Plants, soil and the stability of mountain socio-ecological systems

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Sommaire

1 The who and what - a short presentation

... the long and exhaustive presentation, you'll find in chapter 3 - Curriculum Vitae.

Here, you'll find key points which may contribute to better situating my professional development, the way I lead my research and the topics I work on.

1.1 Who ?

I am a scientific collaborator at *Irstea* (cf. box 1) working on the impact of climate and land-use change on plant-soil interactions and its consequence on the resilience of mountain grasslands.

After having obtained a first diploma as landscape gardener, I continued to work as gardener in Northern and Southern France, before starting my courses at the Technical University of Munich (TUM). During this time, I spent one semester in Angers, before assisting in landscape architecture offices for several months in England and in France. In 2002, I was graduated in landscape ecology and architecture at TUM after having accomplished a diploma thesis on the feeding habitat of manatees in French Guiana. I continued my studies in Switzerland as a PhD student working on land-use, soil nutrient availability and conservation of mountain grasslands. During this time I discovered the huge advantage of long-term datasets in ecology, a topic which continues fascinating me. In 2006 I obtained my PhD in biology from the University of Fribourg. It followed a short post-doctoral stay at CABI Bioscience Europe, before I was appointed scientific collaborator (chargé de recherche) in the research unit Mountain Ecosystems at Irstea in 2006. I continued to work on the long-term effects of nutrient changes on mountain grasslands and started to take over responsibility in the Alps LTSER platform founded in 2008. Between 2009 and 2011, I worked part-time at

Box 1: Irstea

Irstea is a French public research institute focusing on land and water management and formerly known as Cemagref.

Its research aims on the production of new knowledge and technical innovations used by managers, policy makers and private companies to meet specific societal issues in the areas of resource management, development and land-use.

Irstea has inherited the research model finalised by Cemagref which is centred on scientific research that aims producing practical solutions for stakeholders, by concentrating of four fundamental parameters:

- Cooperative research including private partners with a strong technological and method-logical component;
- Scientific cooperation with research bodies and universities;
- Research that supports public policy through strong cooperative links between Irstea and the Ministries for Environment and Agriculture, regional authorities and devolved government services;
- A European and international setting, particularly with regard to involvement in European environmental research networks.

Irstea (30%) and at the Ecole Polytechnique Fédérale in Lausanne (70 %, Laboratory of Ecological Systems – ECOS). At the latter, I was in charge of the project MOUNTLAND where we studied the effect of land-use and climate change on pasture woodlands and the interactions between plants and soil. After three years during which I also acted as adjunct of the ECOS director, I continued working at Irstea on different aspects of mountain ecosystems which I'll expose in the following paragraph.

From 2006-2013, my work at Irstea took place in the team "Ecology and restoration of grassland and mountain river ecosystems". The team's main research topic was the functioning of mountain ecosystems and the ecosystem services associated with them. We were particularly interested in the dynamics of these environments and the interactions between certain characteristics of the ecosystems (beyond others: habitat function, nutrient cycles, plant diversity, forage value) and pastoral and/or agricultural practices, touristic uses and climate change.

Since 2013 I'm leading the team BIODIV 4D. Most of the team's work is centred on the study of effects from interactions between natural and social systems (socio-ecosystems) on mountain ecosystems, and how these interactions affect their persistence over time: meeting the needs of present and future generations, while at least keeping ecological quality, or even increasing it.

The team discusses mountain socio-ecosystems in a multi-scale perspective. Observations and experiments made at scales ranging from μ-meter to the territory contribute - through up-scaling processes - to modelling. The team's study sites are areas of high natural value as protected areas (national and regional parks, natural and wilderness areas) that can be considered in the framework of ecological networks as a source of ecological diversity. More anthropogenic areas such as managed forests, mountain pastures and ski resorts could help identifing the effects of human influence on these ecosystems. Voluntarily the research team concentrates its field work on some major sites as for example the socio-ecological observatory platform "Alps LTSER" which allows establishing long-term observations and contribute to study ecosystem sustainability.

I wrote or contributed to 29 publications in international peer-review journals (plus 6 currently submitted), three book chapters, eight technical publications in refereed journals and more than 50 publications at conferences. I supervised or co-directed four postdocs, one PhD-student, 10 M2-students, 6 M1-students and 4 L3-students and I supervise two PhD-students currently. I was a member of one thesis jury and I attended or I am part of four thesis committees.

Since 2009 I am responsible for a M2 teaching module at the Ecole Polytechnique de Lausanne (70h) where I teach the vast majority of the courses. I give regularly lectures in different master courses in Grenoble (STAGE, BEE).

I am co-coordinator of the Zone Atelier Alpes labelled by the INEE (CNRS, National Centre for Scientific Research) and also labelled long-term socio-economy and ecology research platform (Alps LTSER) and I am head of the task force "Mountain LTER" grouping mountain sites within LTER Europe.

1.2 What ?

In the centre of my research stand the long-term effects of global change on ecosystems under environmental stress and the consequences on the stability of these ecosystems with a particular focus on plant-soil interactions. Although global change can be discriminated into four main groups (atmospheric gases, climate change, land use change, biotic exchange), I am mainly interested in the impacts of climate change and land use change on vegetation and the interaction between vegetation and soil. These two factors (climate change, land use change) requires an adaptation of the ecosystem and its use which then affect the goods (fodder, wood, etc.) and services (water retention, recreation area, etc...) provided by the ecosystem (Figure 1). My research mainly concerns grasslands, but also wooded pastures of the montane and subalpine zone. For this I use observational and experimental approaches and collaborate with modellers to understand the changes over the last 100 years to present day in order to anticipate future changes.

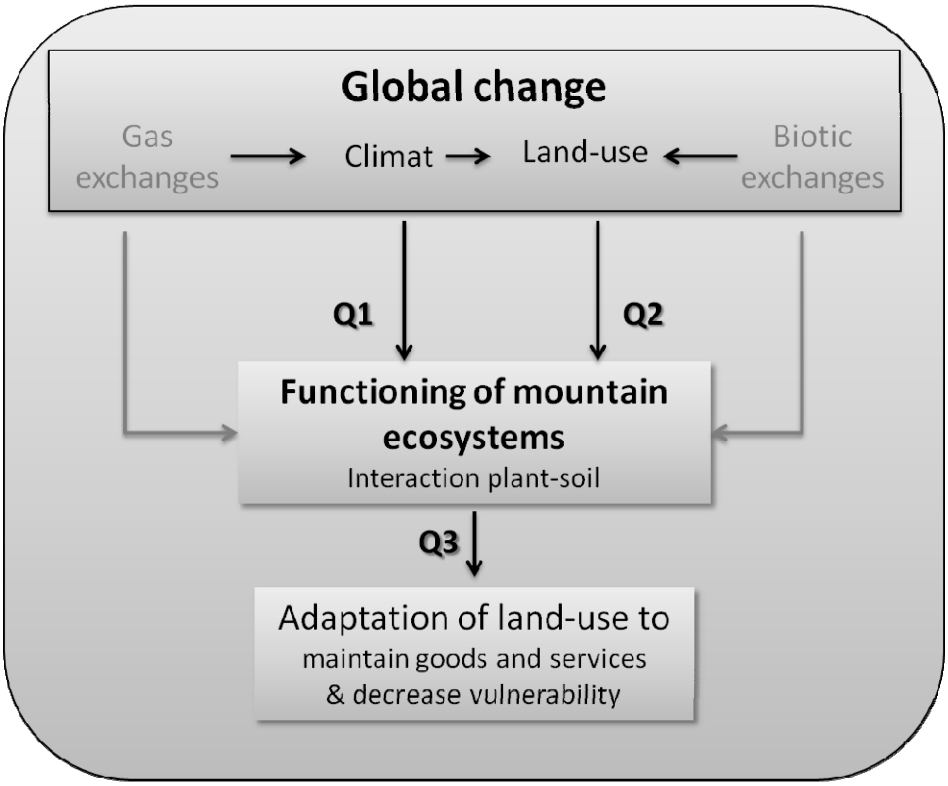


Figure 1: Conceptual framework of my research.

Specifically, I examine the following questions:

- Q1 : How does climate change affect the vegetation and the interactions between vegetation and the soil?
- Q2 : What are the consequences of changing land use on ecosystem functioning and interactions between vegetation and soil?
- Q3 : How can we maintain the functioning of ecosystems and increase their resilience to reduce the vulnerability of ecosystems due to global change?

I studied the resistance of plant communities to disturbances such as droughts (Deléglise *et al.* 2014; Jung *et al.* 2014), but also the increase in average temperatures (Gavazov *et al.* 2013; Gavazov, Spiegelberger & Buttler 2014c; Peringer *et al.* 2013), of land use changes such as intensification or extensification (Spiegelberger *et al.* 2006b; Mariotte *et al.* 2013a). In cases where these disturbances cease, I observe and analyze the resilience of ecosystems (Spiegelberger *et al.* 2006a, 2010; Jaunatre *et al.* 2014; Mills *et al.* 2014) and their possible adaptation to deduce their vulnerability (Gavazov *et al.* 2013; Huber *et al.* 2013b).

The objects of my studies are mainly the vegetation and the plant-soil interactions (Spiegelberger *et al.* 2006a, 2010; Schaffner *et al.* 2012; Dommanget *et al.* 2013a; Puissant *et al.* 2013; Gavazov *et al.* 2014a; Jaunatre *et al.* 2014; Mills *et al.* 2014). My research on plant-soil interactions is situated at different spatial scales ranging from a few centimetres (Spiegelberger *et al.* 2010; Spiegelberger, Steinlein & Schaffner 2014; Spiegelberger *et al.* 2006a; Cassagne *et al.* 2008; Schaffner *et al.* 2012; Mariotte *et al.* 2012, 2013a; Dommanget *et al.* 2013a; Deléglise *et al.* 2014; Gavazov *et al.* 2014a; Jung *et al.* 2014; Mills *et al.* 2014) to several square kilometres (de Thoisy *et al.* 2003; Buttler *et al.* 2012b; Chételat *et al.* 2013; Huber *et al.* 2013b; Peringer *et al.* 2013). Timescales include experiments lasting a few weeks (Dommanget *et al.* 2013a) and retro-perspective modelling and analysis on more than 100 years (Chételat *et al.* 2013; Peringer *et al.* 2013). By combining observational, experimental and modelling approaches, I try to get a complete picture of ecological processes in play (Spiegelberger *et al.* 2012). The overarching aim of my research is reducing the vulnerability of socio-ecosystems. Parts of my work include proposing methods and tools for ecological analysis and making recommendations to land managers and other stakeholders in order to drive the ecosystem towards the desired objectives (cf. technical publications).

In the following chapters I will discuss my progress on each of these research questions by putting them in a more general context.

2 Plants, soil and the stability of mountain socio-ecological systems

In this main part of the present document, I aim at putting my scientific work in a broader context and at rendering clear the links between the different directions of research I took during the last years.

I hold the view that man is part of the ecosystem and I speak therefore of socio-ecosystems, which I'll introduce together with the idea behind long-term socio-ecological research in the first chapter. Chapters two and three are dedicated to the impact of climate and land use change respectively on mountain ecosystems. The findings from the first chapters are used as base for the forth chapter where I focus on the stability and the resilience of mountain ecosystems before investigating up to which limits mountain ecosystems will change in the future. I'll conclude this second part of this report with an outlook on the research questions I hope to focus on in the next years.

2.1 Socio-ecological systems in mountain areas

In the last decades, social and ecological scientists have worked and developed their theories in more or less complete isolation from each other. While the former have often thought "as if nature did not matter" (Murphy 1995), the latter were particularly interested in the biological and physical dimension of nature. Moreover, human influence was and is still today often interpreted by ecologists as a "perturbation" (White & Jentsch 2001) and more rarely seen as part of the complex interactions in nature (Liu *et al.* 2007) while many sociologists regard nature as a purely social construction. Today's environmental challenges, in particular the effects of global change and the predicted human impact via land use change on biodiversity (Sala *et al.* 2000) urges in particular sociologists, economists, climatologists and ecologists to develop common approaches in order to collaborate on one of the most pressing problems in the 21st century. Recognition has grown in all parties over the last years that neither human nor biophysical systems can be studied autonomously. This recognition is the impetus for studying the dynamics of complex and interdependent social and ecological systems as it is done for example in LTSER research (Haberl *et al.* 2006).

2.1.1 Socio-ecological systems

Human impact has substantially change nature and the benefits people can take off from our environment (Millennium Ecosystem Assessment 2005). Today, there are hardly any natural systems without humans; all social systems are built on goods and services provided by nature. Therefore both systems constantly co-evolve and are thus interdependent. Our environment is consequently best viewed as a social–ecological system. The science of socio-ecological systems (SES) integrates both and studies them parallel. Using SES as a study background puts the human in the centre of the investigations. In particular in the context of global change, humankind may adapt to alter climatic conditions, but this may be on the expenses of the capacity of ecosystems to provided service. This complex interaction is the focal point of sustainability science (cf. box 2).

Box 2: Sustainability science

Sustainability science builds toward an understanding of the human–environment condition with the dual objectives of meeting the needs of society while sustaining the life support systems of the planet (Turner et al. 2003).

Sustainability science seeks understanding of the coupled human–environment system in ways that are useful to the different communities of stakeholders. A concern for many of these communities is an improved understanding and projection of the vulnerability of people, places, and ecosystems in the face environmental change, global or otherwise (Turner et al. 2003).

SES are complex and adaptive systems which link the dynamics of ecosystems and the development of human society. SES are governed by adaptive cycles which passes through four phases (Walker *et al.* 2004): a growth and exploitation phase (r) merging into a conservation phase (K), followed by a chaotic collapse and release phase (Ω) that rapidly gives way to a phase of reorganization (α). The Ω and α phases together comprise an unpredictable backloop. The α phase leads into a subsequent r phase, which may be similar or different from the first r phase. Several frameworks have been proposed to study socio-ecological systems. The one I mainly use and which I'll describe in the following is the press-plus dynamics model (PPD; Collins *et al.* 2011). It contains four core components: (1) press and pulse events, (2) a biophysical template, (3) ecosystem services, and (4) a social template. The biophysical and the social template are both influenced by external drives such as the climate and globalisation. This rather general PPD model can be adapted to mountain ecosystems as demonstrated in Figure 2 .

