCH85
<b>Distance variables</b>				
Distance to roads	DRDS	m	Accessibility	Vector25
Distance to settlements	DSET	m	Accessibility	SGCH
Distance to avalanches	DAVS	m	Snow-related disturbance Propensity for future avalanches	DADB

CSD: Climate Station Data from the period 1961 – 1990. DEM25: Digital elevation model for Switzerland at 25m resolution from the Swiss Federal Office of Topography (SwissTopo). BEK200: Soil suitability map 1:200,000 (Bodeneignungskarte der Schweiz, SFSO, 1992). ASCH85: Swiss land-use statistics 1985 (SFSO, 2001). Vector25: Mapped street data, Vector 25 © 2006, Swiss Federal Office of Topography (DV033594). SGCH: Settled areas of Switzerland (Siedlungsgebiete der Schweiz, SFSO, 1992). DADB: Destructive avalanches database (SLF, 2006).

We checked for collinearity of the predictor variables using a hierarchical cluster analysis and selected one representative for groups with a higher Pearson correlation coefficient than 0.8 (Menard 2002), which served to reduce data and avoid the presence of multicollinearity in the models (MacNally 2000; Harrell 2001).

### ***Sampling strategies***

We ran three different sampling strategies in order (a) to determine whether different models resulted, and (b) to identify the most effective strategy (i.e. the strategy that produced the best model in terms of explanatory power and predictive accuracy):

1. An equal number of 250 random data points for each of four land-cover transitions (irrespective of their observed prevalence) = 1000 points in total. The “no change” transition means extensive grasslands remain the same during the 12 study years.
2. A random sample of one quarter of the three observed land-cover transitions representing a change in land cover = 4,785 points in total.
3. A regular sample of those data points that only show cover transitions, with data points 500m apart in both x- and y- directions = 719 points in total.

The distance of 500 m apart in the x- and y- directions was selected on the basis of previous investigations into the presence of spatial autocorrelation in binary logistic regression models of land cover transitions (Rutherford 2006). Ideally the points would be 1000m apart but this would have yielded a very small sample size. We eliminated the no change class from the latter two sampling strategies to reduce the influence of the much more prevalent event (Manel *et al* 2001; Pontius *et al* 2004a). We also did this because we were ultimately interested in comparing the systematic changes in land cover to each other, and not necessarily to the static state. For each sampling strategy, we sampled an independent dataset by the same methods (data-splitting), for subsequent model evaluation (Wear & Bolstad 1998).

### ***Model fitting***

#### ***Multinomial Logistic Regression***

We fit a saturated multinomial model (terms up to quadratic form; no interactions) in R (R Development Core Team 2006) using the `multinom()` function in the `nnet` package (Venables

& Ripley 2002) and reduced the model by performing a backward stepwise procedure, using the Akaike Information Criterion (AIC) for variable exclusion.

### *Ordinal Logistic Regression*

We fit a saturated proportional odds regression model to our data (terms up to quadratic form; no interactions) using the `lrm()` function of the `Hmisc` and `Design` packages (Alzola & Harrell 2002) in R and then reduced the model, as in the multinomial case, by performing a backward selection using the model AIC as the criterion for variable exclusion.

### *Measures of model fit and accuracy*

The many measures of model accuracy in use today include  $R^2$ , Area Under Curve (AUC), Somers'  $D_{xy}$  rank correlation, the Kappa statistic and Correct Classification Rate (CCR).  $R^2$  measures model calibration but not model discrimination, according to Harrell (2001). Johnson & Omland (2004) describe this rather as a measurement of fit but not complexity, but their reasoning mainly applies to non-adjusted  $R^2$ . Harrell (2001) discusses some of the arguments against the use of CCR and the advantages of values such as AUC and the related Somers'  $D_{xy}$ , which are independent of the prevalence of a positive response, provided the prevalence is neither very low nor very high (McPherson *et al* 2004). The kappa statistic corrects for chance agreement and has been increasingly used in land-use and land cover change studies (Monserud & Leemans 1992; Müller & Zeller 2002). McPherson *et al* (2004) recommend the use of AUC, stating that the Kappa statistic is also sensitive to outcome prevalence, but they did not assess the behaviour of weighted Kappa (Cohen 1968) compared to AUC. Given the advantages and disadvantages of the various measures of model accuracy and given that the appropriate measure of accuracy can depend on the question being investigated (Guisan & Zimmermann 2000), there may be good reason to use several measures for any given study (Fielding & Bell 1997).

One of the early uses of the kappa statistic in ecological studies was in remote sensing for assessing the accuracy of land cover maps derived from satellite images, thus for nominal data (Monserud & Leemans 1992). Kappa can be weighted (e.g. Fleiss-Cohen weights) giving more importance to more similar classes, whilst remaining fully chance-corrected (Cohen 1968). We calculated the kappa statistic for each model as a whole (i.e. all classes evaluated at once, as for the evaluation of remote sensing classifications (Monserud & Leemans 1992)) using the `Kappa()`

function of the `vcd` library in R (Meyer *et al* 2005) with Fleiss-Cohen weights (Fleiss & Cohen 1973). Despite the fact that the Correct Classification Rate (CCR) is influenced by the prevalence of positive outcomes (Harrell 2001), we chose to use it as an additional measure of model performance, particularly as we were trialling different sampling strategies. Using it, we were able to ascertain what the points were being falsely predicted as. Müller & Zeller (2002) also followed this method in checking the predictive ability of their multinomial model for land cover change. As a further measure, we calculated the AUC (Swets 1988) for each outcome individually. All measures were determined for both the calibration and independently sampled evaluation datasets. This allowed us to check for a) overfitting of the model (Pontius *et al* 2004b); b) agreement between both datasets, and thus statistical robustness (Wear & Bolstad 1998).

### ***Model similarity***

We checked for model similarity based on the presence/absence of predictor variables, by calculating the Jaccard dissimilarity index in R. This was done using the `vegdist()` function in the `vegan` package (Oksanen *et al* 2006) and is an appropriate index for presence/absence data (Kent & Coker 1995). We then performed an average linkage agglomerative cluster analysis using the `daisy()` and `agnes()` functions from the `cluster` package (Maechler 2005) and plotted the dendrogram to visualise model similarity.

## **Results**

### ***Calibration of the six regression models***

A summary of the variables proving to be statistically significant showed some striking similarities among the models, irrespective of sampling strategy and modelling technique (Table 3). In general climate and neighbourhood variables were most commonly retained. These included three variables - annual average temperature, number of already overgrown neighbours in 1985 and distance to destructive avalanche sites - that were present in all six models. Annual average precipitation, June direct solar radiation and the number of open canopy forest neighbours in 1985 remained in five of the six models. In four out of six models were: May average precipitation, number of precipitation days per year, annual direct solar radiation, continentality, the number of closed canopy forest neighbours in 1985, the number of extensively

**Table 3: Predictor variables resulting from the backward stepwise regression for 3 sampling strategies and the multinomial and ordinal logistic regressions. “Same”, “Reg”, and “Quarter” stand for the three sampling schemes, “Multi” and “Ord” represent the multinomial and the ordinal regression models, respectively. Abbreviations of variables are according to table 2.**

Predictor Variables	Same, Multi	Same, Ord	Reg, Multi	Reg, Ord	Quarter, Multi	Quarter, Ord	Presence Numbers
TAVEy		x	x		x	x	6
^2	x	x	x	x	x	x	
PRCPy	x		x	x	x	x	5
^2	x			x	x	x	
PRCP5	x				x	x	4
^2	x		x		x	x	
MIND5	x	x			x		3
^2	x				x		
PDAY	x		x	x	x		4
^2			x	x	x		
SDIRy		x	x		x		4
^2	x	x			x		
SDIR		x			x	x	5
^2	x		x		x	x	
CIND			x	x	x	x	4
^2			x	x	x	x	
SLOPE				x	x		2
^2					x		
TOPOS	x				x		2
^2					x		
SWB	x				x	x	3
^2					x	x	
SDEP	x				x		2
^2	x				x		
SSTO					x		1
^2					x		
#CCAN	x	x	x		x		4
#OCAN	x	x	x		x	x	5
#OVGN	x	x	x	x	x	x	6
#EXTN			x	x	x	x	4
#INTN					x		1
DSET	x		x	x	x		4
^2	x				x		
DRDS					x		1
^2					x		
DAVS	x	x	x	x	x	x	6
^2	x	x			x		
Total number of variables	15	8	13	9	21	10	

used neighbours in 1985 and the distance to settlements. Soil stoniness, the number of intensively used neighbours in 1985 and distance to roads remained only in the multinomial model calibrated using the random sample of a quarter of all points. This model retained all variables after the stepwise selection. The multinomial regression models were in all cases more complex than their

ordinal counterparts, in that they retained a greater number of predictor variables following a stepwise reduction of the saturated model.

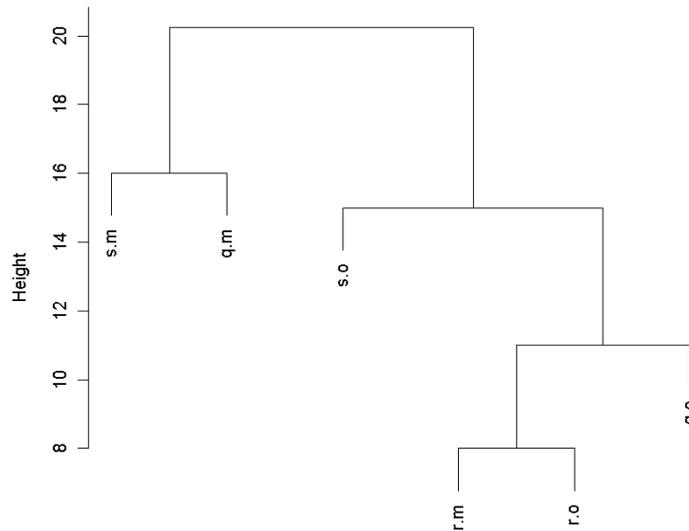
The Jaccard indices showed differences between models based on the presence/absence of predictor variables (Table 4). The models showing the greatest similarity were multinomial models using the same number of sample points per transition type (S.M) and using a quarter of randomly selected points (Q.M), which yielded a dissimilarity coefficient of 0.43. The two models calibrated using the regular sampling method (R.M and R.O) were also more similar to each other than to the other models (dissimilarity coefficient = 0.44). The least similar models were two of the ordinal regression models: that which used a regularly spaced sample (R.O) and that which used a sample of the same number of points per transition type (S.O) (dissimilarity coefficient = 0.85).

**Table 4: Dissimilarity matrix showing the Jaccard dissimilarity coefficients for the 6 models, where similarity is determined by the presence/absence of particular predictor variables, subsequent to the backward stepwise regression. Coefficient values approaching 0 indicate similarity and those approaching 1 indicate dissimilarity.**

	Same multi	Same ordinal	Regular multi	Regular ordinal	Quarter multi
Same, ordinal	0.67				
Regular, multi	0.63	0.65			
Regular, ordinal	0.73	0.85	0.44		
Quarter, multi	0.43	0.70	0.57	0.68	
Quarter, ordinal	0.63	0.71	0.48	0.60	0.57

The dendrogram of the cluster analysis confirmed the statements concerning the most similar models (Figure 3). Note that the nature of the two most similar groupings differed in terms of sampling and modelling strategy. The multinomial models appeared to be inherently more similar to one another (S.M, Q.M) than ordinal models. Likewise models calibrated using a regularly spaced sample (R.M, R.O) were more similar than other strategies.

**Figure 3: Dendrogram showing the model groupings according to their similarity based on the presence/absence of predictor variables. Height refers to the average ‘distance’ between the clusters.**



s.m = same number of sample points, multinomial regression; s.o = same number of sample points, ordinal regression; r.m = regular sample, multinomial model; r.o = regular sample, ordinal model; q.m = quarter random sample, multinomial model; q.o = quarter random sample, ordinal model.