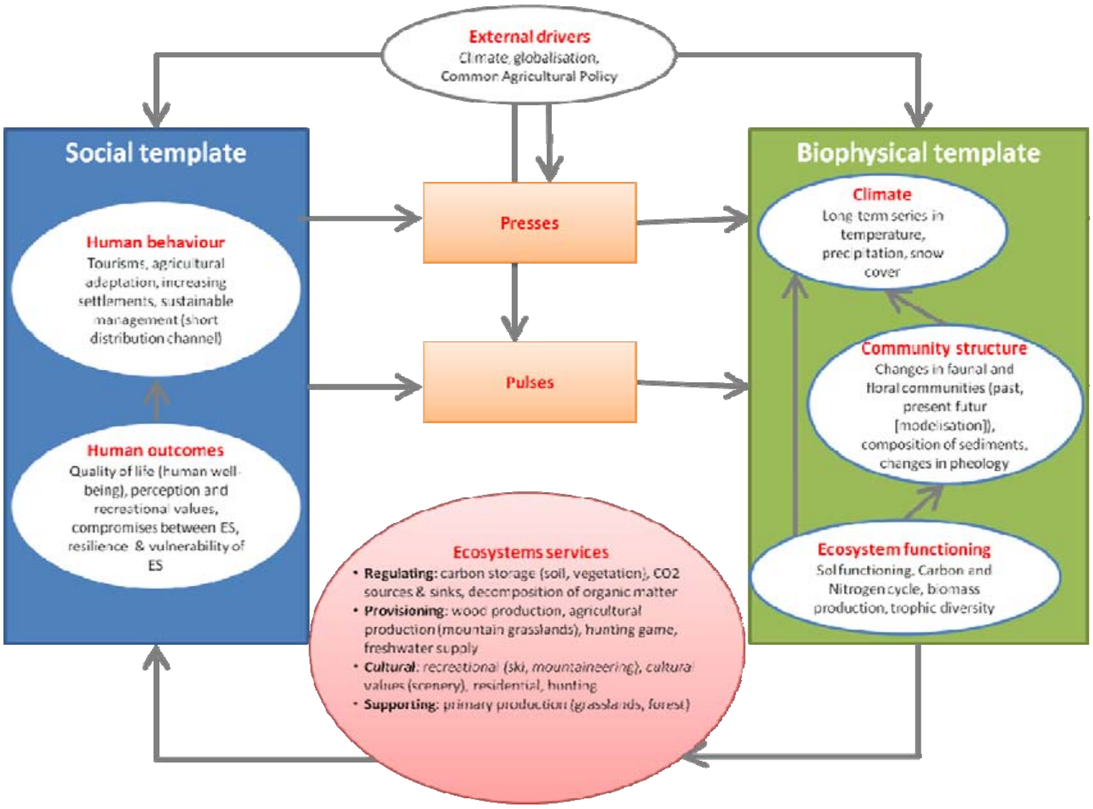
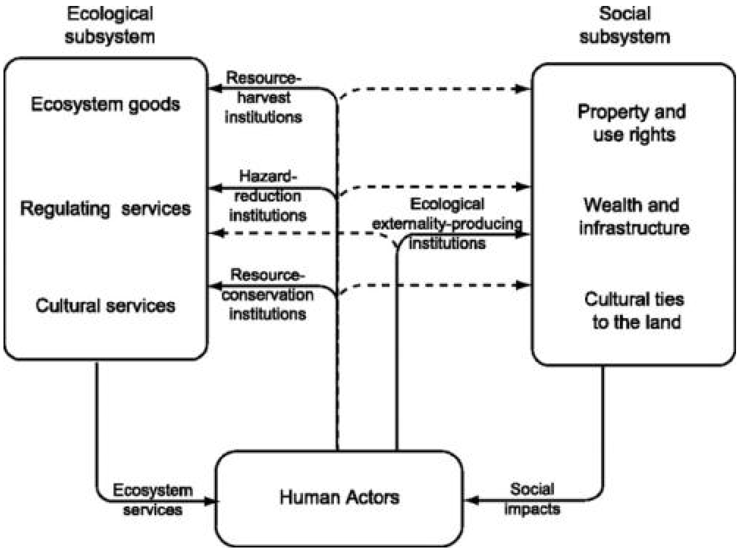


Figure 2: The Press-Pulse Dynamics Model adapted to mountain ecosystems. Figure follows Collins et al. 2011.

According to Collins *et al.* pulse events are relatively discrete and rapidly alter species abundances and ecosystem functioning while press events, such as mean temperature increases, are sustained and chronic. Along the arrows, hypotheses can be dressed (Collins *et al.* 2011). Collectively, altered press and pulse events have quantifiable implications for and impacts on ecosystem goods and services, and changes in these services trigger adaptation of humans, e.g the social template.

Another yet rather similar framework which has it importance in the analysis of SES is the ecological institutions model (Chapin *et al.* 2006). Similar to Collins' model it provides an ecological and a social subset. It explicitly integrates a spatial and a temporal component. Human actors (both individuals and groups) respond to social, environmental, and ecological impacts through a complex web of institutions which mean "the enduring regularities of human action in situations structured by rules, norms, and shared strategies" (Chapin *et al.* 2006, p. 16638). This model also allows an assessment of a suite of at least four policy strategies (adaptability, resilience, vulnerability and transformability) that could be integrated to address the consequences of large directional changes. These approaches differ in their presumed mechanisms.

Common to both frameworks is that the make reference to the concept of ecosystems goods and services. EGS (following the Millennium Ecosystem Assessment; MEA 2005) are goods and services that humans receive from nature. According to MEA,



EGS can be classified in four large categories: provisioning services (providing food, water, etc.), regulating services (regulating climate, floods, etc.), cultural services (aesthetic, spiritual, etc. values) and supporting services (nutrient cycling, soil formation etc.) which are on the base of the three others. In recent years EGS have become a conceptual and empirical link between ecological quality and human wellbeing (Carpenter *et al.* 2009; Collins *et al.* 2011) and a way of communicating the importance of nature conservation to stakeholders (Daily *et al.* 2009).

Biodiversity, meaning the diversity of any kind of genes, species and habitats in a given area, supports EGS and contributes to human welfare and livelihoods. In general human use of biodiversity and ecosystem services is expanding, commensurate with growth in earth's human population and expansion of consumption (Carpenter *et al.* 2009). Moreover, current consumption rates lead to a decrease in particular of regulating services such as air and water quality regulation, climate, natural hazards or erosion regulation, for which mountain ecosystems play a particular important role, and what is foreshading further declines in subsequent services such provisioning or cultural services.

If the concept of ecosystem services is used for sustainable resource management, ecosystem services mapping needs to be conducted. The increasing use of GIS (including digital cartography, remote sensing, image analysis, and simulation) facilitates this task. However, without an understanding of the biophysical reality, any assessment of the impact of climate and land use change on the provision of EGS is futile (Carpenter *et al.* 2009). As plants are on the bottom of all trophical pyramids, approaches which focus on the vegetation may be seen as a rather integrative way to assess subsequent services such as pollinisation. A way this is commonly done is the integration of plant functional traits (PFT) which can be spatially represented into ecosystem service assessments (Quétier *et al.* 2007; Fontana *et al.* 2014), as PFT traits allow the description of important underlying properties of ecosystems and have thus been identified as useful indicators for EGS (Díaz *et al.* 2007; de Bello *et al.* 2010).

2.1.2 Mountain ecosystems

Mountains, which occupy about 16.5 % of the earth surface (Körner, Paulsen & Spehn 2011) are characterised by steep gradients which exemplify "natural experiments" that permit testing ecological theories (Körner 2007). In general, an increase in altitude goes in hand with shorter vegetation period due to reduced ambient temperature, lower atmospheric pressure and CO_2 concentrations and increased UV radiation (Körner 2003). For temperate mountains ecosystems, precipitation increases from low to high altitudes (Körner 2007).

Figure 3: Species-richness mountain grassland in the Swiss prealps.

Within temperate mountains, semi-natural grasslands are widespread components and play an important role by providing fodder for livestock. These ecosystems host species-rich communities with up to 40 plant species per square meter (Figure 3) but are among the most endangered ecosystems in Europe, threatened by both land use (Fava *et al.* 2010) and climate change (Thuiller *et al.* 2005). Indeed, changes in agricultural practices, which have been accelerated since the 1950 in Central Europe are leading to intensification of well accessible sites paralleled by abandonment of less accessible sites in the European Alps (Tasser & Tappeiner 2002; Buttler *et al.* 2012a).

Biodiversity in temperate mountains follows the same pattern as temperature: plant species richness decreases with increasing altitude because of the environmental constraints. However, due to their steep gradients and in consequence the remoteness of same mountain areas, plant diversity of many traditionally managed mountain grasslands is still high, whereas it has dramatically decreased in lowland areas (MacDonald et al. 2000). When traditionally managed mountain grasslands below the tree line are abandoned, their floristic composition changes and their agricultural quality decreases, leading in the long term to reforestation and a significant reduction in biodiversity (Fischer & Wipf 2002). This development is difficult to reverse (Stampfli & Zeiter 2000), because of limited seed dispersal, recruitment and micro-site availability (Zobel & Zobel 2002). Intensification, in particular the application of fertiliser, has also been shown to decrease the species richness of mountain grasslands (Theodose & Bowman 1997; Nagy *et al.* 2003).

Figure 4: Typical pasture woodland from the Jura Mountains.

Wooded pastures are a particular form of semi-natural mountain grasslands (Figure 4). By combining typical forest and grasslands features they serve as refuge habitats for threatened species, because of their richness in vegetation types embedded into a dynamic forest-grassland mosaic and are therefore ecosystems of high conservation value (Olff & Ritchie 1998). Wooded pastures are inherent dynamic systems with progressive and regressive successions being driven by the grazing impacts of cattle. The landscape structure is a dynamic patch-mosaic of different successional stages between grassland and woodland (Olff *et al.* 1999). In mountain areas, these dynamics are very slow because of the longevity of trees and the harsh climate and consequently, the impact of management actions and climate change may be delayed for decades. Overall, livestock stocking rate and climate both directly influence the establishment of trees, their regeneration being a critical stage in grazed systems (Vandenberghe *et al.* 2006, 2007; Vandenberghe, Frelechoux & Buttler 2008; Vandenberghe *et al.* 2009) determining landscape structure in the long run.

In the Swiss Jura Mountains, but also in other regions such as the Vércors in France, pasture-woodlands represent a traditional form of semi-natural landscape (Dufour *et al.* 2006). They depend on multiple and extensive land use, including cattle stocking and logging, that are still practiced or have been practiced until recent times and create small scale mosaics. However, intensification of agriculture has generally resulted in landscape changes from small-grained heterogeneous patterns towards more monotonous and mono-functional landscapes (Brandt 2003). Particularly the multi-functional pasture-woodlands of Western Europe are threatened by a strong tendency towards segregation of land use, which leads to the spatial and functional isolation of large patches of intensively used grasslands from forests.

Mountains provide essential EGS both to people living in the mountains as well as to people living outside mountain areas (Grêt-Regamey, Walz & Bebi 2008). Moreover, they play an important role in the hydrological cycle, as they influence weather patterns and rainfall. Vegetation and soil store rainwater, regulate water drainage and feed the ground water table of lowland areas. As a consequence, mountains can be seen as the "undervalued ecological backbone of Europe" (EEA 2010).

2.2 Impacts of climate change

According to the fourth assessment report of the Intergovernmental Panel on Climate Change (IPCC 2007) the Earth's climate has warmed by about 0.74°C over the past century. Climate scenarios for the 21st century predict further warming, with a best estimate temperature rise of 4.0°C (likely range is 2.4°C to 6.4°C) for the high scenario A1FI (IPCC 2007). It has been suggested that these trends will be particularly pronounced at high latitudes altering snow cover, permafrost stability, growing season length, and productivity in arctic and boreal environments. Recent warming has already caused shifts in vascular plant communities in many cold regions of the world (see overviews in Post *et al.* 2009; Theurillat & Guisan 2001).

Global warming and related changes are expected to have equally a strong impact on high altitude ecosystems in the 21st century (IPCC 2007). In the European Alps, evidence of climatic change in the 20th century was an increase of 1.5° C in mean annual air temperature (Beniston 2006) accompanied by an increase in the maximum summer temperatures and precipitation decrease by 30% which leads to a marked increase in severe and prolonged droughts (Beniston 2009). Observed consequences are glacier retreat, decrease in snow-cover extent and earlier snowmelt (Beniston 2006). Throughout the 21th century, these trends will increase and temperate mountains of the northern hemisphere will experience an increase in the more intensive temperature with a heating rate typically two to three times higher (2.8° C to 5.3° C) than that recorded in the 20th century (Nogues-Bravo *et al.* 2007).

Future consequences of climate change in the European Alps under the hypothesis of an upward shift of the vegetation could be that the nival, alpine and subalpine belt are predicted to lose 81%, 63%, and 9% respectively of their surface to the lower belts with an predicted medium temperature rise of 3.3° Celsius. Moreover, within each belt, the proportion of areas harbouring steep slope will increase what will restrict even more the currently available surfaces for today's species (Theurillat & Guisan 2001) and increasing their vulnerability in the face of climate change (Guisan & Theurillat 2000). Based on these findings the reports of the IPCC have pointed mountain ecosystems as highly vulnerable to global climate change (IPCC 2007).

The capacity of mountain ecosystems to provide key services is therefore also at risk as high biodiversity assure high provision of EGS. Not only is global warming expected to have sudden critical impacts on terrestrial ecosystems in the coming decades (Malcolm *et al.* 2006), but so too are changes in political decision-making at different levels and in socio-economic boundary conditions, as they are driving rapid changes in land use. These transitions pose great ecological and societal challenges, including how to handle the impacts of changes in species performance and ecosystem functioning on the provision of EGS (Schröter *et al.* 2005; Metzger *et al.* 2006). It is anticipated these changes will have severe socio-economic implications and require the adaptation of social systems.

Studies on climate change concerning plant aboveground biomass, have reported different effects starting from an increase in annual herbaceous biomass production with warmer and drier climate (Bruelheide 2003; Sebastia 2007). Others (Harte & Shaw 1995; Zhang & Welker 1996), to the contrary, have observed no cumulative change in aboveground biomass. Drought alone has been found to exert a negative effect on plant biomass (Johnson *et al.* 2011). At the level of plant community composition, these studies fail to give a holistic picture on shifts in diversity resulting from a climate manipulation. Either graminoids or forbs have been shown to successfully dominate after a climatic perturbation. Opportunistic plants may be granted competitive advantage through advanced phenological development (Körner 2003), or through utilization of newly available nutrient resources (Bowman *et al.* 2006). Others may benefit from their inherent tolerance to specific environmental stress (Buchner & Neuner 2003). Overall, more fertile early-successional grassland communities have been shown as more responsive to climate warming and drought, compared to late successional ones, typically found in areas of low intensity management (Grime *et al.* 2000). Drought resistance and recovery potential of plant communities have also been attributed to high species richness (Van Ruijven & Berendse 2010), whereas grazing of highland pastures has been shown to both promote herbaceous richness and decrease evapotranspiration loss and thus water consumption (Spehn, Liberman & Körner 2006). In comparison to grasslands, forests exhibit a more conservative water use and hence cope better with long-lasting heat and drought stress (Teuling *et al.* 2010).

Litter and soil organic matter decomposition represent one of the major carbon fluxes from terrestrial ecosystems (Houghton 2007). Environmental conditions affect directly the rates of litter decomposition (Chapin *et al.* 1997) such that in cold environments, as the Alpine, ecosystems contain most of their carbon in the soil organic matter due to physiological constrains on the decomposers community (Körner 2003). Temperature apparently exerts a hierarchical control on litter decomposition, however soil moisture modulates its direct positive effect and often times causes contrasting directions of the response based on regional precipitation and evapotranspiration regimes (Aerts 2006). Furthermore, indirect climate effects on decomposition are mediated by the vegetation through its litter quality (Cornelissen *et al.* 2007) and its feedback on microclimate (Körner 2003). Concomitant changes in the soil microbial communities further affect the carbon cycle (Bardgett *et al.* 2013), thus exerting indirect climate effects on litter decomposition rates too (Allison *et al.* 2013).

In a changing climate, where mountain systems are said to experience a disproportionately higher increase in atmospheric temperatures (Nogues-Bravo *et al.* 2007), the coupling between land and atmosphere (Seneviratne *et al.* 2006) can induce positive feedbacks with far reaching implications for future terrestrial carbon cycling and litter decomposition in particular. Reports on confounding effects of soil moisture on the response of litter decomposition to climate warming come from both the Arctic (Robinson 2002) and the Alpine (Gavazov 2010), hence the relative importance of temperature and moisture remain hard to disentangle. Considering the dual role of soil moisture regime as both a result and a cause for rise in atmospheric temperatures (Mueller & Seneviratne 2012) one should investigate the effect of these environmental parameters on litter decomposition in concert.

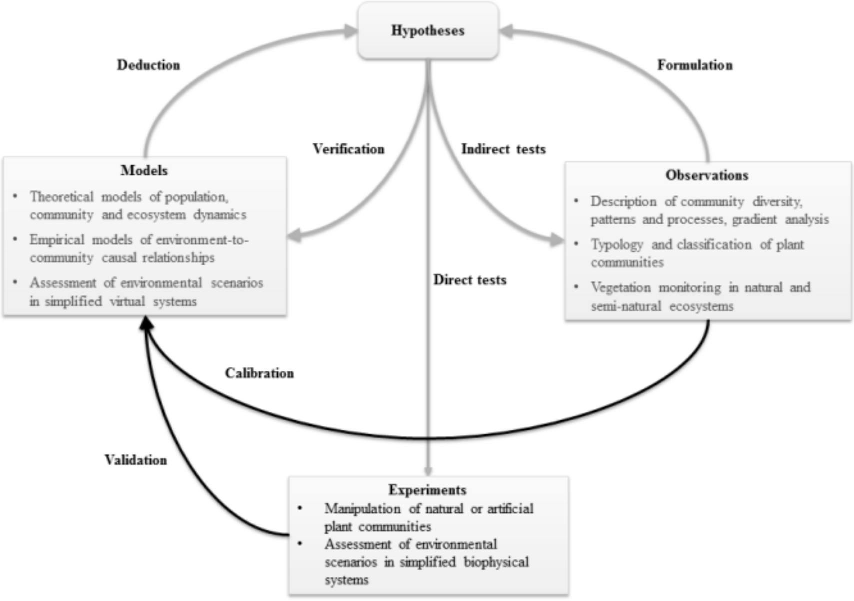


Figure 5: The methodological triad and its application to plant community ecology. Figure following Spiegelberger et al. 2012

The study of climate change can be best approached by combining observations and experiments, as both are strengthened when reconciled (Sagarin & Pauchard 2010) and extended to mathematical models (Reyer *et al.* 2013). The methodological triad (Figure 5) conceptualises the complementarity of the three approaches and shows their interplay (Spiegelberger *et al.* 2012). The ideal way to study ecological communities and interactions is to observe patterns in nature, which allows for the formulation of hypotheses that are focused on a number of factors of potentially high importance as drivers of the patterns observed. Hypotheses can either be formulated based on observations in the field or - if already existing - on models. These hypotheses can then be tested with empirical explanatory models, either directly by manipulative experiments or indirectly by targeted observations for example along altitudinal gradients.