***Same number of sample points per transition, multinomial regression (S.M):***

The AUC values for this model were highest for the no change transition (calibration data: 0.78; evaluation data: 0.77) and the change to overgrown (calibration data: 0.65; evaluation data: 0.62) (Table 5). On average only about half of all points were correctly predicted (Table 6). The best predicted were those that remained the same (no change) in the 12 year study period (68.4%). The outcome that was least correctly predicted was the change to overgrown (38.40%). Misclassifications to other classes were evenly distributed for the no change transition and change to overgrown transition. In contrast, the highest incidence of misclassification of open canopy forest were closed canopy forest and vice versa. The weighted and unweighted Kappa values differed somewhat (weighted: 0.46; unweighted: 0.35) indicating that there was some likelihood of similar classes being classified as one another.

**Table 5: AUC values for the calibration datasets for each land cover change, under each modelling and sampling strategy. The differences between the values for the calibration and evaluation datasets are shown.**

		Model and sampling strategy					
		S.M	S.O	R.M	R.O	Q.M	Q.O
Land cover change	0	0.78 – 0.01	0.50 – 0.00	-	-	-	-
	1	0.65 – 0.03	0.45 + 0.01	0.64 + 0.01	0.69 + 0.03	0.65 – 0.01	0.71 – 0.02
	2	0.69 – 0.03	0.46 + 0.02	0.66 + 0.02	0.69 + 0.02	0.67 – 0.03	0.70 – 0.03
	3	0.68 – 0.03	0.63 – 0.00	0.52 – 0.01	0.50 – 0.00	0.51 + 0.01	0.50 – 0.00

0 = no change; 1 = change to overgrown; 2 = change to open canopy forest; 3 = change to closed canopy forest; S.M = same number, multinomial model; S.O = same number, ordinal model; R.M = regular, multinomial model; R.O = regular, ordinal model; Q.M = quarter, multinomial; Q.O = quarter, ordinal.

**Table 6: Observed vs. predicted land cover transitions according to the multinomial logistic regression model calibrated using the same number of sample points per land cover change. The predicted values were calculated using the evaluation dataset.**

		Predicted by model					% correct
		Same	Overgrown	Open canopy forest	Closed canopy forest		
Observed	Same	171	26	29	24	68.40	
	Overgrown	46	96	56	52	38.40	
	Open canopy forest	30	31	126	61	50.40	
	Closed canopy forest	31	46	53	120	48.00	
	Total predicted	278	201	264	257		

**Same number of sample points per transition, ordinal regression (S.O):**

The overall percentage of correctly classified points was low, which can be largely attributed to the very high misclassification rates of the classes ‘closed canopy forest’ (CCR = 3.6%), mostly as ‘open canopy forest’ (Table 7), and ‘no change’ as either ‘overgrown’ or ‘open canopy forest’. Both overgrown and open canopy forest areas were better classified from this model (40.4 and 65.2%). More than half of the overgrown points were classified as open canopy forest. The latter was the only class which was predicted well and when misclassified, it was predicted as overgrown. Closed canopy forest was rarely predicted (15 out of 1000) in contrast to open canopy forest (530 times). All AUC values were low for this model ranging from 0.45 to 0.63

(Table 5). The weighted and unweighted Kappa values differed greatly (weighted: 0.43; unweighted: 0.15) indicating that similar classes were likely to be classified as one another.

**Table 7: Observed vs. predicted land cover transitions according to the ordinal model calibrated using the same number of sample points per land cover change. The predicted values were calculated using the evaluation dataset.**

		Predicted by model					% correct
		Same	Overgrown	Open canopy forest	Closed canopy forest		
Observed	Same	<b>86</b>	115	49	0	34.40	
	Overgrown	10	<b>101</b>	136	3	40.40	
	Open canopy forest	0	84	<b>163</b>	3	65.20	
	Closed canopy forest	0	59	182	<b>9</b>	3.60	
	Total predicted	96	359	530	15		

**Regular selection of change only points, 500m apart in x- and y- directions, multinomial regression (R.M):**

As with the randomly selected sample, the influence of outcome prevalence on CCR is evident in this model, where the most common outcome was best predicted (87.84%) and falsely classified points were predicted as the most common transition (overgrown) (Table 8). Only two points were predicted as closed canopy forest. The AUC values, ranging from 0.51 to 0.68 (Table 5) indicate poor accuracy (Swets 1988). The weighted and unweighted kappa values (0.22; 0.31) were both fairly low.

**Table 8: Observed vs. predicted land cover transitions according to the multinomial model calibrated using a regularly spaced selection of sample points per land cover change. The predicted values were calculated using the evaluation dataset.**

		Predicted by model				% correctly classified
		Overgrown	Open canopy forest	Closed canopy forest		
Observed	Overgrown	<b>419</b>	58	0	87.84	
	Open canopy forest	94	<b>95</b>	1	50.00	
	Closed canopy forest	58	18	<b>1</b>	1.30	
Total predicted		571	171	2		

***Regular selection of change only points, 500m apart in x- and y- directions, ordinal regression (R.O):***

The regular sample ordinal regression model showed the highest correct classification rates of all the models and sampling strategies, with 73% of the observed changes to both overgrown and open canopy forest areas being correctly predicted (Table 9). Closed canopy forest was only predicted once. Outcome prevalence appears to have a lower influence on the CCR than in the multinomial model calibrated using the same sampling strategy, with false predictions mostly being predicted as the adjacent class and not the most prevalent. The weighted and unweighted kappa values were similar (0.35; 0.34). The AUC values (Table 5) for the changes to overgrown (calibration: 0.69; evaluation: 0.72) and open canopy forest (calibration: 0.69; evaluation: 0.71) indicate that they are useful for applications (Swets 1988).

**Table 9: Observed vs. predicted land cover transitions according to the ordinal model calibrated using a regularly spaced selection of sample points per land cover change. The predicted values were calculated using the evaluation dataset.**

		Predicted by model				% correctly classified
		Overgrown	Open canopy forest	Closed canopy forest		
Observed	Overgrown	<b>349</b>	134	0	73.17	
	Open canopy forest	50	<b>139</b>	1	73.16	
	Closed canopy forest	29	48	<b>0</b>	0	
Total predicted		428	321	1		

***Random selection of a quarter of all points representing a change, multinomial regression (Q.M):***

The influence of outcome prevalence on the CCR was highly evident using the random selection sampling strategy and the multinomial modelling technique, where the most common outcome (overgrown) had a high CCR (87.96%) and the least common (closed canopy forest) a very low CCR (3.82%) (Table 10). This is supported by the fact that a high number of open and closed canopy forest points were classified falsely as the most common transition i.e. overgrown. The AUC values ranged from 0.51 to 0.68 (Table 5), indicating low accuracy (Swets 1988). Both Kappa values were low and similar (weighted: 0.23; unweighted: 0.27; here the unweighted value being slightly higher than the weighted).

**Table 10: Observed vs. predicted land cover transitions according to the multinomial model calibrated using a random selection of a quarter of sample points per land cover change. The predicted values were calculated using the evaluation dataset.**

		Predicted by model				% correctly classified
		Overgrown	Open canopy forest	Closed canopy forest		
Observed	Overgrown	<b>2681</b>	348	19	87.96	
	Open canopy forest	694	<b>501</b>	15	41.40	
	Closed canopy forest	336	143	<b>19</b>	3.82	
Total predicted		3711	992	53		

***Random selection of a quarter of all points representing a change, ordinal regression (Q.O):***

Overgrown areas and open canopy forest were successfully predicted for 70.0% and 69.3% of points respectively (Table 11). However, in all cases the model failed to predict closed canopy forest. The effect of outcome prevalence was less evident in the ordinal regression method compared to the multinomial model above, where the CCR for overgrown and open canopy forest were approximately equal. Falsely classified closed canopy forest tended to be classified as open canopy forest rather than the most common transition (overgrown). This, and the fact that closed canopy forest was not predicted, show that the model did not distinguish between open and closed canopy forest. The weighted and unweighted kappa values were similar (0.31; 0.29). The AUC values (Table 5) were ‘useful’ for both the change to overgrown (calibration: 0.71; evaluation: 0.69) and open canopy forest (calibration: 0.70; evaluation: 0.67) (Swets 1988).

**Table 11: Observed vs. predicted land cover transitions according to the ordinal model calibrated using a random selection of a quarter of sample points per land cover change. The predicted values were calculated using the evaluation dataset.**

		Predicted by model				% correctly classified
		Overgrown	Open canopy forest	Closed canopy forest		
Observed	Overgrown	<b>2126</b>	922	0	70.0	
	Open canopy forest	371	<b>839</b>	0	69.3	
	Closed canopy forest	176	322	<b>0</b>	0.0	
Total predicted		2673	2083	0		

## **Discussion**

We have provided an example of using several models to identify the most important relationships between variables. How a modeller or manager may approach this depends also upon the purpose of the study, where ‘prediction’ requires a single best model fit and ‘explanation’ of pattern may be better answered by the use of multiple models (MacNally 2000). Irrespective of sampling strategy or type of modelling, several variables were consistently retained in our models after the stepwise regression, indicating their proximal importance. The composition of the neighbourhood, a proxy for propagule availability, annual average temperature, direct solar radiation, precipitation and continentality (a measure of large-scale weather pattern, particularly related to temperature and precipitation) are the variables most commonly present. This result seems ecologically meaningful, since we would expect these variables to influence the rate of secondary succession (Prach *et al* 1993; Myster & Pickett 1994; Donnegan & Rebertus 1999; Duncan & Duncan 2000).

Our results indicate that the models that fit the data best were not necessarily those that were the most similar in terms of the predictor variables remaining after stepwise elimination. Two relatively dissimilar models were shown to fit the data better than all others in terms of the diagnostic tests we used here (CCR, kappa, AUC) - the ordinal model using the regularly spaced selection of sample pixels per outcome and the ordinal model with the random selection of a quarter of all pixels representing a change transition. This is further evidence that there is generally more than one plausible model that can be fit to data (Aspinall 2004). It also indicates the importance of a chosen sampling regime and the effect that it can have on results yielded (Olden & Jackson 2000).

There were more predictor variables retained in the multinomial models than that of the ordinal models. Preference may be given here to a simpler model i.e. with fewer variables, due to the principal of parsimony (Harrell 2001), despite the fact that relationships between predictor and outcome variables can be as complex as a model with many variables reflects. This said if the nature of the process under investigation is truly ordinal, then including that ordinality yields a model which can be more easily interpreted (Agresti 1996). It seems from our results that both direct (nominal) transitions and successive (ordinal) transitions occurred in the landscape, and a particular sampling strategy may emphasise one type rather than the other. Results showed a pronounced lack of distinction between open and closed canopy forest, especially those of the

ordinal regression models. We attributed this mainly to two factors: a) we do not have data which may distinguish the two classes, such as disturbance and historical land-use data; b) the Swiss land-use statistics classes based on aerial photograph interpretations are not necessarily the same as a given ecological interpretation (Sager & Finger 1992) and thus our aggregations are not necessarily ecologically accurate (only % density in canopy cover separates the 2 classes according to our definitions, which does not take into account that some of the ‘open canopy forest’ is still agriculturally used). The other explanation is that the proposed sequence of open to closed canopy forest is not in fact ordinal. The process can be construed as ordinal in terms of the broad sequence of land-use to overgrown to forest, as reflected by the good fit of two of the ordinal regression models and their successful classification of overgrown and open canopy forest categories. We suggest that the latter part of the process is represented better by a nominal scale, as evidenced by the multinomial models successful classification of some, albeit few, closed canopy forest pixels. This reflects better the possibility that our open canopy forest class is not necessarily the forerunner of our closed canopy forest class and takes into account the fact that some of the classes within our open canopy forest category are still used for grazing purposes. As an alternative approach, we could have combined the open and closed forest canopy classes in to a simple forest category. We chose not to do so, as we suspected that the process was ordinal but that the assumptions of ordinality may not have been entirely fulfilled.