2.2.1 Studies along altitudinal gradients

Mountains have as common element their steepness (slope angle to the horizontal) (Körner *et al.* 2011). Their steepness shaped by gravity altitudinal gradients which are among the most powerful "natural experiments" for testing ecological responses to geophysical influences, such as changes in temperature and precipitation patterns (Körner 2007). Such elevation gradients can be used as surrogates for climate change driven changes (Körner 2007) avoiding - due to their short latitudinal gradient - confounding effects linked to features such as land use history, differences in soil depth or initial substrate (Beier *et al.* 2012).

Such a short horizontal but steep vertical gradient exist in a permafrost scree next to La Plagne in the Hauts de Chartreuse Nature Reserve, France. Despite being situated in the montane belt, such screes which can be found in many European mountains present distinctive features that would allow classifying them into the alpine zone. The cold microclimatic conditions of the site provide microhabitats with very thick raw humus colonized by many cold living plants and a particular soil fauna. These small-scale habitats which are older than the surrounding biological matrix act as refugia and support communities unable to survive elsewhere in the landscape. Such paleorefugia are expected to be particularly vulnerable to changes in their environmental conditions in particular to climate warming (Nekola 1999; Noss 2001), and may therefore provide a sensitive indicator of climate change processes.

Based on observations done by N. Cassagne, a post-doc at Irstea with whom I collaborated, we used this unique opportunity offered by the La Plagne scree to assess the long-term effect of a temperature increase similar to the predictions of the IPCC climate scenario A1FI on the humus form and the soil fauna (Cassagne *et al.* 2008). In contrast to most other field studies where the effects of global warming are simulated over a limited number of years (Sjursen, Michelsen & Jonasson 2005; Aerts 2006), climatic conditions are similar at La Plagne scree since many centuries. A soil temperature by about 3.8 °C higher in the warmer plots covered by a dense pin forest led over time to a remarkable change in the soil faunal composition favouring in particular Oribatid mites. To date, differences in the pedofaunal community composition did not alter the humus form which may be explained by the extraordinary complexity of biotic soil interactions and the high functional redundancy of the soil fauna.

Our work is among the first which details the ecological components of the alpine ecosystems developed on frozen screes and confirm the importance of spatial and temporal scales in ecosystem response to environmental changes. In conclusion, works on these alpine enclaves could help to predict the effects of changes in soil temperature on the alpine belt and to measure the magnitude of induced process shifts, such as faunal response.

In the Mountland project, my colleagues from the EPFL and I used an altitudinal gradient covering about 1000 elevation meters on a horizontal distance of about 19 km, spanning from Lake Geneva to the first Jura mountain summits in the Western part of Switzerland (Figure 6). This project allowed us to assess both, impacts of climate change and of land use change at different spatial and temporal resolutions. Here I will only focus on the consequences of climate change while findings on land use changes will be reported in chapter 2.3 and combined effects of climate and land use change in chapter 2.4.

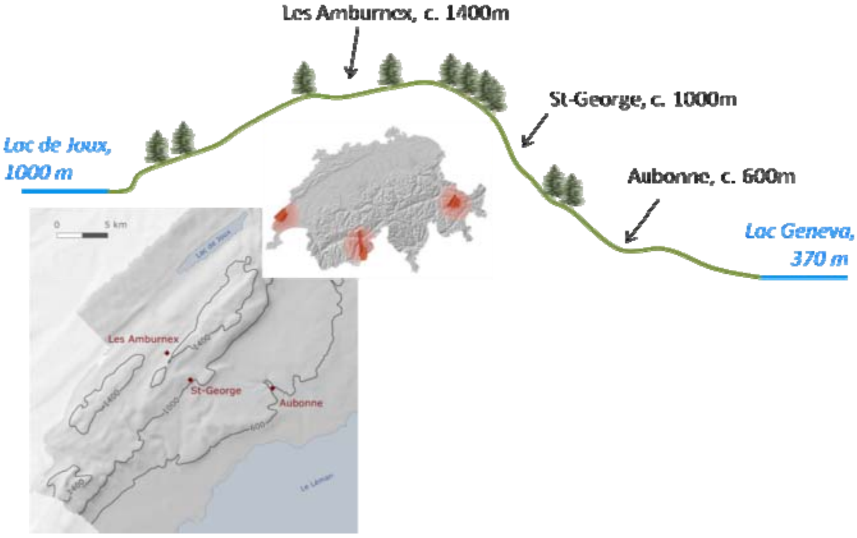


Figure 6: The Mountland Jura Transect and the altitudes of the study sites. Situation within Switzerland is indicated in the small map.

Soil monolith transplantation from high to low altitudes has been shown to effectively simulate warmer climate in various studies (Ineson *et al.* 1998; Hart & Perry 1999; Olofsson 2001; Link *et al.* 2003). It provides a natural year-round experimental warming, which also accounts for associated changes in precipitation, snow-to-rain ratio, snowmelt, and length of the vegetation season. Therefore transplantation experiments along natural climatic gradients offer a powerful method for testing hypotheses about how species and communities are affected by future climatic changes. Although there are relatively few published studies using this technique, some successful attempts have been carried out in contrasting terrestrial environments: in peatlands (Wieder & Yavitt 1994; Breeuwer *et al.* 2010), in montane meadows (Bruelheide 2003), in subalpine grasslands (Sebastia 2007), and in alpine vegetation (Scheepens, Frei & Stocklin 2010). Their interpretation allows a more mechanistic understanding of primary ecological processes occurring along such gradients.

Figure 7: View of the local transplantation site at Col du Marchairuz. Photo by K. Gavazov.

To asses effects of climate change in Mountland, we chose to transplant turfs of mountain pastures in 2009 from the initial donor site in Combe des Amburnex at 1 350 m to four recipient sites (Figure 6): the disturbance control at 1 350 m (Marchairuz, Figure 7), and the downslope sites at 1 010 m (St George), 570 m (Arboretum d'Aubonne) and 395 m (Bois Chamblard). The first site at 1 350 m served as a transplantation control site, with a mean annual rainfall of ca. 1 750 mm including more than 450 mm of snow, and a mean annual temperature of 4.5 °C. The other two sites were chosen to represent a combination of an annual temperature increase of +2 K and a precipitation decrease of −20 % at 1 010 m (referred to as the +2 K scenario hereon), and of +4 K and −40 % at 570 m (referred to as the +4 K scenario hereon). The temperature increments were chosen in accordance with the moderate A1B and the intensive A2 climate change scenarios outlined by the 2007 IPCC report and the predicted concurrent decrease in precipitation for temperate regions (CH2011 2011).

Each mesocosm contained one of the following three land use types: a densely wooded (DW) pasture, a sparsely wooded (SW) pasture, or an unwooded (UW) pasture. This order reflects diminishing canopy cover of the dominant tree species *Picea abies* due to increasing intensity of pasture management. Unwooded pasture vegetation has a higher herbaceous productivity than its wooded pasture counterparts, and is characterized by a higher frequency of graminoids. Both wooded pasture types, in contrast, have higher frequencies of forbs. The three land use types have a similar vascular plant diversity of ca. 30 species m^{-2}.

At each site, 15 mesocosms (i.e., five replicates of each land use type) were transplanted to a common garden according to a completely randomized design. A more detailed description of the sites, material and methods can be find elsewhere (e. g. Gavazov *et al.* 2013, 2014a; Mills *et al.* 2014).

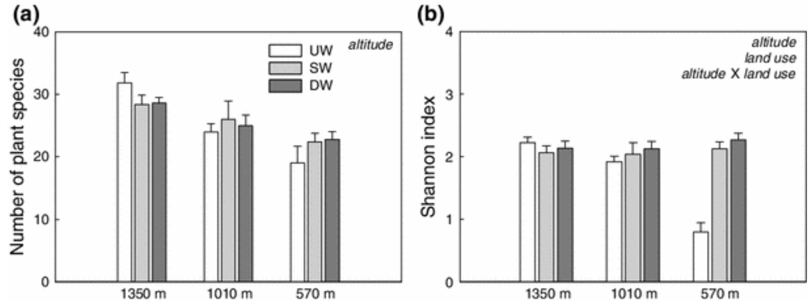


Figure 8: a) Plant species richness and b) Shannon diversity for the vegetation communities in the three land use types: unwooded pasture (UW), sparsely wooded pasture (SW), and densely wooded pasture (DW). Significant (P < 0.05) factors (in italics) and interactions (marked with an X) are shown for each response variable. Figure from Gavazov et al. (2014b).

This experiment, done largely in collaboration with my PhD-student K. Gavazov and two post-docs (A. Peringer and R. Mills), allowed us to show that these temperate subalpine pastures have in terms of productivity and plant diversity a resistance potential at moderate levels of climate change (+2 K scenario). The observed negative impact of the high level of climate change (+4 K scenario) was strongest in the intensively managed unwooded pasture system and only minimal in the extensively used sparsely and densely wooded pastures. This was visible for the plant species richness as well as for the diversity: plant communities that were transplanted in mesocosms to the warmer and drier climate experienced a marked loss in species richness (Figure 8) going up to 30 % at both transplantation altitudes, 1 010 m and 570 m, compared to the control site at 1 350 m. Similarly, total herbaceous biomass across all three land use types decreased to 45 % of that of the control site especially, when there was now shade (UW in Figure 9). This indicates that the pasture-woodlands of the Jura Mountains are internally buffered to moderate climate perturbations, and that stronger impacts of climate change in the future can be circumvented through sustainable land use and by preserving the diversity of the landscape (Gavazov *et al.* 2014c).

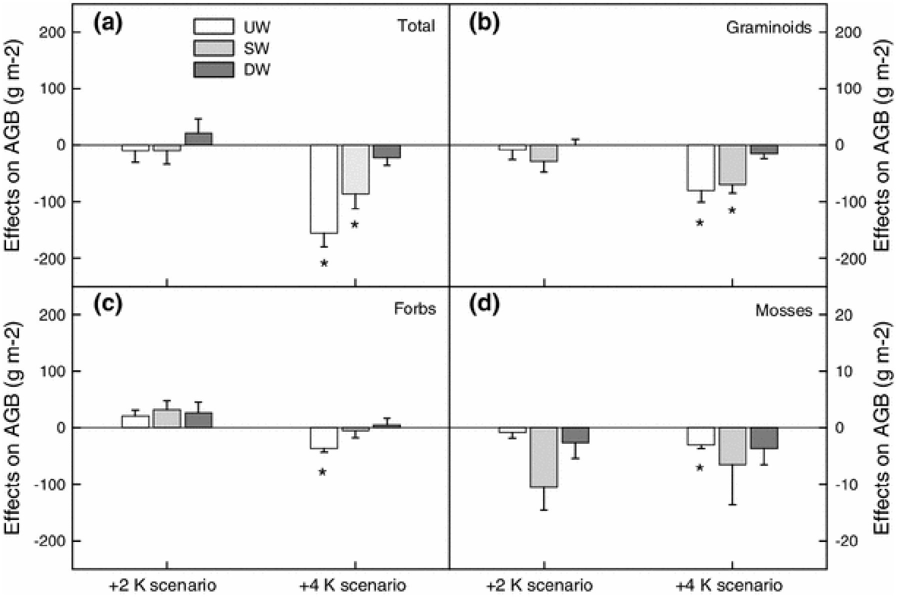


Figure 9: Effect of transplantation to a warmer and drier climate at 1 010 m (+2 K scenario) and 570 m (+4 K scenario) on aboveground biomass (AGB) production. Data presented in the plots are for a) the total biomass and the biomasses of b) graminoids, c) forbs, and d) mosses (y-axis scale varies). The three land-use types are: unwooded (UW), sparsely wooded (SW), and densely wooded (DW) pastures. Asterisks indicate significant differences (P < 0.05) from controls at 1 350 m. Figure from Gavazov et al. (2014b).

From a below-ground perspective, transplantation significantly increased soil temperature and decrease soil moisture compared to reference transplantation at 1 350 m (Figure 10). This combined effect lead to a significantly lower soil respiration at the transplanted sites in the field (Mills *et al.* 2014), but also a lower δ13C rate in unwooded compared to wooded plots (Gavazov *et al.* 2014c). We further assessed a significant and overriding effect of moisture on soil respiration and its temperature response *in situ* in the pasture system (only open pasture plot were used in the study). However, under controlled conditions with the soil moisture effect being level out by watering soil samples to field capacity, respiration responses were site and temperature dependant. We concluded from those observations that the climate manipulations have affected the decomposer community response to temperature in terms of the magnitude of the flux, but not its intrinsic temperature sensitivity under standardised conditions. This highlights the resilience of the microbial community to extreme climatic change, but reinforces the reduction in the capacity to respond, and the consequences thereof for mineralisation processes and soil function.

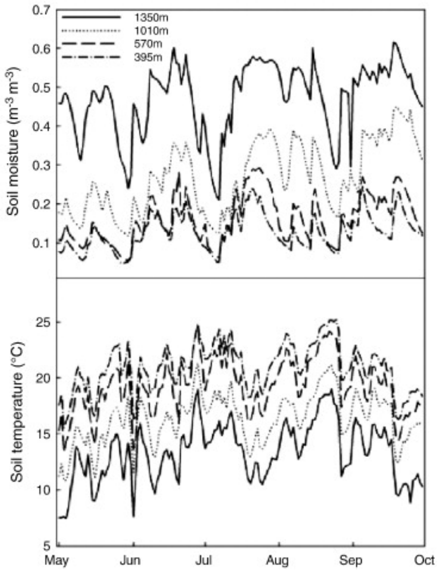


Figure 10: Daily mean soil moisture and temperature across the study period (May–September 2011) for the four study sites with elevation shown in metres above sea level. Figure from Mills et al. (2014b).

These findings were confirmed by a decomposition experiment on the Mountland sites, where we followed decomposition of a standard litter type—senescent leaves of *Fagus sylvatica* collected from a single location over 2.5 years (Gavazov *et al.* 2014b). Decomposition in the drier unwooded pasture mesocosms increased with altitude, likely because of higher moisture at the highest sites. Decomposition in the more mesic mesocosms from sparsely and densely wooded sites was insensitive to altitude, suggesting an overriding moisture, rather than temperature, constraint on decomposition across these sites (Figure 11). The functional composition of decomposer microbial communities (fungal/bacterial ratio) was

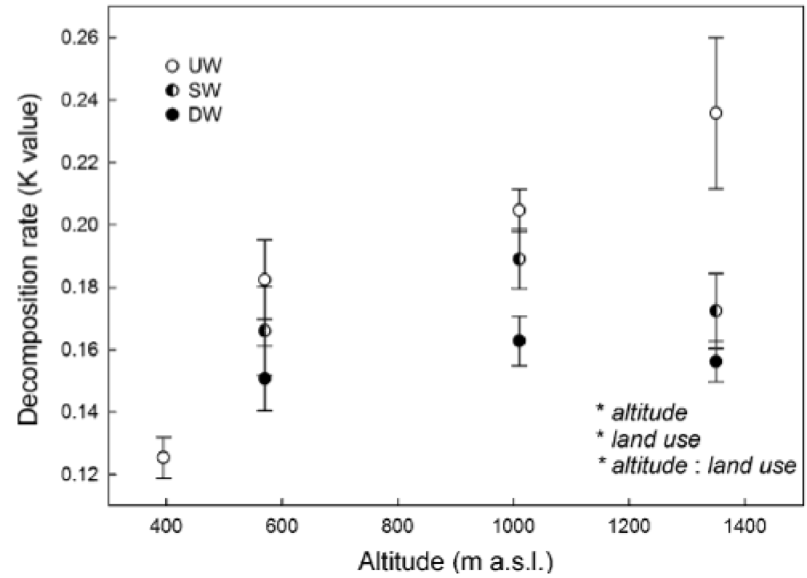


Figure 11: Leaf litter decomposition rates (K values) of *Fagus sylvatica* along an altitudinal gradient with mesocosms from three land-use types: unwooded pasture (UW), sparsely wooded pasture (SW), and densely wooded pasture (DW). Presented are mean values and standard errors for five replicate plots. Asterisks indicate significant effects of the specified factors. Figure from Gavazov et al. (2014b).

similarly insensitive to altitude. These findings add substantial evidence for the controlling role of soil moisture on litter decomposition, as well as for the indirect effects of climate through changes in the decomposer community.