The differences between the AUC values of the calibration and evaluation datasets were not large for any transition or any model. This further suggests statistical robustness, in the sense that the models are not over-fitted and that our samples are representative of the whole dataset, even when the predictive power is not high. In general, the different measures of accuracy, fit and predictive power reflect different aspects of ‘model quality’. The AUC rendered values for each transition within each model, as did the CCR, whereas we used the kappa statistic here as an overall value for each model. Despite the fact that the CCR and kappa statistics are prevalence-dependent, they still yield useful information to the user, since prevalence is often part of the judgment. The comparably low model quality can be explained by the high local variability and stochasticity of land use change processes (Braumoh 2005). Aggregating local points to larger analysis units may be a solution for this, although the ecological crispness of identifying local causes may be lost.

The results presented here are relevant for landscape managers and ecological modellers alike, highlighting the need for consideration of different analytical approaches. As Johnson & Omland (2004) and Aspinall (2004) state, fitting multiple models to data is a valid and useful method of data analysis. This study has shown how inferences (in this case about aspects of land cover change) may be drawn from a set of discrete outcome models. We have successfully identified some of the proximate and underlying factors influencing the successional patterns under investigation. We have also shown that ordinal logistic regression, till now not commonly employed in ecological or land cover change research, is a useful tool in such investigations and can be used to predict future land cover changes based on the processes driving them. However, with too few classes that follow an ordinal sequence, multinomial models are still a valid approach for land cover change analyses and predictions.

### **Acknowledgements**

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#### **4. Analysing spatial and temporal patterns of forest succession on abandoned agricultural land using ordinal logistic regression.**

Rutherford, G. N., Edwards, P. J., Bebi, P. & Zimmermann, N. E. Submission to *Journal of Vegetation Science*.

##### **Abstract**

**Questions:** Which environmental factors influence the rate of secondary forest succession on abandoned agricultural land? How do patterns of temporal change vary in space? Is ordinal logistic regression a suitable tool for the analysis of successional changes at the landscape scale?

**Location:** Switzerland

**Methods:** Using data from the Swiss Land-Use Statistics for two survey periods, 1979/85 and 1992/97, we distinguished changes from extensively used agricultural land to: (i) overgrown with shrubs and small trees; (ii) open canopy forest; (iii) closed canopy forest. To determine which factors potentially influenced the rate of succession during this period, we fit a proportional odds ordinal regression model to our land cover change data using a pool of potential predictor variables. Model quality was assessed using a combination of data splitting and bootstrapping. Somers'  $D_{xy}$ , AUC and the CCR were used as measures of accuracy.

**Results:** Statistically significant predictor variables were: annual average temperature, number of extensively used neighbours at  $t_0$ , continentality, June direct solar radiation, number of overgrown neighbours at  $t_0$ , annual average precipitation, number of open canopy forest neighbours at  $t_0$ , May precipitation, site water balance and distance to historical avalanche sites. The model accurately predicted changes to overgrown and open canopy forest, but not to closed canopy forest.

**Conclusions:** The rate of forest succession and hence land cover change varies considerably at a regional scale in Switzerland, and is dependent on local factors such as propagule availability as well as larger scale climatic factors such as continentality. Ordinal regression is a promising method for investigating land cover change.

##### **Keywords**

Climate, continentality, land cover change, neighbourhood, ordinal regression, secondary succession, temperature.

## **Introduction**

Land-use change takes many forms, ranging from forest clearance, agricultural intensification and urbanisation to the inverse processes of agricultural land abandonment and forest regeneration. It is one of the most important components of cumulative environmental change and strongly influences other types of regional and global change, including climate, atmospheric chemistry, use of natural resources and biological invasions (Turner & Meyer 1991, 1994; Vitousek 1994).

In recent decades, a declining use of marginal areas for agriculture has led to a dramatic increase of forest cover in many European countries including Switzerland (Walther 1986; SFSO 2001; Gellrich *et al* submitted; Gellrich & Zimmermann submitted). This trend has prompted several studies designed to investigate why land is abandoned and how land cover is affected (Bunce 1991; Kristensen *et al* 2004; Vicente-Serrano *et al* 2004; Höchtl *et al* 2005; Rudel *et al* 2005). The results typically indicate that the initial decision to give up agricultural use is determined by socio-economic factors (Turner & Meyer 1991; Verburg *et al* 2004) and reflects peoples responses to economic opportunity (Lambin *et al* 2001), while subsequent changes in land cover are the result of ecological processes; these, in turn, are influenced by environmental conditions (Turner & Meyer 1994) and the history of the site (Hill 1992).

Ecologists have long been interested in how vegetation develops on former agricultural land, and there have been many studies of 'old field' succession, especially in Europe and the Eastern United States (e.g. Brenchley & Adam 1915; Keever 1950; Pickett 1982; Hill 1992; Lavorel *et al* 1998; Cook *et al* 2005). Such successions are usually studied by monitoring vegetation changes at one site over time, or by comparing sites of different ages in space-for-time substitution studies (Pickett 1989; Fukami & Wardle 2005). A typical old field succession begins with the domination of a site by annual weeds and then by herbaceous perennials; after some time, this early vegetation is replaced by shrubs and pioneer tree species and finally by late successional woody species (Ellenberg 1988; Begon *et al* 1996; Crawley 1997). However, closer examination often reveals that most of the plant species in a secondary succession are either present at the outset or colonise within a few years (Miles 1979); thus, changes in the composition and appearance of the vegetation are not due to sequential colonization (as in a primary succession), but largely reflect differences in growth rates and longevity among the plant species already present. The rate at which succession proceeds is influenced by many factors, of

which soil fertility, moisture conditions, solar radiation and surface rock cover or stoniness are often important (Prach *et al* 1993; Myster & Pickett 1994; Donnegan & Rebertus 1999). The availability of propagules, commonly influenced by the surrounding vegetation or the distance to a forest edge, is often also a factor (Duncan & Duncan 2000; Cook *et al* 2005).

The traditional, small-scale approach to investigating ecological succession delivers a wealth of information about how plant species composition changes at one or a few localities. In contrast, in this study we were interested in how the rate of succession varies at a regional scale, and the consequences of such variation for the development of land cover. Specifically, our aim was to identify the most important factors influencing the rate of forest succession on abandoned agricultural land in Switzerland. Our study was based on the assumption that an old field succession is both directional and predictable, and that any differences in outcome starting from the same initial state can be explained in terms of a limited set of environmental factors and local conditions. For example, we might expect forest succession to be faster where soil, temperature, precipitation and location favour the rapid establishment and growth of woody species.

To conduct such a study requires that information on vegetation change is available at a much larger spatial scale than can be obtained using traditional ecological field plots. A secondary objective of this study, therefore, was to evaluate the use of land cover information derived by remote sensing to make inferences about successional processes. The Swiss Land-Use Statistics (ASCH) dataset is derived from aerial photographs and provides detailed information about land-use for the whole country at the resolution of a one hectare raster. Out of 74 ASCH land-use/land cover classes mapped in two consecutive surveys, we selected those land cover classes that correspond to successional stages from extensive agricultural land to closed forest.

Of the several approaches used to forecast successional dynamics in a landscape, two have proved particularly influential. One of these is based on the use of Markov-chain based transition matrices (Horn 1975; Moore 1990; Yemshanov & Perera 2002); these have the advantage of being very flexible in their spatial application, but they are less useful for calibrating spatially explicit drivers, which was one of the aims of our study. The second approach, forest succession models, is based on the concept of gap dynamics and has been widely used for the last 30 years (Botkin *et al.* 1972; Shugart 1984; Bugmann 2001). Although successfully applied in many case studies, their larger-scale spatial application is difficult due to heavy computational requirements. For this reason, it has usually been necessary to make

simplified assumptions (Roberts 1996; He & Mladenoff 1999; Schumacher *et al.* 2004), though recently more realistic models have been possible (Lischke *et al.* submitted).

While these latter approaches are mostly applied to spatial dimensions of  $10^4$ - $10^6$  ha (Sturtevant *et al.* 2004), our method can be applied to millions of hectares. It combines elements of Markov chain models, predictive habitat distribution modelling (Guisan & Zimmermann 2000), and cellular automata, where the explicit neighbourhood is included for predicting future time steps.

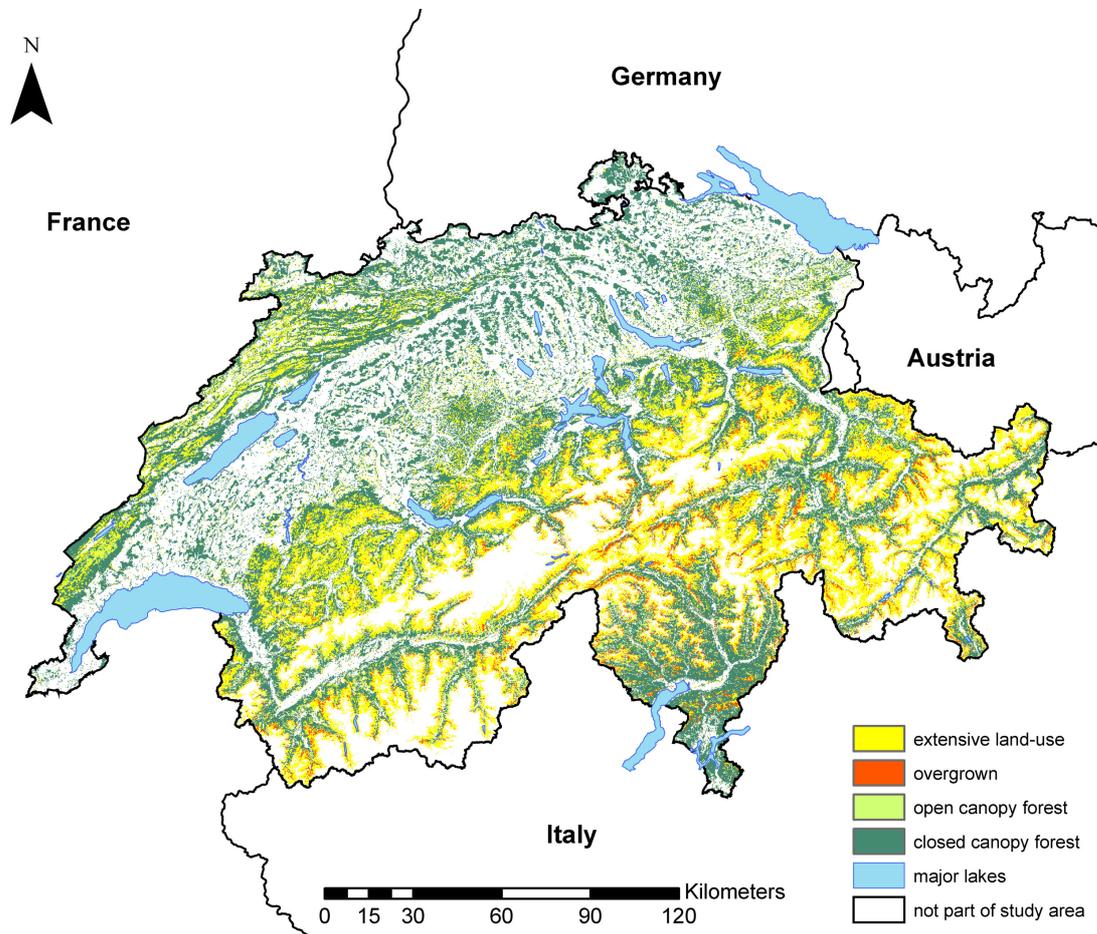
To investigate how environmental variables and landscape structure influence land cover change, we used the technique of ordinal logistic regression. This technique has been used to predict species distributions (Guisan & Harrell 2000; Dirnböck *et al.* 2003), insect development (Manel & Debouzie 1997) and to determine the effect of land-use history on the conservation value of roadside sites (Spooner & Lunt 2004), but has not previously been used in studies of land cover change. The advantage of using ordinal regression instead of developing individual binomial logistic regressions for each land cover transition is that one model can be calibrated for more than one discrete choice outcome, thus yielding transition probabilities for each outcome in relation to the others. Although multinomial regression is also a possible analytical method to address this question (Augustin *et al.* 2001; Müller & Zeller 2002), we preferred ordinal regression models for three reasons. First, succession is an ordered process, meaning that the stages can be viewed as intervals along a time continuum (McCullagh 1980). Second, multinomial regression assumes that the outcomes are mutually exclusive i.e. nominal (Long 1997), while ordinal regression allows for sequential changes. Finally, compared to the mechanism-oriented models discussed above the method of logistic ordinal regression is simple and straightforward.

## **Material and Methods**

### ***Study Area***

Switzerland (4.1 million hectares) is a mountainous country located in the centre of mainland Europe (lat: 47°00'N; long: 8°00'E) (Figure 1) and characterised by its very high topographic and climatic diversity. Its climate ranges from oceanic in the Northwest to continental in the Eastern Central Alps, with a more Mediterranean influence in the South and mean temperatures vary

widely according to altitude (Wachter 2002). Precipitation and number of sunshine hours also vary considerably within the country.



**Figure 1: Map of study area and the spatial distribution of the land cover types under investigation, in 1979/1985 (ASCH85). The surrounding countries are labelled.**

### ***Response variable***

The basic assumption of this study is that secondary succession on abandoned agricultural land proceeds through a sequence of stages - including shrub vegetation, open forest and closed forest - that can be distinguished from aerial photographs. In order to calibrate spatial models of these successional transitions, we used data from the Swiss Land-Use Statistics recorded during the two time periods, 1979-1985 and 1992-1997, referred to hereafter as ASCH85 and ASCH97 (SFSO 1997). Although these time bands are broad, the flight sequence for both periods was for

the most part the same and thus the time difference for most pixels is approximately 12 years, with around 19% of pixels having a difference of 13 years (of which a considerable proportion consisted of land cover classes we did not use in our study) (SFSO 1997). Of the original 74 ASCH classes, 18 were combined to form the four classes of interest in this study (Figure 1; Table 1), covering a total of 18 830 hectares or roughly 0.5% of the Swiss territory. The criteria for these classes are discussed in more detail in Rutherford *et al* (submitted).

**Table 1: Aggregated classes from the Swiss land-use/land cover statistics (ASCH85 & ASCH97) used in this study. Numbers in parentheses represent the official ASCH class numbers (Sager & Finger 1992). The criteria used to aggregate the classes are listed.**

Aggregated class	Classes from Swiss land use statistics	Broad definition
Closed forest canopy	<ul style="list-style-type: none"> <li>• Other forest (10)</li> <li>• Normal forest (11)</li> <li>• Strips and blocks (14)</li> <li>• Bushes (15)</li> <li>• Groves &amp; hedges (17)</li> </ul>	Vegetation height > 3m, Crown density > 60%, Composed of tree species.
Open forest canopy	<ul style="list-style-type: none"> <li>• On non-agriculturally used land (12)</li> <li>• On agriculturally used land (13)</li> <li>• Groups of trees on agriculturally used land (18)</li> <li>• Other groves (19)</li> </ul>	Vegetation height > 3m, Crown density 20 - 60%, Composed of tree species.
Overgrown areas	<ul style="list-style-type: none"> <li>• Overgrown meadows (84)</li> <li>• Overgrown alpine pasture (86)</li> <li>• Shrubs and bushes (16)</li> </ul>	Vegetation height < 3m, Crown density > 50%.
Extensive land use	<ul style="list-style-type: none"> <li>• Pasture in the vicinity of settlements (83)</li> <li>• ‘Maiensässe’, hay alps, mountain meadows (85)</li> <li>• Sheep alps (87)</li> <li>• Favourable to pasturing (88)</li> <li>• Stony alpine pasture (89)</li> <li>• Grass and herb vegetation (97)</li> </ul>	Used for grazing, Use not necessarily year-round, Not machine-accessible.

Our response variable was comprised of three different outcomes with the same starting state, which occurred mostly between 1000 and 2000m a.s.l in the Swiss Alps:

1. 'Overgrown': extensively used agricultural land (1985) became overgrown with shrubs and small trees (1997) – 11 930 hectares.
2. 'Open forest': extensively used agricultural land (1985) became open canopy forest (1997) – 4 836 hectares.

3. 'Closed forest': extensively used agricultural land (1985) became closed canopy forest (1997) – 2 064 hectares.

### ***Predictor variables***

A set of factors likely to influence either land abandonment or subsequent plant growth was selected as potential predictor variables (Table 2). This selection was based partly upon published information (e.g. Prach *et al* 1993; Myster & Pickett 1994; Donnegan & Rebertus 1999) and partly upon the results of an earlier study in which we calibrated binary logistic regression models for each individual land cover change (Rutherford *et al* submitted). All predictor variables were available as georeferenced raster maps at the same spatial resolution as the dependent variables (100m).

### ***Sampling Design***

It is usually desirable to use all available sample points when fitting a statistical model or evaluating it by bootstrapping (Harrell 2001). However, this would have led to problems of spatial autocorrelation (Müller & Zeller 2002), and we therefore chose a sampling regime intended to maximise the independence of individual points and model residuals (Dungan *et al* 2002). To this end, we used data-splitting, where an independent dataset of the same size as the calibration dataset was sampled by the same method and used to evaluate the models (Wear & Bolstad 1998). We randomly sampled a quarter of all available sample points per transition type without replacement, yielding a total of 4 785 points broken down into: extensively used land becoming overgrown (3 037 points), extensively used land becoming open canopy forest (1 248 points) and extensively used land becoming closed canopy forest (500 points), thus account for the prevalence of each transition type. The independent dataset was also sampled randomly without replacement, yielding a total of 4 756 points, with a break-down of 3 048, 1 210 and 498, respectively, for the three transition types.

### ***Spatial pattern of land cover change***

The densities of all three observed land cover changes were mapped in a GIS. To visualise the spatial distribution of the various land cover changes, we calculated kernel density functions (search area = 5 000m<sup>2</sup>) for each change, thus allowing us to display point values over a surface.

**Table 2: Independent spatial variables used to calibrate the predictive model explaining the 3 land cover transitions between extensive use and forest. All grids were available at 100m spatial resolution.**

Variable	Abbreviation	Unit	Proxy for	Source
<b>Climate-related variables</b>				
May moisture index	MIND5	cm/100	Small-scale water availability	CSD/DEM25
Yearly direct solar radiation	SDIRy	kJ/day	Energy input, drought stress	CSD/DEM25
June direct solar radiation	SDIR6	kJ/day	Energy input, drought stress	CSD/DEM25
Annual average temperature	TAVEy	°/year	Potential evapotranspiration Growing degree days, Elevation	CSD/DEM25
Continental index, Gams	CIND		Large scale weather pattern	CSD/DEM25
Annual average precipitation	PRCPy	(1/10mm)/year	Total water input to system	CSD/DEM25
# summer precipitation days	PDAY	number	Frequency of rainfall	CSD/DEM25
May average precipitation	PRCP5	(1/10mm)/month	Precipitation during growing season	CSD/DEM25
<b>Relief-related variables</b>				
Slope	SLOPE	°	Diffuse solar radiation	DEM25
Topographic position	TOPOS	-∞ to +∞	Exposure of site, drought	DEM25
Topographic wetness index	TWI		Moisture accumulation	DEM25
Site water balance	SWB	(1/10mm)/year	Available soil moisture	CSD/DEM25
<b>Soil-related variables</b>				
Soil depth	SDEP	cm	Soil water & nutrient availability	BEK200/DEM25
Soil permeability	SPRM	cm/day	Water infiltration, risk of drought	BEK200/DEM25
Soil stoniness	SSTO	%	Water holding capacity	BEK200/DEM25
<b>Neighbourhood variables</b>				
# closed canopy neighbours	#CCAN	number/25	Woody species seed source	ASCH85
# open canopy neighbours	#OCAN	number/25	Woody species seed source	ASCH85
# overgrown neighbours	#OVGN	number/25	Woody species seed source Density of abandonment	ASCH85
# extensively used neighbours	#EXTN	number/25	Density of extensive use	ASCH85
# intensively used neighbours	#INTN	number/25	Density of intense use	ASCH85
<b>Distance variables</b>				
Distance to roads	DRDS	m	Accessibility	Vector25
Distance to settlements	DSET	m	Accessibility	SGCH
Distance to avalanches	DAVS	m	Snow-related disturbance Propensity for future avalanches	DADB

CSD: Climate Station Data from the period 1961 – 1990. DEM25: Digital elevation model for Switzerland at 25m resolution from the Swiss Federal Office of Topography (SwissTopo). BEK200: Soil suitability map 1:200,000 (Bodeneignungskarte der Schweiz, SFSO, 1992). ASCH85: Swiss land-use statistics 1985 (SFSO, 2001). Vector25: Mapped street data, Vector 25 © 2006, Swiss Federal Office of Topography (DV033594). SGCH: Settled areas of Switzerland (Siedlungsgebiete der Schweiz, SFSO, 1992). DADB: Destructive avalanches database (SLF, 2006).

This made it easier to see rare occurrences of a land cover change amongst clusters of more common events.

### ***Statistical Analyses***

We fit a proportional odds (PO) ordinal logistic regression model to our data in order to distinguish the land cover changes from one another on the basis of the various predictor variables, which represent potential proximate causal factors. PO regression models are based on cumulative probabilities of the response and are multivariate extensions of generalised linear models (McCullagh 1980). The probability of an event is (Equation 1):

$$P(Y \geq j|X) = \frac{1}{1 + \exp(-(\alpha + X\beta))} \quad (1)$$

where  $Y$  is the given response,  $j$  the ordinal level,  $X$  any of the predictor variables,  $\alpha$  the intercepts and  $\beta$  the regression coefficients for the respective predictor variables. Rather than comparing those sites showing a change to the condition of ‘no change’ (i.e. continued extensive use for agriculture), we compared the transitions to open or closed forest canopy with that to overgrown in the same time period. The *Hmisc* and *Design* libraries in R (R Development Core Team 2006) contain functions to fit ordinal regression models and to test the model fits using a bootstrap calibration of all sample points used in the fit of the model (Alzola & Harrell 2002). First, a saturated model was fit to the calibration data using the complete pool of potential predictor variables (linear and quadratic terms; no interactions). We then performed a manual backward variable selection, eliminating variables one by one based upon their Wald  $\chi^2$  statistic values, until all variables in the model contributed explanatory power at the  $P \leq 0.05$  level. ANOVA diagrams showing the relative explanatory contribution of each individual variable were produced for both the calibration and evaluation datasets, based on the calibrated model. Generalised additive models (GAMs) were calibrated for two of the resulting ecologically meaningful and statistically significant predictor variables and were plotted (with twice-standard error curves) against the individual transition types to aid in the ecological interpretation of the model results. To ascertain whether the assumptions of ordinality were fulfilled and to gain further insight into the significant relationships, the kernel density distributions of the resulting

predictor variables were simultaneously plotted for each response. This is a more accurate and transparent method of investigating probability density functions than the plotting of histograms (Venables & Ripley 2002).