Initial observations on changes in the quantity and quality of the SOM-light fraction indicate that accumulations of unprotected organic matter may lead to a greater C and N source for decomposer communities during the winter, therefore potentially shifting a large proportion of the annual C and N budget outside of the growing season. The consequences of reduced function during the growing season carry negative implications for the sustainability of productivity in pasture systems, especially if limiting nutrients are only slowly returned to available pools. Whilst our results do not imply an increase in the losses of C as a function of climate change, a reduction in soil function will alter the storage capacity of C and macronutrients, which in the longer term will inevitably erode the stocks of C and N from organic matter (Mills *et al.* 2014).

We therefore investigate more on the understanding of the seasonal dynamics of nutrient cycling (Gavazov *et al.* 2014a). Observation during winter show that naturally occurring warmer average winter temperatures resulted in thinner and inconsistent snow cover, which promoted soil frost and large diurnal temperature amplitudes. These exerted strong negative effects on soil microbial biomass and respiration rates during the winter. Considering we found below-snow CO_2-efflux to be of greater magnitude than that during the growing season, we conclude that a reduction in microbial activity due to climate warming may impede organic matter turnover and nutrient cycling in these subalpine pasture systems, with broad implications for ecosystem scale processes (Gavazov *et al.* 2014a). The results presented indicate a thermal decoupling of soil respiration under the snow, which is of general interest for the modelling of CO_2 worldwide.

Year-around measurements of soil enzymatic activity brought further evidence of for seasonal changes in soil carbon utilisation (Puissant *et al.* 2014). After four years of transplantations, we measured microbial biomass (MB), microbial community structure (MCS), and soil extracellular enzymatic activities (EEA) of nine hydrolytic and oxidative extracellular enzymes in the transplanted soils on a seasonal basis. We found a strong seasonal sampling date effect and a smaller but significant effect of the climate manipulation (soil transplantation) on EEA. Overall EEA was higher in winter and spring but enzymes linked to N and P cycles showed higher potential activities in autumn, suggesting that other factors than soil microclimate controlled their pool size, such as substrate availability.

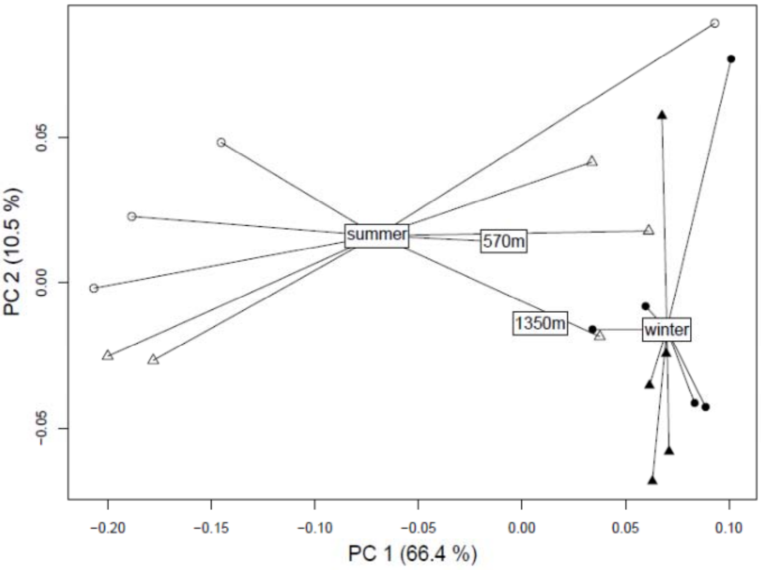


Figure 12: Redundancy analysis (RDA) of EEA (dry soil mass basis) using microbial biomass (MB), microbial community structure (PC 1; PC 2), SOC and C/N as constraining variables. Triangle = control site (1350 m a.s.l.), circle = lowest site (570 m a.s.l.); filled in = winter, empty = summer. Gray arrows and black arrows represent non-significant and significant explanatory variables, respectively ($p<0.05$).

The climate manipulation decreased EEA in most cases, with oxidative enzymes more concerned than hydrolytic enzymes. In contrast to EEA, soil MB was more affected by the climate manipulation than by the seasons. Transplanting soils to lower altitudes caused a significant decrease in soil MB, but did not affect soil MCS. Conversely, a clear shift in soil MCS was observed between winter and summer. Mass-specific soil EEA (EEA normalized by MB) showed a systematic seasonal trend, with a higher ratio in winter than in summer, suggesting that the seasonal shift in MCS is accompanied by a change in their activities (Figure 12). Surprisingly, we observed a significant decrease in soil organic carbon concentration after four years of soil transplantation, as compared to the control site, which could not be linked to any microbial data. We conclude that four years warming and decreased precipitation strongly affected MB and EEA but not MCS in subalpine grassland soils, and that those shifts cannot be readily linked to the dynamics of soil carbon concentration under climate change (Puissant *et al.* 2014).

2.2.2 Drought experiments

Extreme weather events are projected to increase in magnitude and in frequency due to climate change (IPCC 2007), calling for a shift from "trend-focused" to "event-focused" climate change experiments (Jentsch, Kreyling & Beierkuhnlein 2007). Plants, as sessile organisms, are likely to be particularly exposed to an increasing frequency of extreme events. Understanding the mechanisms that underlie the response of plant communities which are on the base of the trophic cascade to such extreme weather episodes is a major challenge for predicting climate change effects on biodiversity (Smith 2011).

Besides the increase in the average temperature, the increase of droughts is a second phenomenon predicted for mountains worldwide (Beniston 2003). For Central Europe, extreme summer droughts are expected to be among the main consequences of climate change: the occurrence of dry summers droughts, comparable in severity to the summer drought in 2003, may represent the norm by the end of the 21st century in which precipitation deficits might reach 70% in extreme years (Calanca 2007). For France, the number of summer heat waves will increase by about 1/3 for the future (2080 to 2099), as well as their duration which will last about 14 days in the future compared to about 10 days in the period 1961-1990 (Meehl & Tebaldi 2004).

Given the key role of climate to vegetation distribution, a majority of scholars agree that extreme climatic events will induce vegetation shifts. However, it is also possible that no vegetation shift occurs after extreme climatic events due to site quality, variations in species and individual responses (tolerance, plasticity, and phenotypic variability), taxonomic and functional diversity, and biotic interactions such as facilitation or lowered competition leading to a high resilience of ecosystems to droughts (Lloret *et al.* 2012).

Figure 13: Rain-out shelter in a subalpine mountain grassland in the Vercors. Photo: V. Jung

Based in the results from the Mountland study indicating temperature sensivity at 1350 m, but soil moisture limitation at lower altitude, we studied in collaboration with my postdoc V. Jung in an experimental approach one of the mechanisms that could explain the resilience of grasslands to droughts: intraspecific variability of functional traits (Jung *et al.* 2014). We analysed the short-term functional response of subalpine grassland communities to a simulated drought by focusing on four leaf traits (LDMC: leaf dry matter content, SLA: specific leaf area, LNC: leaf nitrogen concentration, LCC: leaf carbon concentration). We therefore set up four rain shelters (Figure 13) in a species-rich subalpine grassland vegetation in the Vercors Mountains and intercepted rain fall during five weeks, corresponding to a rainfall deficit of 115 mm (62 %) from the June-July average rainfall (based on the 1952-2009 data from Meteo-France). Control plots were watered twice a week following the local June-July average rainfall. Plant species were recorded twice, immediately before and after the drought event using the "point-quadrat" sampling method. Leaf traits were measured in each plot for the most abundant species with standard protocols (Cornelissen *et al.* 2003).

After evaluating species turnover and intraspecific variability separately, we determined their relative contribution in the community functional response to drought, reflected by changes in community weighted mean traits. We found significant species turnover and intraspecific variability, as well as significant changes in community weighted mean for most of traits. The relative contribution of intraspecific variability was more important (42 – 99 %) than the relative contribution of species turnover (1 – 58 %). Intraspecific variability either amplified (for LDMC, SLA and LCC) or dampened (for LNC) the community functional response mediated by species turnover (Figure 14). We demonstrated that the small contribution of species turnover to the changes in community mean LDMC and LCC was explained by a lack of covariation between species turnover and interspecific trait differences. These results highlight the

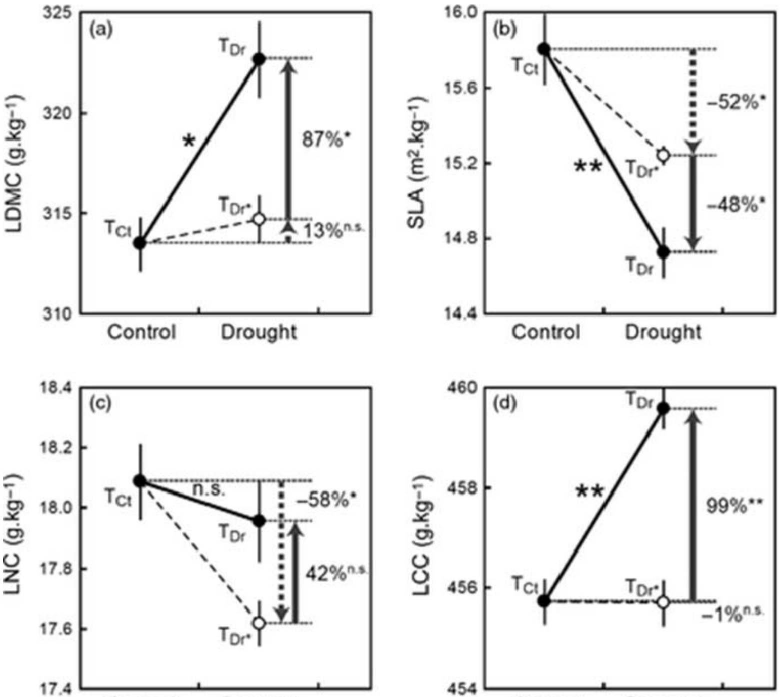


Figure 14: Changes in community-weighted mean trait values due to both species turnover and intraspecific variability (solid line) and due to species turnover only (dashed line). TCt and TDr correspond to the observed community mean traits in control plots and in drought plots; TDr* corresponds to the community mean trait in drought plots recalculated from trait values measured in control plots. Data are means ± standard errors of community means of LDMC (a), SLA (b), LNC (c) and LCC (d). Arrows indicate the contributions of species turnover (CTurn; dashed line arrows) and of intraspecific variability (CIntra; solid line arrows) to the changes in community mean traits. CTurn and CIntra are expressed as percentages of their cumulative magnitude (Significance levels: *P < 0.05, **P < 0.01, n.s. not significant). Figure from Jung et al. (2014).

need for a better consideration of intraspecific variability to understand and predict the effect of climate change on plant communities. While both species turnover and intraspecific variability can be expected following an extreme drought, we report new evidence that intraspecific variability can be a more important driver of the sort-term functional response of plant communities. This indicates that vegetation can adapt quickly by its intra-specific variability, as species-rich communities such as the grasslands under study are most often rich in plant functional traits.

In a further step, we crossed in a second drought experiment in collaboration with my former Master student C. Deléglise, now at Agroscope Changins, CH, reduced precipitation with real grazing by sheep (Figure 15). Simulating grazing by clipping or mowing as widely applied in other experiments (Mariotte *et al.* 2013b) does not represented mechanisms correctly compared to grazers. We therefore aimed at predicting the effects of drought on the vegetation of temperate grasslands when grazed with real animals, which has, as far as we know, never been investigated and this despite the fact that cattle grazing is the main grassland management worldwide (WallisDeVries, Bakker & Van Wieren 1998). In many cases grazing is simulated trough cuttings, which are rarely applied in a selective manner, but for reasons of feasibility applied uniformly to the spot under study. However, grazing animals have feeding preferences due to their anatomy and their nutritional requirements. Moreover, through defoliation, dejections, and trampling, grazing can have positive or negative interactions with above and below-ground components of grassland ecosystems (Kohler *et al.* 2006) and impact the spatial structure of the vegetation in various ways (Adler, Raff & Lauenroth 2001). In addition, numerous are the regions which are usually intensively grazed in a rotational systems which triggers a much more frequent utilization than under traditional mowing as

Figure 15: Pair of sheep grazing under a rain-out shelter during the simulated drought. Photo: C. Deléglise.

illustrated for the Jura Mountains (Jeangros & Scehovic 1996). While in general frequent grazing reduces the annual dry matter production, repeated defoliation forces plants into an active growing and tillering phase instead of maturing naturally which leads to a higher nutritive value to the forage (Bruinenberg *et al.* 2002). It is therefore likely that grazing influences the response of the vegetation to drought to another extent than mowing.

Similarly to other drought experiments, we observed strong negative drought effects on forage production and, to a lesser extent, on the nutritive value of the forage with sheep grazing being more constraining than mowing (Deléglise *et al.* 2014). Changes in community weighted-mean traits (e.g. decrease in specific leaf area) accompanied these shifts, attesting for a decline in plant growth rates and an investment in structural tissue by plants, whereas species composition remained rather stable (Figure 16). Recurrent defoliation due to grazing and associated less leaf area remaining maintained vegetation in an early regrowth stadium more sensitive to water stress.

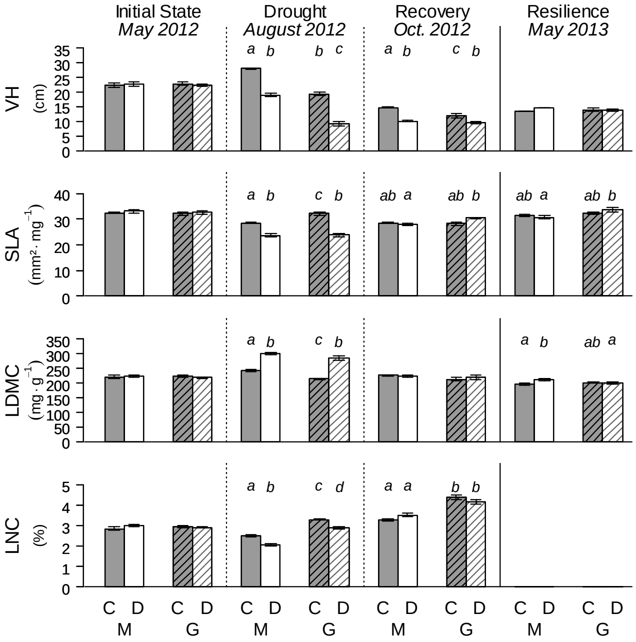


Figure 16: Community weighted mean traits in control (C) and drought (D) conditions in the mowing (M) and grazing (G) managements at four periods. VH: vegetative height; SLA: specific leaf area; LDMC: leaf dry matter content; LNC: leaf nitrogen content. Bars are means ± SE (n=4). Within each period, significant differences between treatments are indicated by different letters above bars ($P < 0.05$, Tukey's post-hoc tests). Figure from Deléglise et al. (2014)

During the recovery phase after cessation of the drought, management effects remained visible, but resilience was observed for both managements in spring of the following year. Our results suggest that grazing increases drought effects, but reversible trait variation ensure stability of grasslands after a short-term drought event, i.e. preventing long lasting shifts in species and trait composition, and therefore in forage production, even under a fairly intensive management.