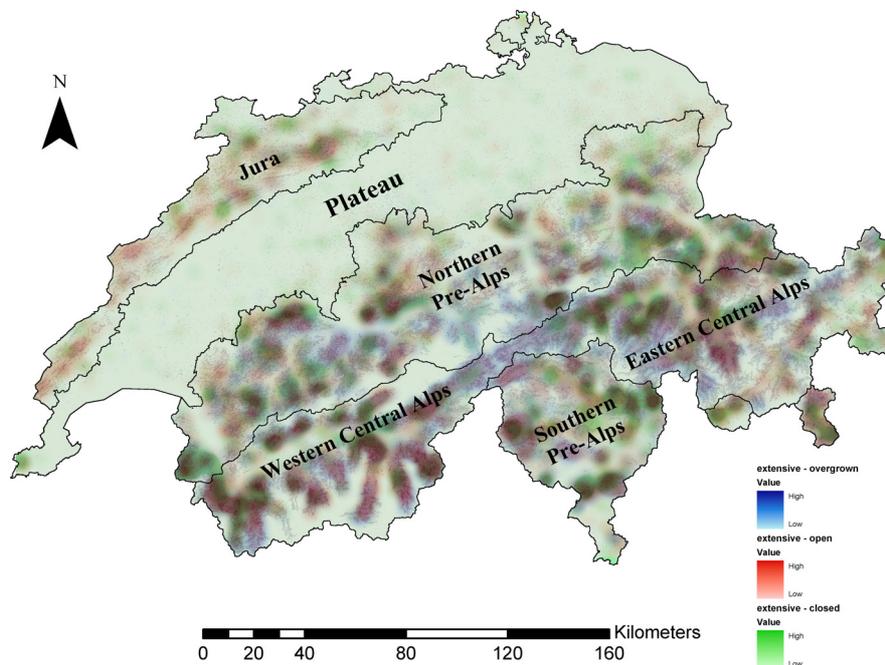
Output values of Somers'  $D_{xy}$  rank correlation were used to assess the model's success in discriminating between predicted probabilities and observed responses (i.e. to show the difference between concordance and discordance probabilities). When  $D_{xy} = 0$ , the predictions of the model are random and when  $D_{xy} = 1$ , the predictions discriminate perfectly (Harrell 2001). This measure is insensitive to the prevalence of positive responses - in contrast to the often used correct classification rate (CCR) - and is therefore a more robust measure of diagnostic discrimination. The AUC was additionally calculated as a measure of model accuracy (Pontius & Schneider 2001), as was the CCR for each transition, in order to gain insight into whether some transitions were predicted better than others. By using this combination of approaches, we aimed to avoid problems arising from the drawbacks of the individual values. We also used bootstrap resampling ( $B=50$ ) of both the calibration and evaluation datasets as an additional method of checking model accuracy and to obtain a bias-corrected result (Harrell 2001; Alzola and Harrell 2002) and plotted the resulting curves. This method is available within the aforementioned R Libraries and tests observations vs. model predictions. Mean Square Error (MSE), Mean Absolute Error (MAE) are automatically returned upon model calibration and validation, as was the bias correction which corrects for potential sample bias introduced into the model calibration (Harrell 2001).

## **Results**

### ***Spatial pattern of land cover change***

In some regions all three of the recognised land cover transitions occurred with relatively high frequency. However, in other areas one type of transition dominated, sometimes to the exclusion of the other two. The most pronounced example of this was the marked concentration of the change from extensive agricultural land-use to overgrown in the centre of the central Alps (Figure 2). A relatively high density of this transition can also be seen in the Eastern central Alps and the South-Western Central Alps, with patches in the remainder of the Western Central Alps and sparse patches in the Northern and Southern Pre-Alps. The change to open canopy forest over the same time period was more concentrated in the Southern part of the Western central

Alps and the central part of the Eastern central Alps, with patches also in the Jura Mountains, Northern and Southern Pre-Alps. The change to closed canopy forest was more patchily distributed, with high densities where the Eastern Northern Pre-Alps border the Eastern Central Alps and where the Western Northern Pre-Alps border the Western Central Alps. A high density was also observed in the Southern Pre-Alps. Most of these areas are located at lower elevations. None of the changes investigated was common in the Swiss plateau, a lowland region which is densely populated and intensively used for agriculture and forestry (Wachter 2002). One exception is the very Western part of the Plateau on the border towards France.



**Figure 2: The observed density of the three land cover changes under investigation between 1985 and 1997 in Switzerland, calculated using a kernel density estimator in a GIS. The five main biogeographic regions are shown.**

### ***Proportional odds model***

The resulting model contained ten variables that significantly contributed to the prediction of whether an area would change to overgrown, open or closed canopy forest (Table 3). These included four neighbourhood variables related to the character of the surrounding area at  $t_0$  (surrounding open forest and overgrown cover, number of extensively used neighbours, distance to historical avalanche sites) and six variables related to climate and relief (June direct solar

radiation, May precipitation, annual average temperature, continentality, site water balance and annual precipitation). Six of the variables showed a significant quadratic relationship with the response: Annual average temperature, continentality, June direct solar radiation, May precipitation, annual average precipitation and site water balance. Predictor variables exhibiting a negative relationship with the likelihood of land cover change were: the number of extensively used neighbours in 1985 and the number of already overgrown neighbours in 1985. The remaining two variables (the number of open forest canopy neighbours in 1985 and distance to historical destructive avalanche sites) exhibited a positive relationship. The Somers' *Dxy* and AUC values reflect an average predictive ability (0.48 and 0.47) and fair to good model accuracy (0.74 and 0.74) for the calibration and evaluation datasets (Table 4). The difference between the values for the calibration and evaluation datasets was small and thus indicates a low level of calibration bias and a high degree of model robustness. The breakdown of the CCR of the actual observed and model predicted classes (Table 5) shows that the transitions to overgrown and open canopy forest were reasonably well predicted (70.0% and 69.3%), whilst the transition to closed canopy forest was not predicted at all.

**Table 3: Predictor variables shown to be significant in the PO ordinal logistic regression of extensive land-use becoming overgrown (y = 1; 3037 points), open canopy forest (y = 2; 1248 points) or closed canopy forest (y = 3; 500 points) between 1985 and 1997.**

	Coefficient	S.E.	Wald Z	P
y>=2	4.774e+01	9.474e+00	5.04	0.0000
y>=3	4.591e+01	9.473e+00	4.85	0.0000
Annual average temperature	4.756e-03	1.541e-03	3.09	0.0020
Annual average temperature <sup>2</sup>	-1.818e-05	2.393e-06	-7.60	0.0000
# open canopy neighbours	6.068e-02	1.235e-02	4.91	0.0000
# overgrown neighbours	-6.036e-02	1.037e-02	-5.82	0.0000
Continentality	-6.092e-02	1.038e-02	-5.87	0.0000
Continentality <sup>2</sup>	2.031e-05	4.596e-06	4.42	0.0000
# extensively used neighbours	-5.580e-02	7.674e-03	-7.27	0.0000
June Direct Solar Radiation	-3.619e-04	1.120e-04	-3.23	0.0012
June Direct Solar Radiation <sup>2</sup>	8.889e-09	2.348e-09	3.79	0.0002
May precipitation	2.431e-03	9.375e-04	2.59	0.0095
May precipitation <sup>2</sup>	-8.927e-07	2.712e-07	-3.29	0.0010
Distance to avalanche sites	9.437e-06	4.666e-06	2.02	0.0431
Annual average precipitation	-1.823e-03	3.453e-04	-5.28	0.0000
Annual average precipitation <sup>2</sup>	3.346e-08	6.228e-09	5.37	0.0000
Site water balance	4.421e-04	1.068e-04	4.14	0.0000
Site water balance <sup>2</sup>	1.123e-07	3.565e-08	3.15	0.0016

**Table 4: Measures of model fit and predictive ability for the calibration and independently sampled evaluation datasets.**

	Calibration data	Evaluation data
MSE	0.00038	0.00037
Corrected Somers' $D_{xy}$	0.48	0.47
AUC	0.74	0.74
CCR	0.64	0.62

MSE = Mean Squared Error; AUC = Area Under Curve; CCR = Overall Correct Classification Rate.

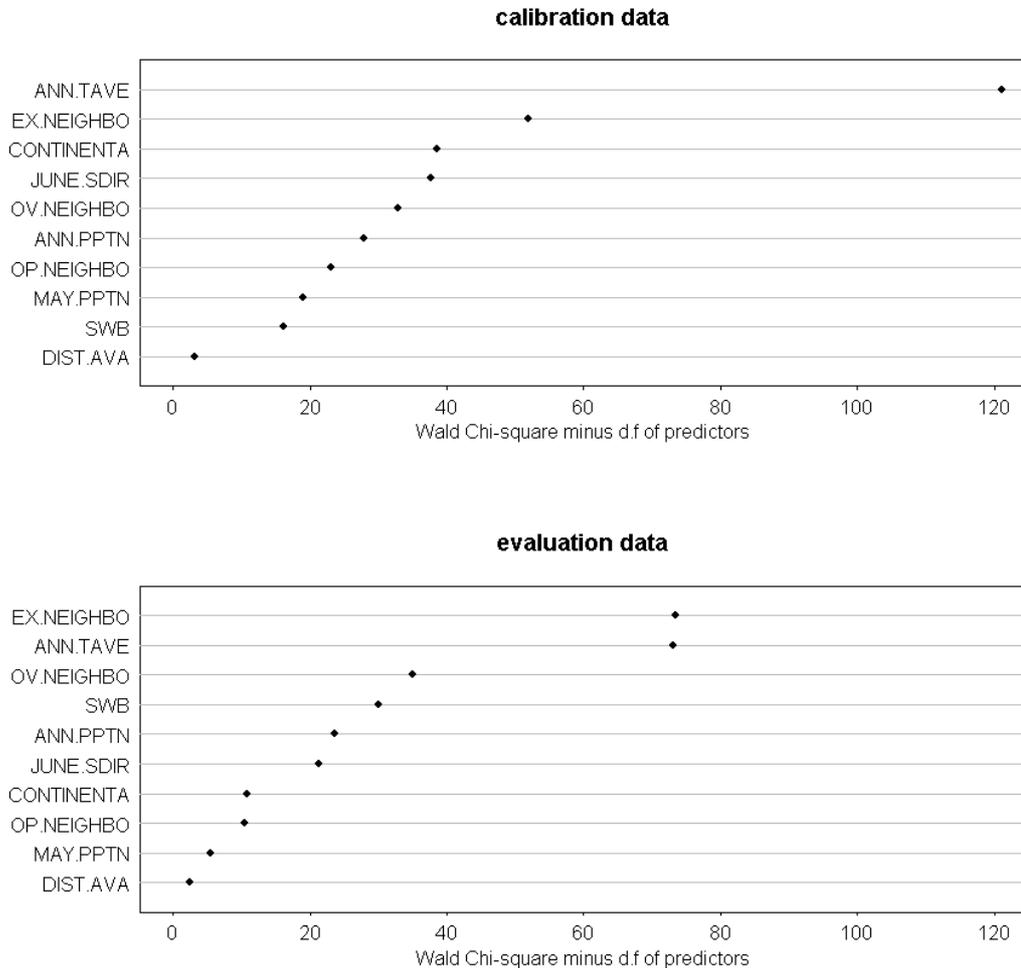
**Table 5: Breakdown of the observed vs. predicted classes for the independent evaluation dataset.**

		Predicted by model			% correctly classified
		Overgrown	Open canopy forest	Closed canopy forest	
Observed	Overgrown	<b>2126</b>	922	0	70.0
	Open canopy forest	371	<b>839</b>	0	69.3
	Closed canopy forest	176	322	<b>0</b>	0.0
		2673	2083	0	

In both the calibration and evaluation datasets, annual average temperature and the number of extensively used neighbours were the variables that best explained the recorded land cover changes (Figure 3). Continentality, SWB, June direct solar radiation, annual average precipitation and the number of already overgrown neighbours in 1985 also had explanatory power, but their order of importance varied between the two datasets. May average precipitation and distance to historical avalanche sites, although statistically significant, contributed the least to the explained variation.