To go further from these two experiments, we also collected root samples from common plant species which are currently under study for assessing their mycorrhizal infestation rates. I wish to explore the consequences of two aspects of climate change (higher frequency in drought recurrence and increased temperature) on the interactions between plants and soil with a particular attention on the relationship between plants and mycorrhizal fungi (AMF). However, there could be a trade-off between positive (higher temperature at lower altitude increases mycorrhizal hyphae length and thus soil volume explored by AMF) and negative effects (increased drought frequency reduces AMF colonization rates of roots) due to climate change. Following these changes, I hypothesize that the interactions between plants and AMF slide towards the parasitic part of the mutualism-parasitism continuum at intermediate altitudes and towards the mutualistic part at lower altitudes due to drought stress (Figure 17). This hypothesis is currently explored by my PhD student Anne-Lena Wahl.

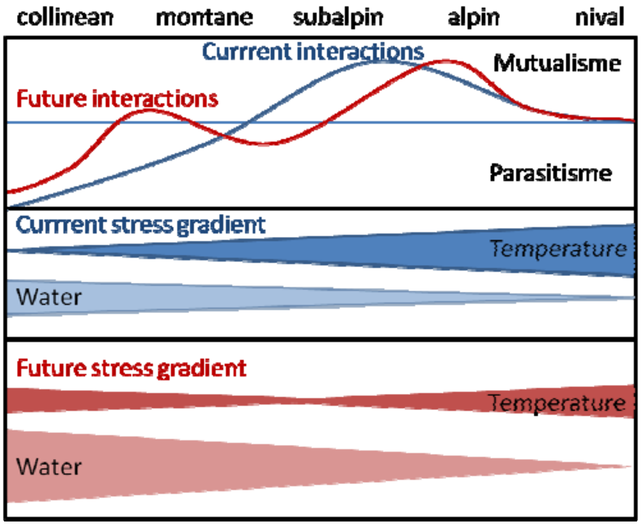


Figure 17: Current (blue) and future interactions between plants and mycorrhizae at different altitudinal zones due to thermal and water stress.

Conclusion

I showed with the works presented in that chapter that subalpine and montane ecosystems are resistant against increase in temperature until a threshold which is situated in our case between +2 K et +4. I further demonstrated that collinean ecosystems are more water limited concerning soil functioning, but that vegetation at this altitudinal belt absorbs temporal decrease in water availability by intraspecific variability.

2.3 Consequences of land use changes

In Europe, grassland biodiversity has declined dramatically in the lowland due to agricultural intensification, while in many mountain areas grasslands are still managed in a traditional way (MacDonald *et al.* 2000). Semi-natural mountain grasslands are widespread components of north-temperate landscapes and play an important role by providing fodder for livestock and acting as reservoirs for both carbon (Follett & Reed 2010) and biodiversity (Mariotte *et al.* 2013c). These ecosystems host species-rich communities with up to 40 plant species per square metre but are among the most endangered ecosystems in Europe, threatened by both climate (Mariotte *et al.* 2013b) and land use change (Fava *et al.* 2010). Changes in agricultural practices may lead to land use changes, which have been accelerated since the 1950 in Central Europe. Land use changes may be triggered by simple adaptations to currents managements (decreasing mowing intensification from 2 cuts per year to 1cut/year, adding fertiliser to increase biomass productivity, increasing cattle density per land unit, etc.) or by radical shifts as fallowing or transformation from haymeadows to pastures. At present, the intensification of easily accessible sites and in parallel abandonment of less accessible sites in the European Alps (Tasser, Mader & Tappeiner 2003) and in the Jura (Chételat *et al.* 2013) became a reality.

Land use changes can act at different spatial scales. One of the most evident impacts because easily visible is the complete or gradual abandonment of an agricultural field which I qualify as changes at the "landscape scale". However, as plant community structure (species diversity and composition) is largely the result of management (e. g. regular grazing) of seminatural grasslands, land use changes are likely to modify this structure and, as a consequence, perturb community stability and ecosystem functioning which in general acts at smaller spatial scale, which I call "local scale".

Accordingly, I'll present my scientific contributions in two chapters: a first which focuses on the small scale impacts resulting from the adaptation of current management where I priviledged an observational or experimental approach and in a second chapter where models were used to asses impacts of land use change on the landscape level.

2.3.1 Local impacts on vegetation and its interaction with soil

While intensive forms of land use are essential for humans to obtain natural products such as food and fibre, they have contributed to the transformation of ecosystem patterns and processes (Foley *et al.* 2005). In particular, human activities have altered the rate, pathways and efficiency of the movement of nutrients within and between the various biotic or abiotic ecosystem compartments. These changes in nutrient cycles do not only affect today's ecosystem functioning but may also result in long-term legacy effects on ecosystem processes, thereby changing the resilience of ecosystems and their adaptive capacity to sustain ecosystem services in the face of uncertainty and global change (Folke *et al.* 2002; Elmqvist *et al.* 2003; Carpenter *et al.* 2009).

Nutrient manipulations trough soil amendments (lime, fertiliser, carbon)

So far, most emphasis in terms of terrestrial nutrient cycling has been put on carbon (C), nitrogen (N) and phosphorus (P), because of their key roles in primary production and climate regulation (Galloway *et al.* 2008). For example, the effects of continuous fertilization of grasslands (Wedin & Tilman 1996; Stevens *et al.* 2004; Suding *et al.* 2005; Silvertown *et al.* 2006), and to some extent also the changes after cessation of fertilization (Spiegelberger *et al.* 2006a; Hrevusova *et al.* 2009; Pierik *et al.* 2011), have been well documented. Less well understood are the short-term and long-term effects on ecosystem patterns and processes of the addition of elements other than C, N or P, although they are also known to affect ecosystem functioning.

Calcium (Ca) is a key base cation in the soil influencing various physiological and structural processes both in animals and plants (McLaughlin & Wimmer 1999). Ca is a component of the soil buffering system, as $CaCO3^{-}$ and $HCO3^{-}$ are important sinks for protons with a high buffering rate and consequently affects soil pH and all major soil processes that are modulated by soil pH. Furthermore, Ca as a bivalent cation with a rather strong sorption capacity is very effective in binding to soil particles, thereby increasing aggregate formation in soils and improving soil structure significantly, and an important early indicator of disturbance of nutrient cycling in terrestrial ecosystems (McLaughlin & Wimmer 1999). Large amounts of lime are applied to croplands, pastures and forests in many regions of the world (Jandl, Alewell & Prietzel 2004; Isselstein, Jeangros & Pavlu 2005; West & McBride 2005), and they are expected to further increase globally due to the expansion of intensive land use practices (Tilman *et al.* 2001). While liming can improve plant health in naturally or anthropogenically acidified soils (Shortle & Smith 1988; Alewell *et al.* 2000), it may also contribute to the loss of rare and threatened species (Tilman *et al.* 1994; Isselstein *et al.* 2005; Spiegelberger *et al.* 2006a) and is discussed controversially as either decreasing (Hamilton *et al.* 2007) or increasing the CO_2 sink capacity of soils (Fornara *et al.* 2011). Processes that influence Ca availability are therefore highly relevant to ecosystem regulation and management (Shortle & Smith 1988; Schaberg, DeHayes & Hawley 2001; Fornara *et al.* 2011).

In several publications, I show that liming can have a significant impact and a long lasting effect on the vegetation (Spiegelberger *et al.* 2006a, 2010), but also on the soil micro-organisms and nutrient cycling (Spiegelberger *et al.* 2006a, 2010; Schaffner *et al.* 2012) which I'll explain more in detail in the following paragraphs.

By revisiting an experiment (Figure 18) setup in the early 1930ies on the Schynige Platte (Switzerland), I revealed together with colleagues that more than 70 years after the last addition of lime, the effects of liming performed for only four years were still visible in the composition of the vegetation on the limed plots (Spiegelberger *et al.* 2006a), but also in the recycling of carbonates (Schaffner *et al.* 2012). Similar results were found by my master student, C. Deléglise, on plots in the Beaufortin (France) where 14 years after the last lime application, soil pH was still significantly higher on the limed plots (Spiegelberger *et al.* 2010). I conclude that only a few years use change can significantly influence vegetation composition and lead to a significant change in nutrient cycling in the meadow.


Figure 18: Photo of the set-up of experimental plots next to the Alpine Botanical Garden at Schynige Platte (in the back). Plots are temporally marked with yellow tap during the vegetation relevées done in 2003.

Our results indicate that a significant amount of the added Ca is still present in the top soil layer and in the vegetation more than 70 years after the last liming treatment. Little is known about the migration velocity of Ca in the soil, assuming Ca to have a similar migration pattern as strontium (Bossew *et al.* 2004), the major fraction of Ca should not have migrated more than 14 cm in depth. Of the added Ca still stored in the soil only 15% was found in the exchangeable Ca-fraction. The latter is noteworthy, because this implies that the major part of the Ca is, either organically or as a mineral non-exchangeable fraction, bound in the soil. However, observed differences in vegetation between limed and unlimed plots are nevertheless likely to be related to differences in Ca.

There are two possible explanations for the long-term effects of liming: 1) liming induced a general shift towards a higher nutritional level of the soil resulting in a relatively stable new state for the whole ecosystem (considering that the effects of 2–4 years of liming are still visible after more than 70 years), or 2) the added Ca is stored in stable "permanent" forms and thus not easily leached from the soil. Even though the soil pH is still enhanced in limed plots (Spiegelberger *et al.* 2006a), no effect was observed on the other macro-nutrients (Mg, P, N, K). Thus, our data do not provide evidence that the whole system shifted towards a state of higher nutritional status. Rather, our findings suggest that long-term storage of the added Ca in relatively stable soil pools is responsible for the long-term legacy effect of single liming events on this subalpine ecosystem. As already observed by Lüdi (1959) liming favoured plant species that have high rates of nutrient acquisition and high relative growth rates. We propose that a significant amount of lime that was applied in the 1930 was incorporated in plant or microbial biomass. The dead, Ca-enriched biomass that remained in the field was then incorporated into the soil organic matter pool, thereby increasing the Ca fraction that was more permanently bound. Since mountain grasslands can, despite the dominance of perennial species, undergo relatively rapid species turnover at small scales (Herben *et al.* 1993), we propose that the current plant species composition is still affected by the altered soil Ca levels in limed plots. This implies that the more permanently bound Ca fractions are available to plants and/or microorganisms, or are affected by longer term weathering.

The exchangeable cation pool in soils is a very old concept in soil science dating from the beginning of the 20th century (Ross, Matschonat & Skyllberg 2008). Several studies have challenged the concept and asked for a redefinition considering (i) organically bound nutrient cations, especially in acid soils (Ross *et al.* 2008), and/or (ii) the existence of pools available to plant and microorganisms other than the "exchangeable pool" (van Breemen, Lundstrom & Jongmans 2000; Jandl *et al.* 2004). It has been suggested, that Ca can be made directly available from rocks, most likely via mycorrhizal fungi, which are able to dissolve Ca from Ca feldspars and apatite (van Breemen *et al.* 2000; Blum *et al.* 2002). Hence, plants with their symbiotic fungi in the limed plots might be able to take up Ca from non-exchangeable pools in the soil, thereby refilling the exchangeable Ca pool, or they use Ca from the exchangeable pool that is continuously refilled through weathering/decomposition of the Ca enriched 'non-exchangeable fraction'.

Our study provides unique experimental evidence of the long-term memory of subalpine soils to single events of liming. Despite the small size of the experimental plots and the continuous removal of the above-ground biomass, the Ca-concentration in all ecosystem compartments investigated differed between plots that were limed in the 1930s and unlimed plots, and these patterns continue to affect ecosystem processes.

While the increase in primary production by the legacy of the liming treatment may be considered beneficial from an economic point of view, it has detrimental effects on biodiversity since it led to a replacement of rare species by ubiquitous species adapted to increased nutrient availability (Spiegelberger *et al.* 2006a). Thus, from a general perspective, our findings suggest that small-scale human and natural perturbations might cause long-lasting small-scale patterns in nutrient cycling and hence influence below-ground and above-ground community composition in acid mountain grasslands (Spiegelberger *et al.* 2006a).

From the more specific view of sustainable ecosystem and soil management, the results indicate that the widely used practice of soil liming might have long-lasting effects on plant and soil microbial biodiversity as well as on the chemical composition of soils (pH_{soil}, Ca and Al content), at least for several decades or even centuries. Long-lasting legacies of human activities might be particularly common in mountain ecosystems, which are characterized by low rates of nutrient cycling (DeAngelis, Bartell & Brenkert 1989). The management of mountain ecosystems should therefore be based on a thorough understanding of the interrelationships between the legacy effects of historical land use, ecosystem resilience and the sustainability of socio-ecological systems in order to sustain or restore desirable ecosystem patterns and processes in the face of global change (Folke *et al.* 2002).

Figure 19: Plot with sawdust added (left) and control plot (right) at one of the study site (La petite Ronde, Switzerland) in the 2nd study year (2003).

Such anthropogenic nutrient enrichment through liming, but also through fertilisation of mountain grasslands boost in praticular grasses and fast-growing unpalatable plants at the expense of slow-growing species, resulting in a significant loss in biodiversity (Spiegelberger *et al.* 2006b). A potential tool to reduce nutrient availability and aboveground productivity without destroying the perennial vegetation is carbon (C) addition (Blumenthal, Jordan & Russelle 2003). However, little is known about its suitability under severe climatic conditions. I setup in 2002 a 3-year field study assessing the effects of sawdust addition (Figure 19) on soil nutrients, aboveground productivity, and vegetational composition of 10 grazed and ungrazed mountain grasslands (Spiegelberger *et al.* 2009). Of particular interest was the effect of C addition on grasses and on the tall unpalatable weed *Veratrum album*. After 3 years, soil pH, ammonium, and plant-available phosphorus were not altered by sawdust application, and nitrate concentrations were marginally higher in treatment plots. However, the biomass of grasses and forbs (without *V. album*) was 20–25% lower in sawdust-amended plots, whereas the biomass of *V. album* was marginally higher. Sawdust addition reduced the cover of grasses but did not affect evenness, vegetation diversity, or plant species richness, although species richness generally increased with decreasing biomass at our sites. With these results I could show that sawdust addition is a potent tool to reduce within a relatively short time the aboveground productivity and grass cover in both grazed and ungrazed mountain grasslands as long as they are not dominated by tall unpalatable weeds. The technique has the advantage that it preserves the topsoil and the perennial soil seed bank.

One of the potential explications of the observed pattern is that plants thriving under severe climate conditions profit overproportionally from interactions with arbuscular mycorrhizal fungi (AMF) which I'll present in the following chapter.

Interactions between plants and soil fungi favours particular species

Nutrient availability is one of the major determinants of above-ground productivity of plants, and nitrogen (N) the limiting factor in many terrestrial ecosystems (Vitousek et al. 1997). Schematically, soil N cycling in mountain grasslands starts with plants producing litter which is incorporated by soil macro-organisms into the soil organic matter. In cold climate ecosystems like mountain grasslands, where litter input is low and decomposition and N cycling are slow, plants and microbes compete primarily for N at the organic stage i.e. the amino-acids (Schimel & Bennett 2004). Microbes are relatively N limited (Schimel & Chapin 1996), but some of the N would be mineralised to ammonium, and, if nitrifiers are present, small part will also be reduced to nitrate.

In semi-natural, extensively managed grasslands, the roots of almost all plants are heavily colonised by AMF (Read & Haselwandter 1981). AMF often form large mycelial networks throughout soil and greatly facilitate acquisition and uptake of scarce or immobile mineral nutrients, particularly phosphorus (Johnson, Leake & Read 2001). In alpine ecosystems, AMF facilitate the direct access to organic nitrogen for the plant (Lipson & Monson 1998; McKane *et al.* 2002; Nordin, Schmidt & Shaver 2004).

In a greenhouse study I confirmed that AMFs are central for N-uptake of alpine plants (Spiegelberger 2006): application of the fungicide benomyl which decreases the biomass of AMF (Fitter 1986; Merryweather & Fitter 1996), reduced the above-ground biomass of the highly AMF-infested plant *Festuca rubra*, but did not influence the above-ground biomass of the less AMF-infested *Poa alpina* (Figure 20). Decreasing the AMF infestation rate through benomyl application probably harms or interrupts the direct access to organic nitrogen which may explain the lower biomass production of *F. rubra*.

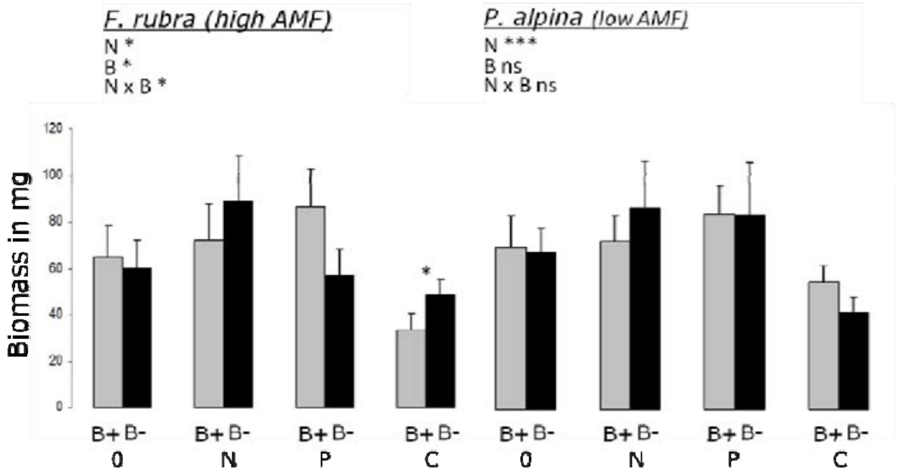


Figure 20: Productivity expressed as above-ground biomass in mg of a highly AMF infested plant (*Festuca rubra*) and a less infested plant (*Poa alpina*). Letters in the bottom line indicate field treatment (0, control; N, nitrogen addition; P, phosphate addition; C carbon (sawdust) addition. Letters in the second line indicate fungicide treatment (B+, application of benomyl; B-, no application of benomyl). Figure from Spiegelberger (2006).

In forming mycelial networks, individual mycorrhizal fungi can be supported by several host plants, and so the hyphae can facilitate seedling establishment (van der Heijden 2004) and affect plant competition. Whilst the AMF symbiosis is typically considered a mutualistic one, increasing evidence points to a more diverse range of interactions. In a meta-analysis, around 45 % of studies found positive effects of AMF on plant growth, 30 % showed no effect and 25 % showed negative effects (Van der Heijden & Horton 2009). This analysis supports the idea that AM fungi act along a continuum between mutualism and parasitism (Johnson, Graham & Smith 1997) and species competitiveness could be increased as well as decreased in the presence of AM fungi.

Observations of plant species abundances in semi-natural grasslands reveal distinct frequency distributions, with some species found frequently and in high abundance (dominants), and some also found frequently but in low abundance (subordinates; Grime 1987). Some species may also be considered transients because they rarely persist (Whittaker 1965). Dominant species are generally few in number, tall and account for a large proportion of the total community biomass. In contrast, subordinate species consistently co-occur with particular dominants, are often small in stature and contribute marginally to the total biomass of the community, although they are the most diverse component of communities.

One mechanism behind this pattern could be the interaction between plants and AMFs what may flatten out the plant dominance hierarchy when dominant species are more reduced than subordinate species in an unfavourable, meaning parasitic, AMF relationship. Together with P. Mariotte, we tested whether the presence of the AMF *Glomus intraradices* affects the competitiveness of two dominant (*Taraxacum officinale* and *Agrostis capillaris*) and two subordinate (*Prunella vulgaris* and *Achillea millefolium*) grassland species grown in greenhouse pots in the presence or absence of the fungus, in monoculture and in mixtures of both species groups with two and four species (Mariotte *et al.* 2012). In the absence of *G. intraradices*, dominants were clearly more competitive than subordinates. In inoculated pots, the fungus acted towards the parasitic end of the mutualism–parasitism continuum and had an overall negative effect on the growth of the plant species. However, the negative effects of the AMF were more pronounced on dominant species reducing the differences in competitiveness between dominant and subordinate species. Dominant species were negatively affected from the AMF in mixtures, while subordinates grew identically with and without the fungus (Mariotte *et al.* 2012).

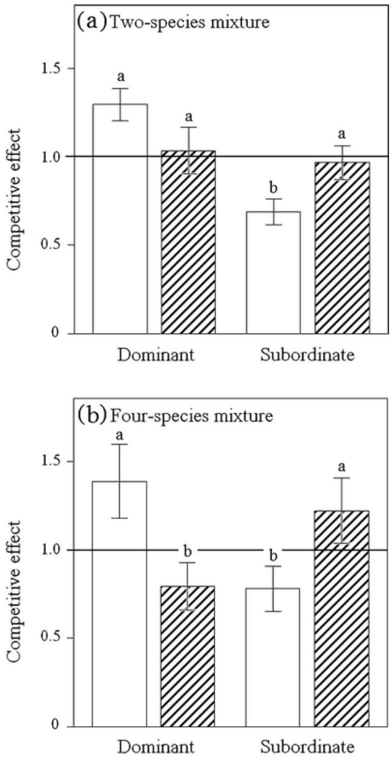


Figure 21: Total plant biomass (±1 SE) of dominant (*Taraxacum officinale* and *Agrostis capillaris*) and subordinate (*Prunella vulgaris* and *Achillea millefolium*) growing with (hatched bars) and without (white bars) *Glomus intraradices* in a) two- and b) four-species mixtures. Bars sharing a letter are not significantly different (P>0.005). Figure from Mariotte et al. (2012).

Vegetation patterns induced by land use

The role of dominant species in ecosystem functioning has received considerable research attention and, according to the "mass ratio" theory (Grime 1998), ecosystem properties are determined by dominant species independent of changes in species richness that involve variations in the number of subordinate species. However, more recent studies show that less abundant species may have a larger influence on ecosystem properties and functioning than their relative abundance suggests (Boeken & Shachak 2006; Mariotte 2014). Thus, it becomes important to consider the factors that determine the abundance not only of dominants but also of subordinates.

I was able to demonstrate that increased mountain pastures use induces a reduction of plant diversity (Spiegelberger *et al.* 2006b), but when these grasslands below treeline and traditionally managed are abandoned, their floristic composition changes and agronomic quality decreases (Spiegelberger *et al.* 2006b), resulting in long-term reforestation and a significant reduction of biodiversity (Fischer & Wipf 2002). In collaboration with several other researchers, we underpinned my own findings by analysing conjointly several datasets on species-richness of grazed and abandoned sites (Mariotte *et al.* 2013a). The results confirm the humpbacked diversity-productivity relationship in semi-natural grassland, which is due to the increase of subordinate species number at intermediate productivity levels (Figure 22). Grazed communities, at the lower or higher end of the species diversity gradient, suffered higher species loss after grazing abandonment. Species loss after abandonment of pasturing was mainly due to a higher reduction in the number of subordinate species, as a consequence of the increasing proportion of dominant species (Mariotte *et al.* 2013a).

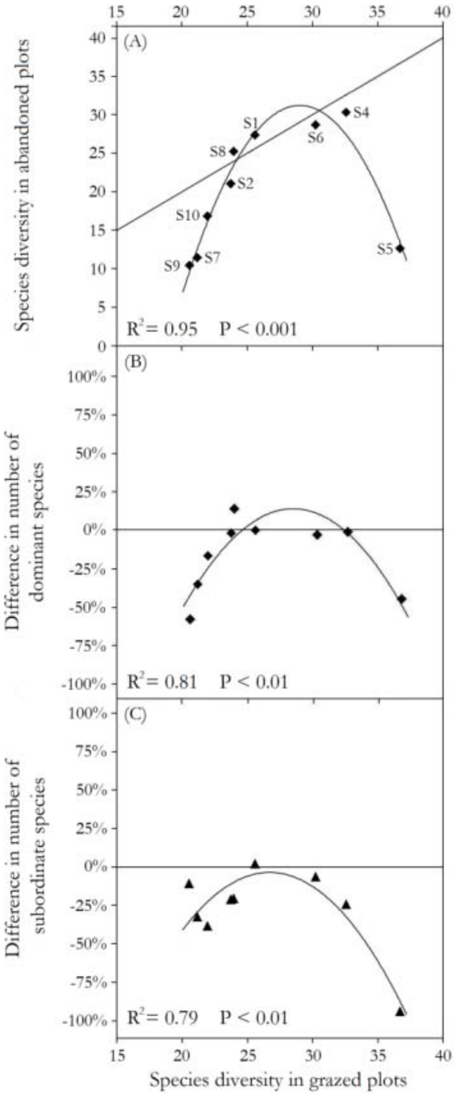


Figure 22: Relationship between species diversity (mean species number per plot) in grazed plots and (A) species diversity in abandoned plots, (B) difference in number of dominant species, and (C) difference in number of subordinates in abandoned plots compared to grazed plots for nine semi-natural grassland sites. Polynomial curves represent the significant models fitting the relationships. Straight lines indicate neutral effects of abandonment. Figure modified from Mariotte et al. (2013a).

However these patterns of dominance in the vegetation are not only governed by AMF as shown above, but also by seed rain, availability of space and light, and the impact of herbivores. In a field study, I was able to demonstrate that the overrepresentation of certain plants in the floristic composition is essentially linked to a better germination and holes in the existing vegetation providing space for germination, but was on the other hand limited by the action of molluscs. The results of this study demonstrate that a combination of niche-and dispersal-assembly factors such as seed addition (dispersal), microsite limitation (niche) and disturbance by herbivores (niche) increases or attenuates the initial differences in seed emergence rate of species groups (Spiegelberger *et al.* 2014).

Conclusion

My works on small scale impact of land use changes through soil amendments and land abandonment in mountain grasslands show that both intensification and abandonment of traditional land use decreases plant species richness and this on the long-term. As underlying mechanisms I could identify a shift from mutualistic to parasitic interaction between mycorrhizae and plants, and the recycling of calcium in limed ecosystems. I further provided a new explication of the hump-backed relationship between species richness and productivity due to a high number of subordinate species at intermediate productivity.

2.3.2 Past land use changes at the landscape level

Land use change has be classified of one of the major issues decreasing biodiversity worldwide (Millennium Ecosystem Assessment 2005). In mountain areas land use change has steadily increased in the last decades in Europe (Mottet *et al.* 2006), but also on a worldwide scale (Spehn *et al.* 2006).

Land management is influenced by local factors as well as by global forces. Besides the natural conditions in which land use takes place, the socioeconomic opportunities and constraints—notably changes in agricultural and forest policy—impact farmers' and foresters' decisions on land management (Lambin *et al.* 2001; Huber *et al.* 2013a). Thus, land use responds to changes driven by biophysical and socioeconomic systems (cf. chapter 2.1) and in turn influences them (Figure 2). Understanding the contexts and influences on land use change is therefore of primary importance to guarantee sustainable use of mountain ecosystems, and to preserve its characteristic landscape with a high biodiversity (Eichhorn *et al.* 2006).

At the landscape level, we show in a retrospective analysis, based on statistical data of land use between 1985 and 2009, a certain resilience of silvopastoral landscape structure in the mountain region of the Park Jura Vaudois (Switzerland, PJV). In the PJV, a vaste area of 542 km^2 comprising 31 municipality in the Swiss Jura, areas of lower elevation (<1000 m) suffered a higher transformation towards intensification (Figure

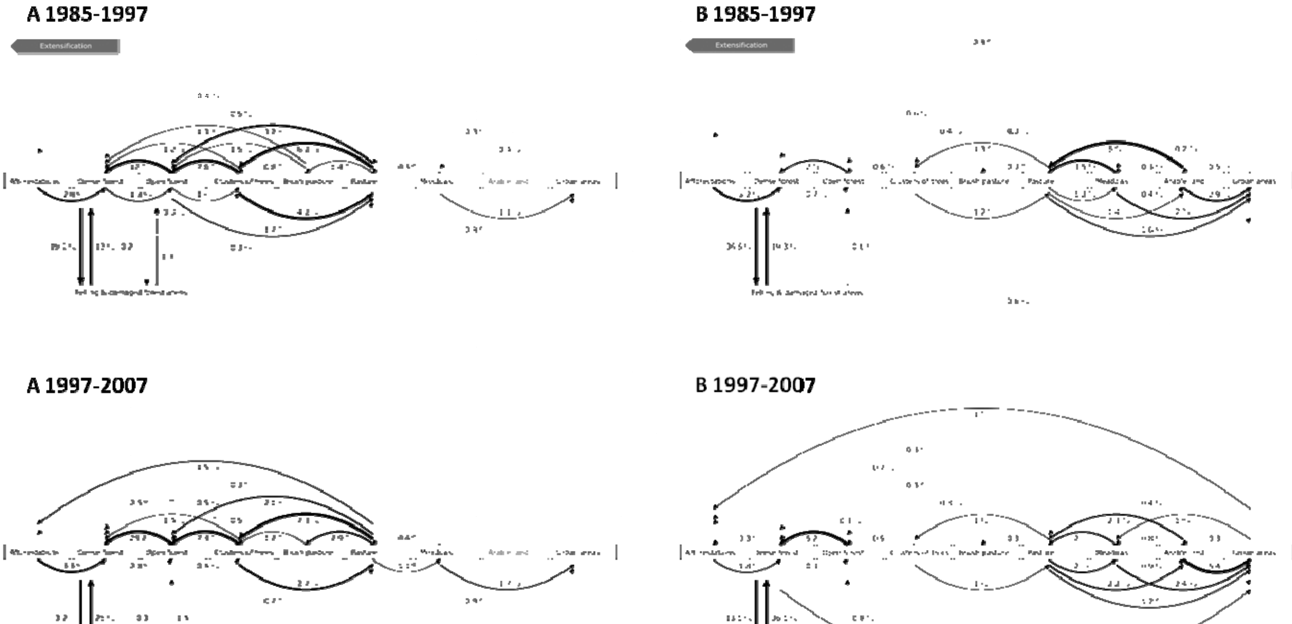


Figure 23: Change of land use in mountain areas of the Jura Regional Park at altitudes a) above 1000 m and b) below 1000 m for the period 1985-1997 (top) and between 1997 and 2009 (bottom). Values represent the rate of change in% compared to the overall changes in the reporting period. Figure modified from Buttler et al. (2012b).

23), despite a tendency towards segregation between closed forests and pastures at higher atltitudes (Buttler *et al.* 2012b). The lowland region suffers a high rate of change, including conversation from agricultural land to urban areas (18.0 %), while only 4.5 % of mountain areas are urbanized underlining the trend towards increasing urbanization in lowland areas (Figure 23). In mountain regions the extensification process prevails, with wooded pastures being transformed toward open forests (7.3 %), of which 25.2 % are transformed to dense forests (Buttler *et al.* 2012b).