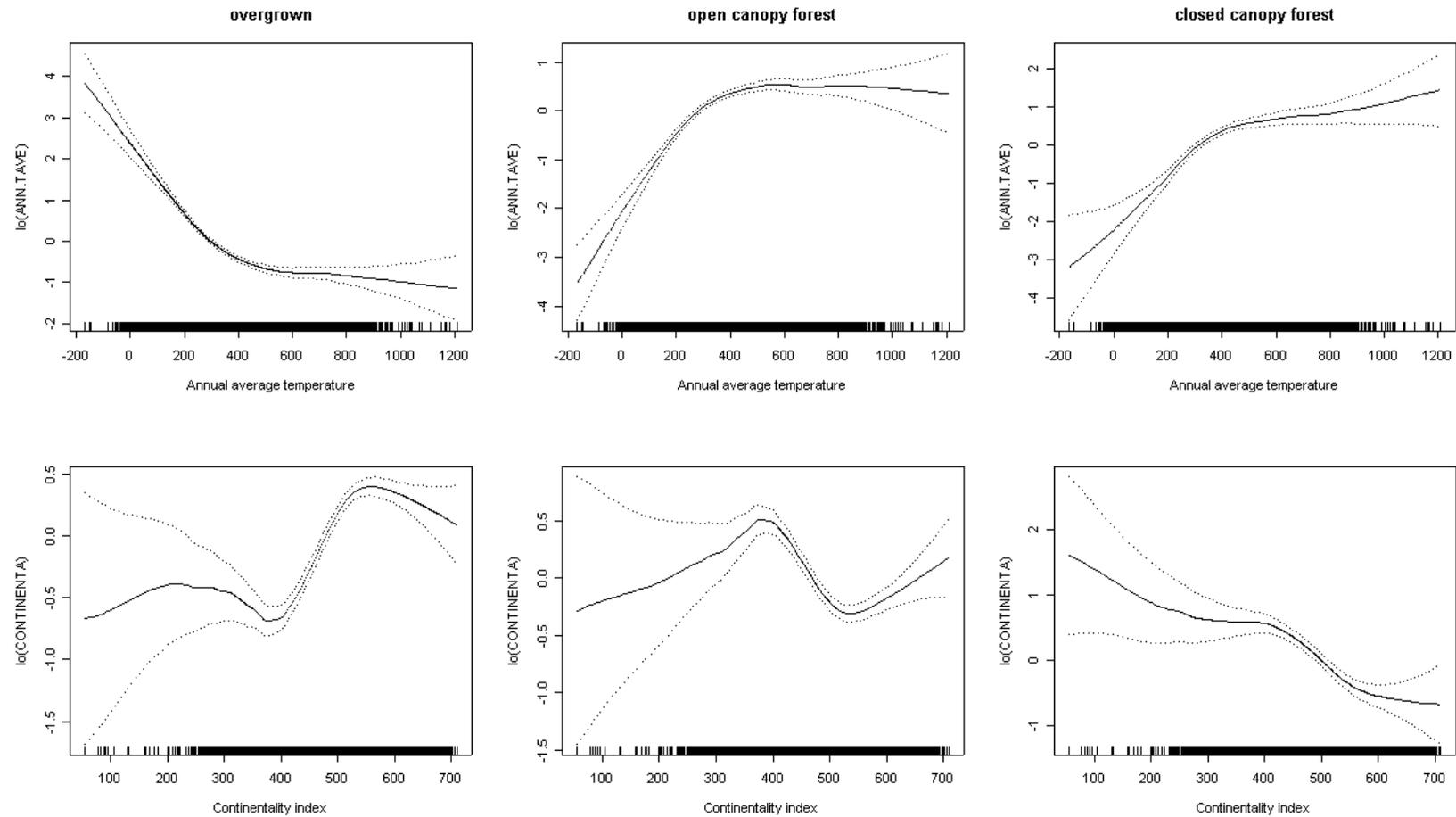
The GAM plots of the relationships between annual average temperature and continentality and the three land cover changes reveal marked differences (Figure 4). Where annual average temperature was lowest, the change to overgrown was more likely than the change to open or closed canopy forest. With increasing temperature, the likelihood of the change to overgrown decreased and the change to either open or closed canopy increased. Differences between the relationship between the change to open or closed canopy forest were not clearly discernible from the temperature GAM plots. At mid to high temperatures, both transitions were

**Figure 3: The importance of the predictor variables as shown by an ANOVA for the calibrated model and its' independent evaluation dataset (4785 and 4756 points respectively). Quadratic terms are automatically included with the parent variable.**



**ANN.TAVE = Annual average temperature; EX.NEIGHBO = # of extensively used neighbours in 1985; CONTINENTA = Continentality; JUNE.SDIR = June direct solar radiation; OV.NEIGHBO = # of overgrown neighbours in 1985; ANN.PPTN = Annual average precipitation; OP.NEIGHBO = # of open canopy forest neighbours in 1985; MAY.PPTN = average precipitation in May; SWB = Site Water Balance; DIST.AVA = Distance to historical avalanche sites.**

similarly possible. Note the narrowness of the standard error curves around the plotted smoother. The relationship between continentality and the three land cover changes was more complex. For extreme values of any of the three changes the standard errors were high. For the range of approximately 300 – 600 (index) the standard errors were low and the trends in continentality between the land cover changes markedly different. With increasing continentality the likelihood



**Figure 4: Plots of GAMs showing the (non-linear) relationship of Annual average temperature and Continentality to the three land cover transition types of extensively used agricultural land (1985) to: overgrown, open canopy forest or closed canopy forest (1997). Dotted lines indicate 2 x standard error.**

of a change to closed canopy forest decreased, accompanied by an increase in the likelihood of a change to open canopy forest at medium continentality. As continentality further increased, the likelihood of a change to open forest decreased and that of a change to overgrown areas increased accordingly. In summary, changes to forest were most likely to occur at higher temperatures (low elevations) and moister climates (low continentality) within the 12 year study period. Under dry-continental and cool climates, the most likely transition was to overgrown only.

The standardised kernel density distributions of the predictor variables showed some clear differences between the land cover changes (Figure 5). While some showed a displacement of the transitional stages along the predictor gradients (e.g. # extensively used neighbours), others showed differences in their contribution intensity (e.g. # of overgrown neighbours). The most pronounced of these was with the number of already extensively used neighbours in 1985; on average, a high value of this variable was associated with change to overgrown. Where the peak in the density distribution is the same for all responses, the difference in the peak height addresses the contribution strength to the various transitions. The density curves are standardised and thus the area under the curve is the same for all responses. The contribution of such variables to the successional development varies between the simulated successional stages; for example, proximity to historical destructive avalanche sites is associated with a slower than average development, with the vegetation mainly proceeding to the overgrown condition. For most predictor variables, it is apparent that the changes to open or closed canopy forest are not easily distinguished, shown by the very similar density distributions e.g. annual average temperature.

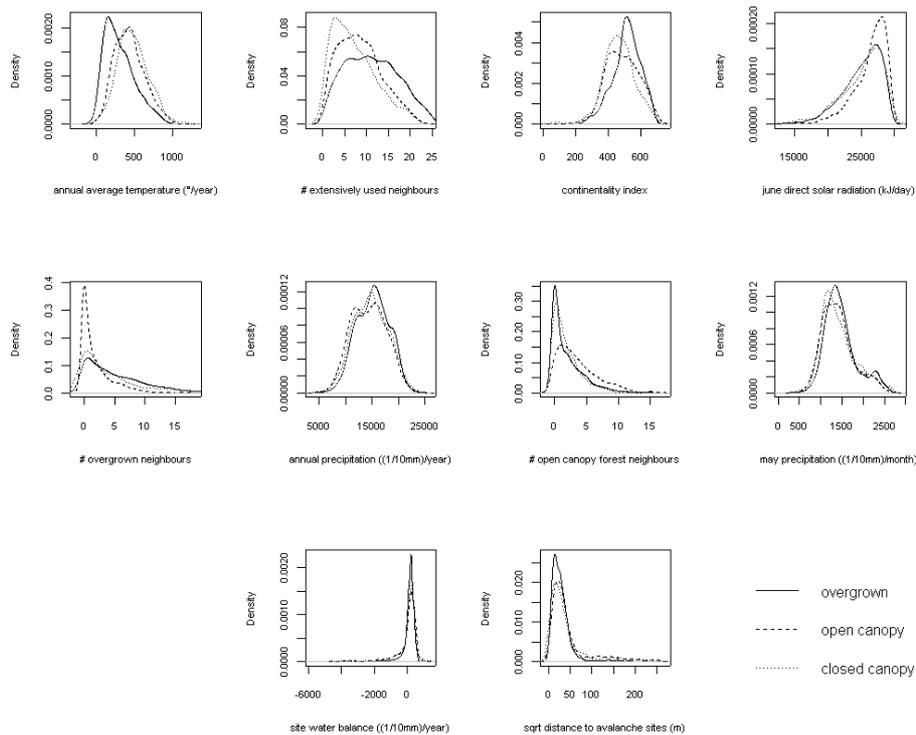
The bootstrap calibration of the model showed a reasonable fit as did the evaluation dataset (Figure 6). The model underestimated probabilities less than 0.2 and greater than 0.65 and overestimated the probabilities between. The apparent and bias-corrected lines are almost exactly the same, indicating that the model is virtually unaffected by sampling bias.

## **Discussion**

In this study we used land cover data derived from aerial photographs to investigate the degree of vegetation change on former agricultural land between two sample dates 12 years apart (or 13 years in the case of a minority of pixels). All of the pixels investigated were under extensive agricultural use when first surveyed, and at some time during the following 12 years this land-use

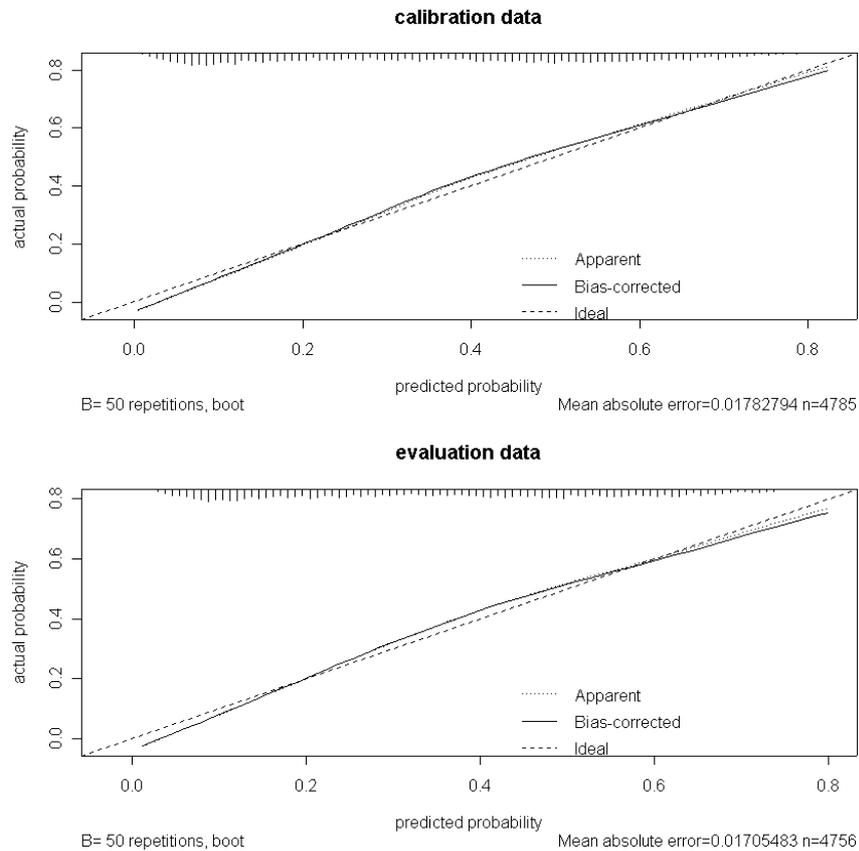
was given up and a secondary succession commenced. It is important to remember that the land cover classes used in our analysis are based upon the interpretation of aerial photographs, and the

**Figure 5: Standardised kernel density distributions of land cover changes for each predictor variable remaining in the model after backward stepwise reduction.**



definitions used therefore reflect the kinds of features that can be observed in such photographs. Our definitions of successional stages, e.g. closed canopy forest, may therefore not carry the same meaning as those used by an ecologist in the field (see definitions in table 1). Also, because we do not know when the land-use changed, it is not possible to calculate an exact rate of succession. For example, some pixels in areas favourable for tree growth will be at the overgrown stage simply because the land was not abandoned until toward the end of the 12 year period; however, land under similar conditions but abandoned earlier could have reached the closed canopy stage. In contrast, the development of closed canopy forest within 12 years would be impossible in areas where conditions for tree growth are unfavourable (cold, dry). Thus under a particular set of environmental conditions, only a minority of pixels may show the potential vegetation change that can occur in a 12 year period. The problem of not being able to account

**Figure 6: Bootstrap resampling model calibration using the calibration dataset and the independent evaluation dataset for the model calibrated using a quarter of transition points and evaluated with another quarter (4785 and 4756 points respectively).**



B = number of Bootstrap resampling repetitions used (Harrell 2001)

for time invariance in such empirical models has been identified and discussed by a number of authors (Aspinall 2004; Verburg *et al* 2004). However, because the data-set is very large and covers a wide range of environmental conditions, even comparatively weak trends are visible and the data can therefore still be used to obtain useful information about the factors affecting the rate of forest succession. Thus, we were able to identify meaningful patterns of spatial variation to make inferences about temporal dynamics (Pickett 1989; Fukami & Wardle 2005).