The analysis of land use dynamics is often limited to observing changes in the biophysical environment as above, without addressing spatial transformations (Verburg *et al.* 2004), and to relating them to the socioeconomic context. A spatially explicit approach based on geographic information sciences and integrating not only natural but also socioeconomic, political, technological, and cultural factors is therefore needed to produce more explanatory results (Taillefumier & Piegay 2003). In addition, land use transition analysis is generally limited to broad spatial occupancy changes (Plieninger & Schaar 2008). More subtle transformations within a land-cover category are rarely addressed though they have significant implications on the ecological functions, production potential, and symbolic value of landscapes (Plieninger & Schaar

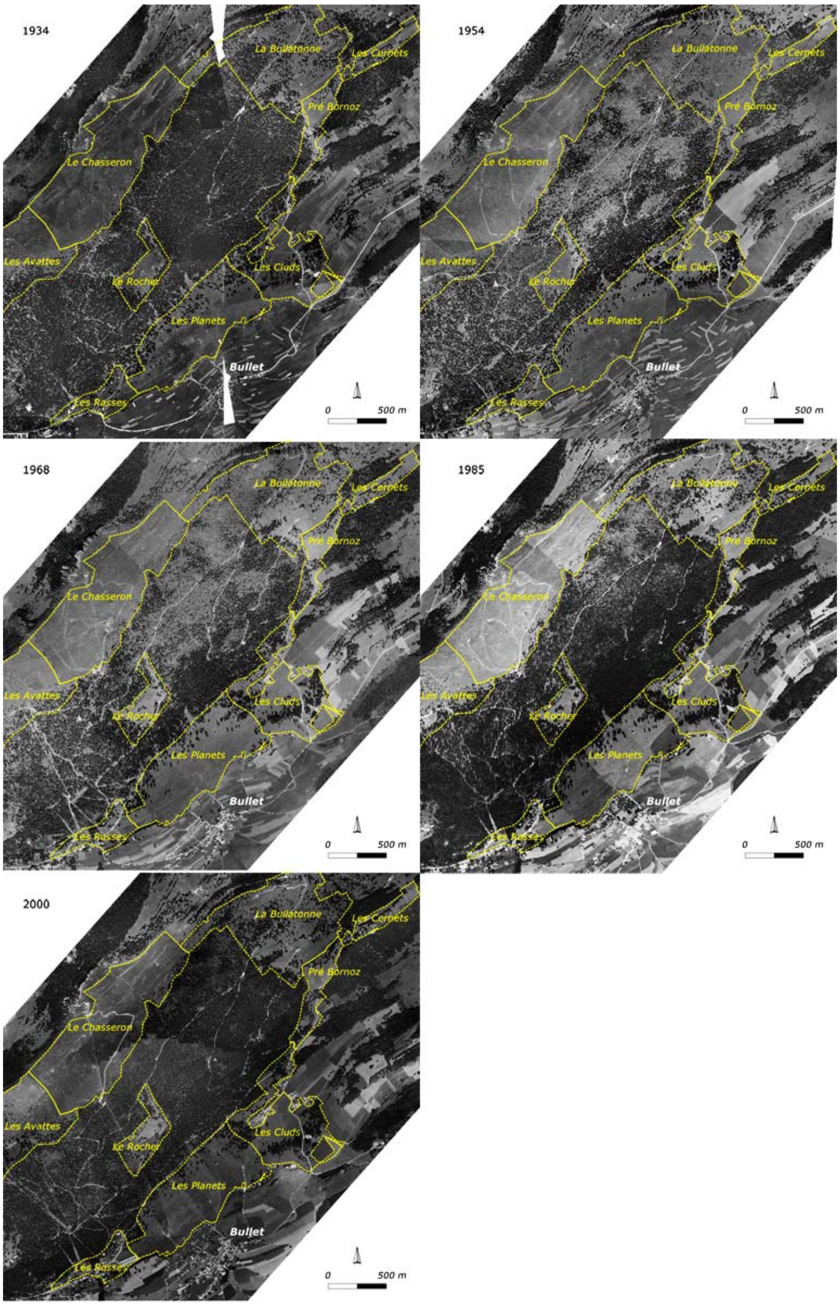


Figure 24: A serie of aerial images of the pastures in Bullet from 1934 to 2000 showing their spatial organization, including the farms of Les Rasses, Les Planets, and Les Cluds. Figure from Chételat et al. (2013).

2008). These implications are particularly true for wooded pastures characterized by a complex mosaic of herbage with various tree densities. However, time series of aerial photographs (Figure 24) can only show the combined consequences of recent land use extensification and climate warming, i.e. forest encroachment and homogenization of the grassland-forest mosaic during the last century. The impacts of these two factors are difficult to disentangle. We used a transdisciplinary approach documenting the contemporary evolution of mountain pastures based on aerial photographs and related the changes to the environmental context, the land policy framework, and the management practices.

I contributed together with several colleagues from the EFPL in Lausanne to that retrospective analysis for two pastures in the Jura by analyzing five sets of aerial photographs acquired between 1934 and 2000. Agricultural policies substantially influence the afforestation rate, but differed depending on the local situation: nearby village sites allowed a better rationalization leading to intensification, while remote site suffered more abandonment (Chételat *et al.* 2013). Pastoral management and forestry policy as well as extreme weather events (storms) produced in the 20th century changes in landscape structure without that the latter has undergone substantial ruptures. These changes were particularly important during the period 1934 - 1954 (Figure 25) where logging was most intense after World War II and significant damage due to storms and drought took place (Chételat *et al.* 2013).

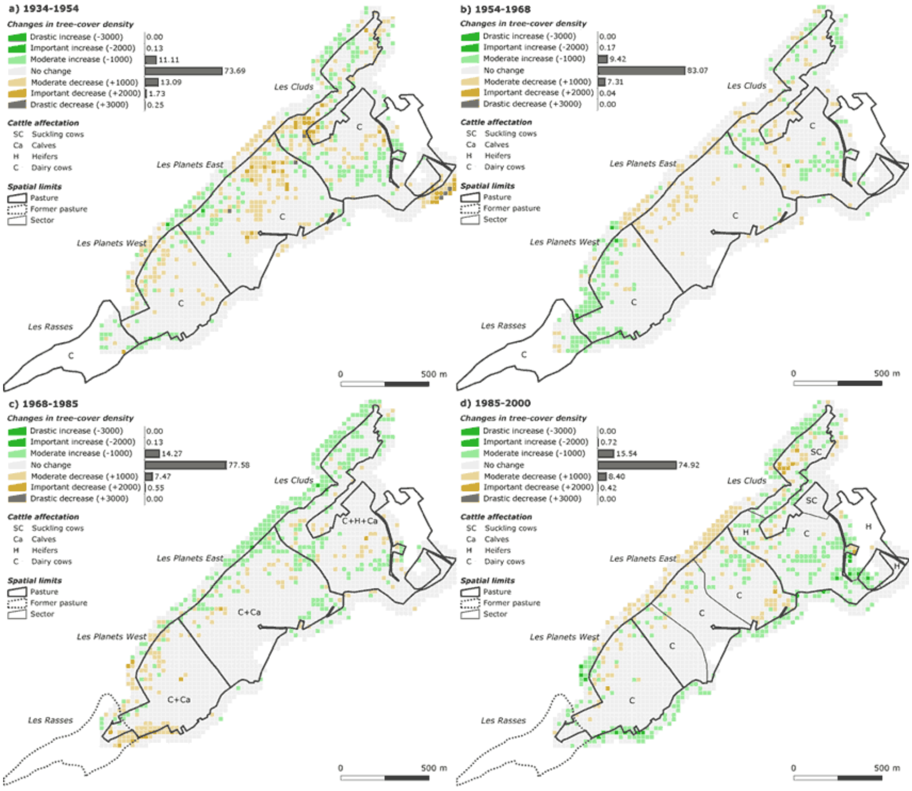


Figure 25: Evolution in management structures and in tree-cover categories between 1934 and 2000 in Planets-Cluds. Figure from Chételat et al. (2013).

Based on these analyses, the spatially explicit dynamic model WoodPaM (Gillet 2008) was adapted to take into account impacts of climate change such as temperature fluctuations and heat waves, or precipitation shift from summer to winter and drought (Peringer *et al.* 2013) to study the long-term impact of historical (warm Middle Ages, Little Ice Age) and future climate change under quasi static, but contemporary stocking constraints (low stocking in the Middle Ages, enhanced stocking with improvements of agricultural practice in the 20th century). We compared the outcome of simulations to aerial photographs of the year 2000 and found that densely wooded pasture in the less frequently grazed corners of the pastures and along ridges of rock outcrops fitted well the observed patterns from aerial photographs (Peringer *et al.* 2013).

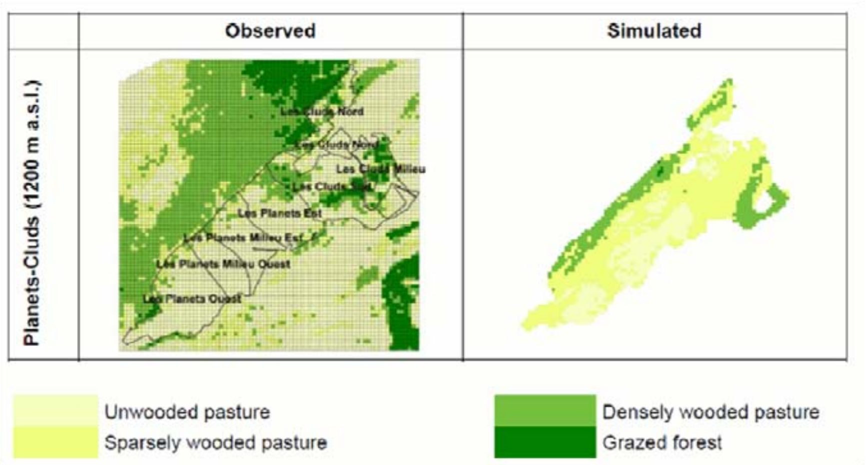


Figure 26: Long-term historical simulations (1100 AD – 2000 AD) and observed (2000 AD) landscape mosaics in the pastures of Planets-Cluds. Squares represent 25-m grid cells used for both photo-interpretation and model simulation. Figure modified from Peringer et al. (2013).

Conclusion

My works on past land use changes presented in that chapter show the bipolar processes of intensification at nearby sites and extensification on remote sites on mountain ecosystems and how local demands (fire wood, increased agricultural demand) transform ecosystems on a small scale. We proved further that by taken into account climate change and life stock density the model WoodPaM can be used to simulate land use changes accurately.

2.4 Stability of mountain socio-ecological systems

Research on stability of ecosystems has a long history in ecology. Already Elton (1958) noted that a simplification of the natural environment leads to less stable ecosystems. However, 15 years later, this view was challenged by mathematical approaches which show the opposite behaviour (May 1973). The question remains, what does "less stable" mean?

A large number of authors give definitions or interpret their understanding of stability which led and still leads to confusions when discussing stability (Grimm & Wissel 1997). For the sake of clearance, I will use Grimm's and Wissel's definition for the following chapters which proposes that the three fundamental properties "constancy", "persistence" and "resilience" contribute to the stability of an ecological system. **Constancy** means that the system stays essentially unchanged, what requires either a certain reference state (which may be an equilibrium), or dynamics (could be oscillations, or irregular but limited fluctuations). **Persistence** refers only to the question whether a system persists as an identifiable entity and therefore perseveres through time. **Resistance** is the capacity of staying essentially unchanged despite the presence of disturbances. A fourth concept is "elasticity" or the speed of return to the reference state (or dynamic) after a temporary disturbance. Resistance is an interpretation of constancy, elasticity an aspect of resilience, which I'll introduce more widely in one of the following chapters.

Vulnerability is another concept which is linked to ecosystem stability. Vulnerability in ecosystems describes the degree to which a system is exposure to hazards and its difficulty in coping with them (Millennium Ecosystem Assessment 2005). Three major dimensions of vulnerability are involved: a) its exposure to stresses, perturbations, and shocks; b) the sensitivity of people, places, ecosystems, and species to the stress or perturbation, including their capacity to anticipate and cope with the stress; and c) the resilience of the exposed people, places, ecosystems, and species in terms of their capacity to absorb shocks and perturbations while maintaining function (Millennium Ecosystem Assessment 2005). This recognition requires revisions and enlargements in the basic design of vulnerability assessments, including the capacity to treat coupled socio-ecological systems and those linkages within and without the systems that affect their vulnerability (Turner *et al.* 2003a).

2.4.1 Future of mountain grassland under climate changes

Both, climate change and land use change, as I have developed in the previous chapters, are likely to change our environment in the future, increase its vulnerability and decrease their stability. However, these changes will bring great uncertainty about how ecosystems in general, and mountain ecosystems in particular, will respond to the changes. Currently, one of the main research questions in ecology with regard to global changes concerns the stability in time of ecosystems.

In several approaches during the project Mountland, we simulated future land use and the consequences of both, climate and land use change on the species distribution and on the land cover. I'll illustrate these changes based on simulations done with the before introduce model WoodPaM. I use therefore the example of the intensively grazed pastures of Planets-Cluds already shown before (Figure 24- Figure 26) and the climate change scenarios B2 and A1FI (Figure 27).

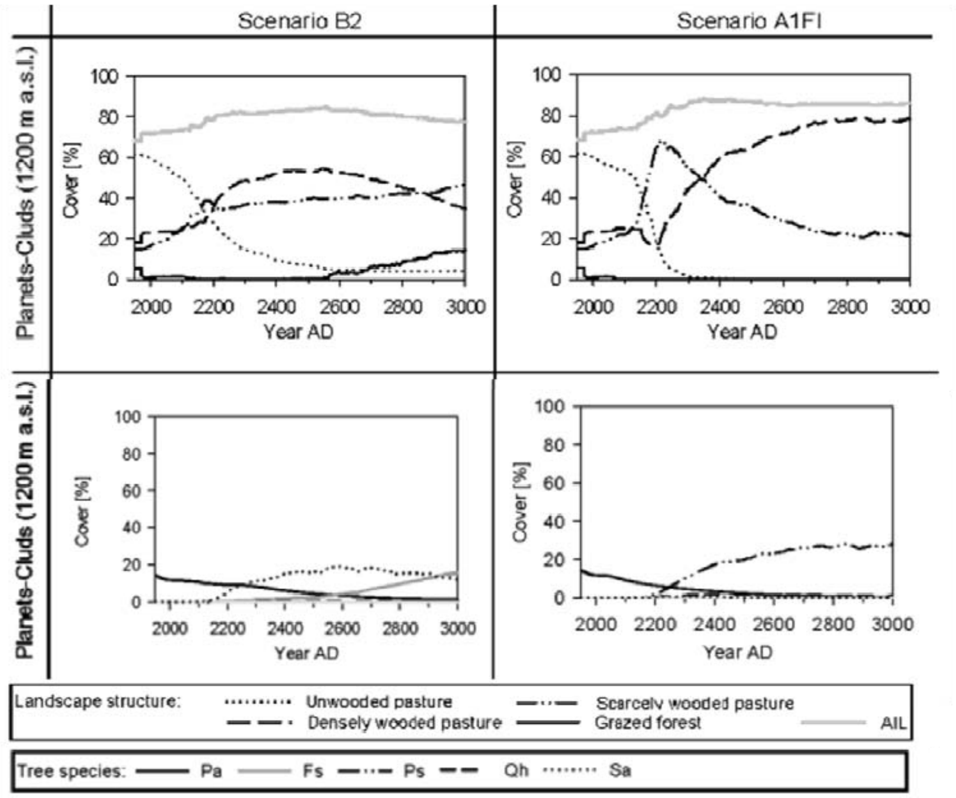


Figure 27: Landscape dynamics and tree species shift following climate change in the wooded pastures Planets-Cluds. Species not occurring during the simulation are kept in light grey. Species abbreviations: Pa: *Picea abies*, Fs: *Fagus sylvatica*, Ps: *Pinus sylvestris*, Qh: *Quercus pubescens*, Sa: *Sorbus aucuparia*. Figure modified from Peringer et al. (2013).

After the initial spin-up phase, only minor changes occurred in the scenario B2 with transformations of unwooded pastures into sparsely wooded pastures and densification of densely wooded pastures into grazed forests until 2050. Afterwards, this successional trend was accelerated until approximately 2200 and succession lines diverged according to the degree of warming. By this period, in the moderate scenario B2, densely wooded pastures dominated, while in the extreme warming scenario A1FI, forests as well as densely wooded pastures decreased and sparsely wooded pastures temporarily dominated (around year 2200). From 2200 on, in both scenarios progressive forest succession took place again, however towards different forest types and landscape patterns: in the B2 scenario, a segregation into grazed forest and sparsely wooded pastures with some open grasslands took place, while after 1000 simulation years (calendar year 3000) the mosaic turned into a homogenous landscape consisting of densely wooded pastures only in the A1FI scenario (Figure 28). The landscape structural heterogeneity decreased in the period 2000-2100, as indicated by a high landscape aggregation index. Ongoing tree species shift temporarily increased landscape heterogeneity in the moderate scenario B2, but later segregation led to a simplified landscape. The extreme warming scenario A1FI showed the inverse process: here tree species shift led to temporary simplification, and then pine wooded pastures implied a high structural diversity.