The data suggest that forest succession following land abandonment proceeds most slowly in the central region of the Central Alps (fig. 3), specifically at treelines, probably because of the relatively dry climate, and at higher altitudes also because of lower mean temperatures. Thus, the model makes ecological sense. However, as is clear from the breakdown of the CCR values, not

all transitional stages were equally well predicted, with changes to closed canopy forest being less well supported than those to overgrown areas and open canopy forest – thus lowering the overall accuracy measures (AUC and Somers'  $D_{xy}$ ). Three explanations may account for the poorer prediction of certain transitions. First, the Swiss Land-Use Statistics may not distinguish adequately between open and closed forest. According to our definitions, these phases are distinguished on the basis of tree density, with values of 20-60% for open forest and >60% for closed forest, but this criterion may be difficult to apply precisely (Sager & Finger 1992). Second, our set of potential predictor variables may not include all the relevant factors. For example, particular types of disturbance such as grazing, rockfall or erosion that were not represented in our data may be important (although distance to historical avalanche sites may represent a proxy for a more generic disturbance variable). Similarly, land-use prior to the first inventory may also be an important factor, but we have no information about this. Finally, closed canopy forest does not necessarily represent a more advanced successional stage than open canopy forest, especially where site conditions prevent the establishment of closed canopy forest.

Despite these limitations, the variables which are significant in the model - propagule source (neighbourhood), moisture (precipitation and soil moisture), light and temperature - are those expected to influence the rate of secondary forest succession on abandoned agricultural land. Since seed availability is known to be one of the major factors limiting early succession (Myer & Pickett 1994), it is not surprising that overgrown neighbours and forest consistently appear as highly significant predictor variables. Thus forest was more likely to establish within a 12 year period in areas which were already surrounded by forest than in those where there was a high proportion of agricultural land.

The retention in the model of the quadratic terms for six of our predictor variables shows the complexity of the relationships with the land cover changes. The GAM plots (fig. 4) and density distribution diagrams (fig. 5) allowed us to interpret the model results where non-linear relationships were evident. It is also important to note that while we did not model interactions between the predictor variables, in reality there may be an interactive link between climate, soil and other variables.

The relationship between annual average temperature and rate of forest development is as expected. Not only do cooler annual average temperatures directly reduce tree growth but they are also associated with a shorter growing season (Kimmins 1997). The relationship of

precipitation to a change to forest could be a reflection of water-logging, retained in the model as SWB. Combined with lower temperatures, increased precipitation with increasing altitude (Tivy 1993) also indicates greater snow longevity and hence an ecological factor limiting the establishment and survival of small seedlings (Kimmins 1997).

Site water balance is a predictor that integrates the difference between monthly precipitation and potential evapotranspiration over a soil bucket for a full water year (Grier & Running, 1977). The bucket size depends on soil properties and topographical position (for details see: Roberts *et al.* 1993; Zimmermann & Roberts, 2001). It expresses the amount of water that is annually available to plants accounting for the water holding capacity of the soil, and the balance between incoming precipitation and loss through (potential) evapotranspiration. Negative values express situations where evapotranspiration exceeds rainfall in the majority of months, with only few months available that allow plants to grow. The response (fig. 5) shows a clear decline of all transitions under very dry conditions. This is in good agreement with theory.

Continentality (expressed here as the adjusted Gams continentaliy index) is a measure of large-scale weather patterns and expresses the amount of rainfall per given temperature (Zimmermann & Kienast 1999), reflecting the evaporative (water) demand for changes in temperature. Our results suggested that the more continental a site (and thus drier for a given temperature), the slower forest succession proceeds which is as expected from the perspective of site water balance but is also contrary to what might be expected where warmer summer temperatures occur that would promote tree growth. Overall, we hypothesise that the slower rate of forest succession in more continental areas may be due both to reduced tree recruitment and to slower growth rates. Possible factors contributing to low recruitment include: 1. relatively dry conditions together with a lower frequency of mast years at high elevations (Tranquillini 1979); 2. dense cover of dwarf shrub communities at higher altitude sites (Jäderlund *et al* 1997); 3. longer duration of snow cover leading to a reduced heat sum (Kimmins 1997); 4. differences in the predominant tree species e.g. the more drought tolerant *Larix decidua* and *Pinus cembra* dominate at higher altitudes in the more continental areas, compared with *Picea abies* in less continental areas (Ellenberg 1988). Reduced growth of established trees can be related to a shorter growing season with relatively low temperatures and low precipitation.

The distance to historical destructive avalanche sites emerged as a significant predictor in the model, though the response to this factor does not appear to meet the assumption of strict

ordinality. However, it discriminates well between slow (conversion to overgrown only) and fast (conversion to open or closed forest) succession, and such differentiation can also be considered an ordinal response. Successional development appears to be slower at sites close to historical destructive avalanche paths. Reasons for this may be: 1. Quick return time of the disturbance itself; 2. The persistent vegetation cover formed and perpetuated by repeated disturbance (e.g. *Alnus viridis*) (Kulakowski *et al* 2006).

Soil depth (and thus water and nutrient-holding capacity) was not shown to be a significant factor, although rates of forest succession are known to be higher on more fertile sites (Prach *et al* 1993). However, this may be due to the fact that although soil depth acts as a proxy variable for nutrient-capacity, it is not a measure of soil nutrients at any point in time and does not take into account the fact that the changing vegetation composition of a site in turn changes the nutrient content of the soil (Leuschner & Rode 1999). Here, soil depth - and thus indirectly nutrient-holding capacity - may already be accounted for by the site water balance variable. This is because SWB directly includes water-holding capacity (corrected for soil depth), as well as the potential in- and output of water into the soil.

## **Conclusions**

The economic and social factors leading to the abandonment of agricultural land have been well studied. This study has highlighted another important aspect of the phenomenon: that the giving up of agriculture marks the beginning of ecological changes that influence land cover for many years. Our results confirm previous studies in showing that the rate of vegetation development varies greatly according to environmental conditions. Under the most favourable growth conditions in Switzerland, closed canopy forest (albeit representing an early successional stage) can be reached in as little as 12 years. However, under the more severe, continental conditions of certain Alpine regions the succession proceeds much more slowly, and after 12 years there is only a cover of shrubs and small trees. Such quantitative information is important because it enables us to understand better the long term environmental consequences of economically induced changes in land use. For example, the statistical model developed in this study could be used to make predictions about future land cover changes rates resulting from the abandonment of agriculture. And this information would help us to evaluate how land-use changes are likely to affect biodiversity and other ecosystem services.

From a more technical point of view, this study has shown ordinal regression to be a promising method to investigate factors influencing the rate of land cover change. The method is particularly useful where data from two time points are available and the assumption of sequential change - as in a secondary succession - is valid. The model presented here predicted on comparably small spatial scales (local neighbourhood, soil conditions) as well as on larger regional scales (climate patterns). It is thus also a successful demonstration of including several acting scales in one model. The variables identified as important predictors of temporal pattern of forest succession provide a basis for future investigations of landscape scale land cover change.

### **Acknowledgements**

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## **5. Outlook**

### ***5.1 General comments and introduction to outlook chapter***

As can be seen from the analyses conducted in the papers presented in this thesis, there is considerable scope for investigating land cover change in Switzerland with the available data and the use of predictive statistical models. However as is the case with any scientific research, in answering one question more questions are raised and different aspects of the research - such as strengths and weaknesses of the data and resulting models and the further applicability of the models - are highlighted. This outlook attempts to briefly describe and make suggestions toward dealing with some of these aspects.

### ***5.2 The Swiss Land-Use Statistics dataset***

#### ***5.2.1 Strengths***

There are a number of strengths and weaknesses associated with the use of the Swiss Land-Use Statistics. These must be acknowledged and taken into account both when using the data itself in a raw form and when interpreting results of models derived from the data. One of the greatest strengths is simply the existence of such a large scale spatially explicit dataset measuring land cover and land-use at regular intervals. The analyses presented here represent just one of many ways in which the data could be used. Not only do the data provide extensive information about land cover and land-use in Switzerland and the changes between the two time periods measured to date, but they are also compatible with European and other international datasets which are also often measured on a 1 hectare raster. And providing that the classification systems are also compatible, this allows for direct comparison across geographical borders.

A further strength of the Swiss Land-Use Statistics lies in the detail of the classification system, with a total of 74 classes that can be further aggregated according to the needs of the investigator and the questions addressed. The research presented here used an aggregation of classes covering the continuum from intensive agricultural land-use to closed canopy forest. As long as the level of class detail is truly representing what it claims to and as long as related error can be quantified or minimised (see next section), then the resulting conclusions can be considered credible.

A third strength of the Swiss Land-Use Statistics is that the use of such a large dataset potentially means that any noise is more than compensated for by a large amount of accurate data: thus, the more common a class, the less frequent the error. For the same reason, conclusions are more likely to be accurate for those types of land cover/land-use that are represented by ‘area cover’, such as forest and agricultural use, than for linear elements such as hedges or streams (BfS, 2006).

### **5.2.2 Limitations**

There are a number of limitations associated with using remote sensing data in the investigation of land cover and land-use change. The most widely recognised of these are the different types of error that are introduced in interpreting images and in quantifying changes (Green & Hartley, 2000). The following two types of error are both potential limitations of the data and analyses presented here: thematic error and positional error. Both types of error have the potential to introduce noise into the data and therefore into the statistical models, thus reducing their reliability or accuracy.

Thematic errors during the process of photointerpretation can result in classes being falsely classified. This is particularly evident when consulting the definitions used by the Swiss Federal Department of Statistics for particular classes where they state that certain classes can at times only be distinguished from others with great difficulty. The aggregation of the classes presented here sought to minimise this phenomenon but its effect has not been quantified.

Positional errors in class boundaries can occur so that a change may be recorded where there was no change or vice versa (Green & Hartley, 2000). Theoretically, a larger sample should reduce both forms of error, which is one of the reasons I devoted so much effort to understanding how results are affected by different sampling strategies. Nevertheless, little information is available as to the magnitude of either type of error for the Swiss Land-Use Statistics, apart from a coarse measure of estimation error based on the number of sample points used (BfS, 2006), and must therefore be taken into account as a caveat of the investigations presented here.

A final limitation that became apparent when interpreting the results presented in the papers of this thesis is the question as to whether the classification system is ecologically meaningful. For example, does ‘open canopy forest’ actually mean the forerunner to ‘closed canopy forest’?; and does ‘overgrown’ truly represent early successional forest or does it also

comprise sites whose vegetation ‘permanently’ consists of shrubs and small trees? Such aspects would benefit from groundtruthing or some other form of verification.

### ***5.2.3 Potentials***

Despite these limitations, the Swiss Land-Use Statistics are an invaluable source of data for investigating processes related to land cover in Switzerland. What can they then be used for? Aside from providing information about the land cover and land-use of Switzerland on a hectare raster in a spatially explicit fashion, the dataset provides input into national monitoring programmes such as those monitoring biodiversity, spatial development and other indicator systems (BfS, 2006). Amongst purposes unrelated to this thesis, the following appear to be the most promising: monitoring the state of land-use, and identifying and describing different trends at local, regional and national levels. These factors are relevant not only for scientific research in itself but as an information basis for land managers and policy makers.

### ***5.2.4 Possibilities with the third Swiss Land-Use Statistics***

A third step in the time series means that models can be calibrated on data from the first time-step and evaluated with independent data from the second time-step. Further, possible trends in land cover and land-use change may be more evident and thus more easily identified over two time steps and effectively 25 years. An additional positive aspect with this particular ‘third step’ is that the Swiss Federal Department of Statistics is also re-evaluating the first and second series in an effort to reduce some of the errors described above, especially positional error. This will ensure much greater consistency also in the process of photointerpretation between the three time-points/two time-steps.

## ***5.3 Statistical Predictive Models of this Thesis***

As is the case with data, there are a number of strengths and limitations which arise out of the development of statistical models which represent a simplification of an ecological process.

### ***5.3.1 Strengths***

One of the greatest strengths of such models is that they allow the user to predict future land cover change. This aspect was not a component of this thesis but some of the models presented

here have been used by other researchers to implement future scenarios of land cover and land-use change under different climatic and socio-economic conditions (see thesis Introduction).

When the same group of variables is consistently found to predict land cover change, regardless of sampling or modelling strategy, it seems safe to conclude that the models are robust. This also highlights the usefulness of multiple models in such investigations, where there may not be one correct model (Johnson & Omland, 2004).

Such models can also contribute towards explaining the observed and measured land cover change even though some predictor variables represent proximate (or accompanying) causes. Although the mechanistic link between pattern and process is not proven (see below), the results still serve in directing the user towards possible true causal factors and can serve as a basis for further investigations where ‘explanation’ is the key question.

Spatially transition-based models, such as those presented here, are an extension of the aspatial Markov-chain technique but also integrate aspects of cellular automata, explicitly assuming that the transition probability of any one cell is influenced by neighbouring areas. These can therefore be performed at a high spatial resolution, with simple rules but nevertheless integrating the dynamic nature of land cover change (Theobald & Hobbs, 1998). This approach can help in the understanding of how individual land-use decisions and land cover changes can create and yield a cumulative trend over space and time (Theobald & Hobbs, 1998). This is of further interest when examining the effects of globally cumulative environmental change.

### ***5.3.2 Limitations***

The error derived from the data (both thematic and positional) introduces ‘noise’ into the models (see above). This may partly explain why many of the models were relatively low in explanatory power – reflected by medium measures of accuracy (AUC). Without accurate measures of the magnitude and types of error in the data, it becomes difficult to quantify the resulting error in the models. Given that some AUC values and  $R^2$ , where measured, were relatively low, one must conclude that such noise has been introduced. And this noise may also contribute to the failure of some land cover types to be predicted. This point was particularly evident in the grouped ordinal and multinomial models where closed canopy forest was seldom predicted.

Given that some of the land cover changes investigated here involved the abandonment of agricultural land, some of the models would probably be improved with the inclusion of further

socio-economic information. Other data representing disturbance and site history could also serve to increase the accuracy of the models as well as possibly helping to distinguish between the open and closed canopy forest categories.

A further point, which is more a comment than a limitation, is that these are not mechanistic models and therefore do not link the spatial and temporal patterns of land cover and land-use change to the underlying processes. Such a linkage would be required in identifying the causal factors behind the observed changes. This is however the trade-off among various types of models - generalised, empirical or mechanistic - and the emphasis of any model must depend on the question being investigated (Guisan & Zimmermann, 2000).

The final limitation to be noted here is that of spatial autocorrelation. The presence of spatial autocorrelation violates statistical assumptions of independence. As is often the case in ecological studies, this aspect was only dealt with rather crudely (using neighbourhood variables to represent spatial autocorrelation, sampling points a maximum possible distance apart), and there is considerable scope for improvement in this area. One of the most promising possibilities would be to include the spatial autocorrelation as a variable in the models.

### ***5.3.3 Potential***

Taking into account the strengths and limitations described here of the statistical models, they are shown to be a useful tool in investigating spatial and temporal patterns of land cover change, even where certain aspects such as error quantification can be improved. The greatest opportunities offered by the models presented here lie in predicting future land cover change and in identifying which areas are most likely to change.

## ***5.4 Questions Raised by the Research Presented Here***

### ***5.4.1 In reality is the data a true representation of the phenomenon that is being investigated?***

This is particularly relevant to the open and closed canopy forest categories where there appears to be a substantial amount of noise in the data and in the models. The question of missing data which would distinguish the two categories better has been discussed in previous sections. The benefit of added groundtruthing must be considered in order to add reliability to the data and the aggregation of the data.

#### **5.4.2 Is the aggregation of the data appropriate?**

What should be done with linear elements in the landscape, such as hedges, which may not constitute ‘closed canopy forest’ for a field ecologist but according to the criteria used here (density, tree height and woody species), must be classed as such? In addition to this they are noted classes which introduce error into the Swiss Land-Use Statistics (BfS, 2006).

#### **5.4.3 Are the models globally or even regionally applicable?**

Whether any of the models presented here can be applied to other areas both within Switzerland and outside depends on a number of aspects, such as the question being investigated, the particular variables which influence the process under investigation and the available data. Care must be used in even extrapolating model results for the most similar environments where similar processes appear to be at work. To know whether a model can successfully be transferred and accurately predict events in other areas, it must be tested. Below are some examples of possible applications and what might be required in order that particular models can be transferred and used in other areas.

- (i) Areas of Switzerland. A good example of the applicability of the models developed here is to areas such as the TWW which comprise a subset of the extensively used agricultural land class used here. With a sampling strategy designed specifically for the TWW areas, the models could be recalibrated to a) determine which variables help to predict abandonment of these areas and b) to identify TWW areas at a higher risk of becoming overgrown.
- (ii) Other agricultural areas. There is a complex and dynamic pattern of land-use in Europe due to environmental and social variability and also the variety of agricultural policies (Verburg et al, 2006). This may limit the applicability of the models to other agricultural areas with regards to reasons for abandonment but given that the variables here are generalised and more likely represent the real factors causing abandonment, they may be applicable.

#### **5.4.4 Does the transition to closed forest really occur within a 12-13 year period?**

As stated in Zoller *et al* (1984) not even 30 – 35 years is long enough to capture the full transition from agriculturally used land to closed canopy forest. However, as identified here and by several

other authors (Surber *et al*, 1974; Walther, 1986; Bebi & Baur, 2002), this does vary regionally. For example, in the Canton of Ticino a transition to closed canopy forest has been observed within as little as 15 years (Zoller *et al*, 1984). The results would benefit from the groundtruthing of aerial photos and closer field investigation of selected sites to better determine what degree of ‘closed canopy forest’ has been reached.

## **5.5 Implications**

### **5.5.1 Ecosystem Services**

There are several benefits, but also some negative aspects, associated with the increase in forest cover in Switzerland. Probably the most commonly cited benefit of increased forest cover is that of carbon sequestration, which increases with the increase of wood biomass. Another ecosystem service that is provided is added soil protection, long term, although this is at times initially reduced with the abandonment of agricultural use and the onset of natural forest regeneration. Erosion prevention is also a particularly important benefit in such a topographically diverse country as Switzerland. Negative aspects include several cultural and social factors such as the loss of a cultural pastoral landscape. Further ecological aspects are the loss of biodiversity and an increased risk of fire. All of these factors have been well covered by a number of authors and will not be further detailed here.

### **5.5.2 Potential impact of climate change**

The importance of temperature and precipitation in predicting slower or faster rates of land cover change (see Paper 3) imply that a changing climate could heavily influence the rate of forest succession. The reverse may also be true where changing land cover and land-use can affect the local, regional and, ultimately, even the global climate (Foley *et al*, 2003).

## **5.6 Were the aims of the thesis fulfilled?**

The main aims of this PhD were: 1) to determine whether large landscape scale statistical datasets can be used to investigate ecological processes such as semi-natural secondary forest succession that are normally studied at a smaller spatial scale; and 2) to use these data to understand and predict spatial and temporal patterns of forest development. I conclude that large landscape scale statistical datasets can indeed be used to investigate ecological processes such as semi-natural

secondary forest succession that are normally studied at a smaller spatial scale. However, there is considerable scope for improvement and therefore the production of even more useful results if the different types of error were to be measured, described and quantified and if the potential effects of spatial autocorrelation were to be either eliminated or integrated in a fashion where they could also be quantified. It is also valid to conclude that the second aim of this thesis was fulfilled, where the data was used to further understand and predict spatial and temporal patterns of forest development. This was done on the basis of statistical modelling and the availability of a large pool of ‘predictor variables’. Climate information, such as temperature and precipitation, and the nature of the surrounding neighbourhood of each site were consistently shown to be the most valuable in predicting both spatial and temporal patterns of land cover change.

### ***5.7 Topics for Further Research***

*5.7.1 Applicability of models to other areas – how globally relevant are the models presented here?*

*5.7.2 The calibration of regional models to identify high risk areas and to recommend management strategies accordingly.*

*5.7.3 The use of the third Swiss Land-Use Statistics (and the corrected versions of the first and second) to test the accuracy of the models and to better model a time series of land cover change for Switzerland.*

*5.7.4 Include variables which quantify the spatial pattern of the statistical model residuals so that spatial autocorrelation is thus quantified but still retained as a variable, rather than eliminated for statistical purposes. This is especially important as spatial autocorrelation itself represents spatially dependent processes occurring in the landscape, of which there are many.*

*5.7.5 The spatially explicit socio-economic data generated by Mario Gellrich (Gellrich, 2006) could be extended to the whole of Switzerland and used as predictor variables, thus providing a better socio-economic background and proving more likely to be identifying the underlying causes of land abandonment.*

5.7.6 *The integration of spatially explicit historical land-use data at the same extent and resolution as the Land-Use Statistics and other explanatory data including the intensity of use (mowing, fertilising, number of cattle per hectare) and nature of the use (whether it was fertilised, Wiese/Weide, sheep/cows/goats)*

5.7.7 *Calibrate the models at different scales e.g 1km raster and compare the results as an investigation of the effect of scale.*

5.7.8 *Investigate the rate of forest succession at the species level to see if there are differences between the species. This may also prove to highlight another set of predictor variables such as water- and nutrient- holding capacity as these factors are thought to determine the pattern/mosaic of species establishment, especially of pioneer species (Zoller et al, 1984; Donnegan & Rebertus, 1999).*

5.7.9 *Attempt to solve the issue of the lack of distinction between open and closed forest by: (i) Introducing a dummy variable for maintained use (such as grazing)/non-use; (ii) Finding a way to factor in other forms of disturbance;*

5.7.10 *Investigate the link between land cover change and climate change and how they interact and feedback onto themselves.*

In conclusion, there remains considerable scope for further research of land cover change in Switzerland and beyond. The research presented here provides another step in understanding this process. Land cover change is a dynamic process which occurs at multiple scales and affects and is in turn affected by a myriad of other processes. Such research contributes a building block to the science of understanding such phenomena.

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Gillian

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## **Gillian Nicole Rutherford**

Born 06.12.1973 Auckland, Aotearoa (New Zealand).

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- 2002 – 2006     **PhD** thesis at the Swiss Federal Research Institute for Forest, Snow & Landscape (WSL) and the Swiss Federal Institute of Technology, Zürich (ETHZ). Title: *The use of land-use statistics to investigate large-scale successional processes.*
- 2003 – 2005     **Post-Graduate Course in Applied Statistics** at the Swiss Federal Institute of Technology, Zürich (ETHZ).
- 2000 – 2002     Logistics at Chris Sports Systems, Tagelswangen, Switzerland
- 1999 – 2000     Research assistant, Department of Environmental Sciences, University of Zürich.
- 1998             Environmental Consultant, Waitakere City Council, Waitakere City, New Zealand.
- 1996 – 1998     **MSc** (Environmental Sciences) with 1<sup>st</sup> class Honours at the University of Auckland, New Zealand. Thesis: The current vegetation of Kaitoke Swamp, Aotea (Great Barrier Island).
- 1992 – 1994     **BSc** (Biology/Botany) at the University of Auckland, New Zealand.
- 1987 – 1991     Secondary Education, Waitakere College, Waitakere City, New Zealand.
- 1979 – 1986     Primary Education, Swanson Primary School, Waitakere City, New Zealand
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