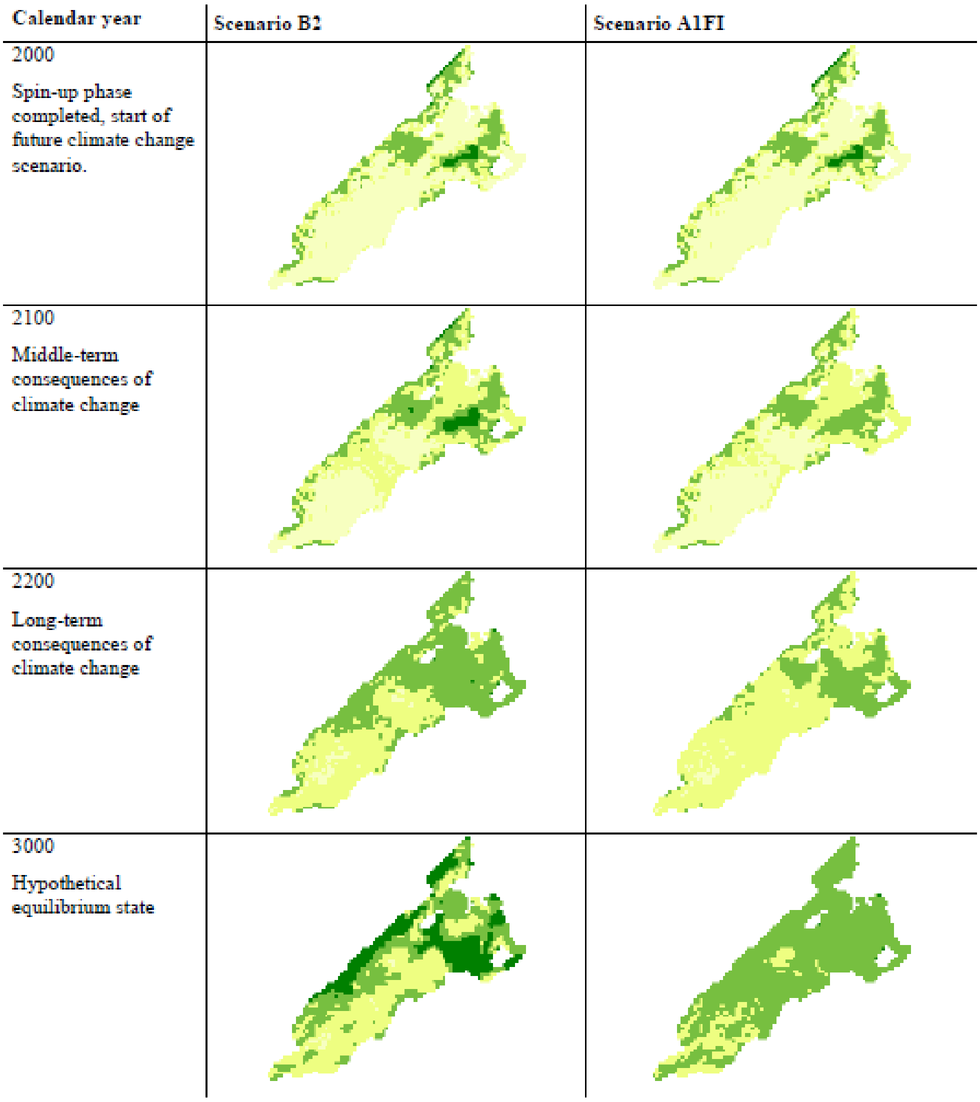


Figure 28 : Landscape structural changes in the climate change scenarios B2 and A1FI in Planets-Cluds. Colours correspond to the local total tree cover: unwooded pastures (white: 0 ≤ Total tree cover (Ttc) < 1%), scarcely wooded pastures (yellow: 1% ≤ Ttc < 20%), densely wooded pastures (light green: 20% ≤ Ttc < 70%) and grazed forests (dark green: 70% ≤ Ttc ≤ 100%). Figure from Peringer et al. (2012).

In both scenarios, Norway spruce (*Picea abies*) declined from year 2000 on. Consequently, a temporary decrease in tree cover appeared between the years 2050 and 2200 corresponding to the shift in tree species composition driven by climate change. In the moderate scenario B2, spruce was replaced by beech (*Fagus sylvatica*) from year 2100 on, but waiting year 2600 to reach significant cover at landscape scale. At this time spruce cover was reduced to approximately one third of its current cover. The early successional stage indicated by rowan (*Sorbus aucuparia*) as a pioneer tree lasted longer under moderate warming (B2). In the extreme warming scenario A1FI, spruce was replaced by Scots pine (*Pinus sylvestris*).

From a spatial point of view, the simulations showed climate change impacts being delayed for decades and centuries after warming started in calendar year 2000 and future landscape structure and vegetation types being strongly dependent on the degree of climate warming, while stocking densities were held constant during simulations (Figure 28). In the pasture Planets-Cluds with high grazing intensity, forest encroachment was slower compared to the other pastures which were less heavily grazed, but regressive succession occurred at similar speed. Nevertheless, they higher grazing intensity led to a comparatively large proportion of unwooded and sparsely wooded pastures.

In the short term and on a small spatial scale, climate change leading only to slightly higher temperatures may have an important impact on the forage quantity provided. In collaboration with my PhD-student K. Gavazov and my Post-doc A. Peringer, we simulated utilisation rates of provided fodder by the pasture woodlands of Planets-Cluds. Even under the moderate climate change scenario B2, utilisation rate increases above 100% indicating an insufficient amount of forage on intensively used pasture relative to the current demand (constant livestock) in hot years, but also reach this limit in cooler years (Figure 29). However, rangelands under forest cover remain productive, probably because of the insulation by trees (Gavazov et al. 2013).

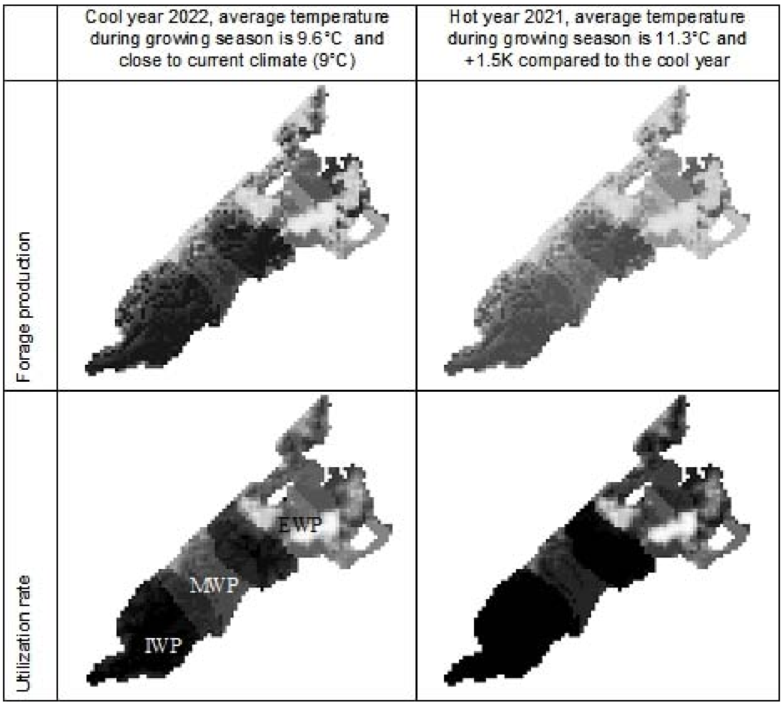


Figure 29: Maps of forage production and local utilization rate at Planets-Cluds in two arbitrarily chosen years—a hot one (2021) and a cool one (2022), based the moderate climate change scenario B2 with contrasting average temperatures in the vegetation period (+ 1.5 K). Darker tones indicate higher values of the respective parameters. Grazing intensity indicated as EWP, light grazing; MWP, medium grazing; and IWP, intensive grazing. Figure from Gavazov et al. (2013).

Wood-pastures depend on a balance between the (natural) successional trend towards forest development and the oppression of tree establishment by browsing. Our simulations underpin the observed sensitivity of wood-pastures to land use change

(Chételat *et al.* 2013) and provide a mechanistic explanation for climate change impacts. Most important, climate change scenarios demonstrate that future climate will cause qualitative shifts in the landscape mosaic regardless grazing pressure (Vandenberghe *et al.* 2006; Huber *et al.* 2013a). Although simulations of future climate do not predict immediate landscape structural changes of similar speed and magnitude as observed after recent extensification, this does not mean that wood-pastures are resistant to climate change. To the contrary, shifts in landscape structure, tree species composition and thus ecosystem service provision are predicted to occur even more rapidly and drastically than known from the past after a delay of approximately 50 years.

In the framework of the Swiss project Mountland we found that farmers in the Jura Mountains are unlikely to increase the number of large domestic herbivores on their farms, although this would be needed to maintain the ecosystem under climate change. Results from an agent-based farm model integrating socio-economic driving forces and the above-mentioned ecological modelling framework (Huber *et al.* 2013a) suggest that economic incentives (in the form of payments for ecosystem services) counteract land use segregation to a certain extent. However, the long-term consequences of a change in economic incentives depend on historical and current land use as well as on ecological boundary conditions. For example, in areas that are currently used less intensively, a future increase in stocking density might not suffice to change long-term vegetation dynamics and selective tree felling might be necessary (Peringer *et al.* 2013).

Land-cover types usually do not respond linearly to climate change, but rather feature threshold behaviour. Spatial heterogeneity in a pasture-woodland mosaic, for instance, implies thresholds for both pressure from cattle grazing and vegetation dynamics through neighbourhood effects (Chételat *et al.* 2013). Such effects were particularly pronounced in the dependence of fodder production on the mosaic structure and the resistance of trees in different

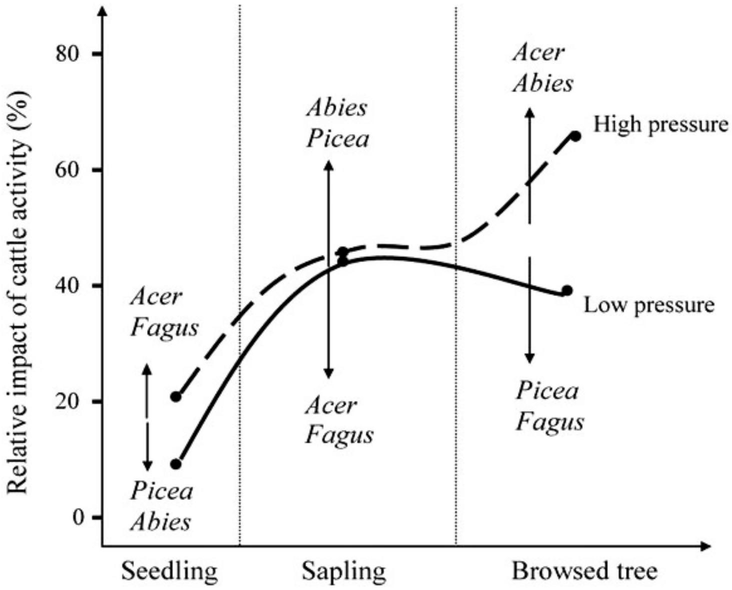


Figure 30: Nonlinearities and thresholds in a Swiss mountain wooded pasture of cattle activity on seedlings (< 1 year old), saplings (1-3 years), and browsed trees (4-8 years) relative to other survival and growth limiting factors. Trees were exposed to low (solid line) and high (dotted line) grazing pressures. Arrows indicate a higher (up) or lower (down) impact of cattle. Figure from Huber *et al.* (2013b).

development stages to cattle activity (Figure 30). For example, Norway maple (*Acer pseudoplatanus*) and beech (*Fagus sylvatica*) seedlings (< 1 year old) were found to have lower survival and growth rates than Norway spruce (*Picea abies*) and silver fir (*Abies alba*) when cattle were present. Once the seedlings have developed to saplings (1-3 years), the relative impact of cattle activity on survival and growth rates is higher for silver fir and Norway spruce (Vandenberghe et al. 2007). In general, the impact of grazing increases with higher development stages and high grazing pressure. In contrast, low grazing pressure reduces the relative importance once the seedlings have developed to browsed trees. Deciduous species are generally more vulnerable to cattle activity, with the exception of the sapling stage when coniferous species are more sensitive. With changing management regimes, different tree species will show nonlinear survival and growth rates that may result in species shift under changing climatic conditions.

Transferred to the landscape scale, the simulation of forest dynamics suggests a considerable shift in species composition and tree density as a result of climate change (Peringer *et al.* 2013). Irrespective of the management alternatives, ecosystems will be unable to return fully to their former state and new states will develop (Huber *et al.* 2013a) what indicates also a threshold due to changes induced by climate change at the landscape scale. The consideration of the feedback loop between structural changes in farming and vegetation dynamics thus accentuates the importance of such thresholds in silvopastoral landscapes.

The main challenge facing the silvopastoral system in the Jura is the segregation of forest and grassland management, resulting in the loss of fine-grained specific ecotones and particularly biodiversity. Moderate warming forces segregation of the pasture mosaic into closed forest and sparsely wooded pasture or grassland. Extreme warming homogenizes the landscape pattern to an almost uniform distribution of densely wooded pastures (Peringer *et al.* 2013). Furthermore, the concomitant shift in tree species will also determine the landscape structure (Peringer *et al.* 2013). The analysis of the herbaceous production showed that a slight increase in air temperature may be beneficial for forage production in the more cold-adapted vegetation of wood-pastures, but drought associated with much higher temperatures may have the opposite effect in large open pastures because of the evaporative loss of soil moisture (Gavazov *et al.* 2013). Insulating forest canopy cover, but also structural landscape diversity, grants wooded pastures a buffering potential in the face of climate change in the forthcoming decades. In contrast, in open pastures, carbon stocks in the soil organic matter will become depleted due to leaching and increased soil respiration (cf. chapter 2.2.1).

The analysis in the Mountland illustrates the effects of a changing biophysical context on the growth of specific tree species, fodder production, or changes in soil carbon cycling in experimental settings simulating climate change. The linkage of socio-economic and ecological models in Mountland allows a successful exploration of a range of scenarios designed to quantify the impacts in mountain regions under a joint set of assumptions linked to climate and land use change. For example, considering land use and climate changes together (this chapter) resulted in a distinctly different landscape pattern than if climate change effects (chapter 2.2.1) had been addressed in isolation.

Conclusion

My works on future land use changes assessed by modelling approaches with colleagues from the EPFL presented here in this chapter show that mountain ecosystems will continue under climate change to suffer from a segregation of the grasslands and woodlands accompanied by tree species changes. This will probably lead at a larger scale to homogenisation of the landscape followed by a decrease in biodiversity.

2.4.2 Ecological resilience and adaptive management

Past human activities have already reduced the capacity of ecosystems to cope with environmental changes (Scheffer *et al.* 2001). The resilience of ecosystems may be an essential factor underlying the sustained production of natural resources and ecosystem services faced with uncertainty (Gunderson 2000). Ecological resilience seems to depend on the a) taxonomical and/or functional diversity of the ecosystems, b) its material or nutrient fluxes and, c) on the connectivity within the system.

Biological diversity appears to play a substantial role in ecosystem resilience and in sustaining desirable ecosystem states in the face of change (Peterson, Allen & Holling 1998). Ecological redundancy, meaning that multiple species or functional types (Leps, Osbornova-Kosinova & Rejmanek 1982; MacGillivray, Grime & The Integrated Screening Programme (ISP) Team 1995) contribute to provide similar functions to the ecological system and therefore guarantee the provision of ecosystems services even in the face of changes (Naeem 1998), seems therefore important to be maintained. A high diversity of functional groups in a dynamic ecosystem undergoing change, and a high species diversity within these groups seems important in helping to maintain ecosystem services (Luck, Daily & Ehrlich 2003) in general and particular in grasslands (Tilman & Downing 1994). Such diversity has been demonstrated to increase the resilience in our drought experiment on the High Plateaux of the Vercors, where intra-specific variability over-proportionally contributes to the high resistance to environmental change and the resilience of those sub-alpine pastures to extreme droughts events (Jung *et al.* 2014). However, resilience is likely to vary also among components and processes within a same ecosystem (Lavorel 1999; Diaz & Cabido 2001). For example, recovery of vegetation cover may be relatively fast, while recovery of vegetational composition might be considerably slower as demonstrated by N. Fontvieille, a master student, I co-supervised. By comparing vegetation samples of different sites, we found that in La Crau, France, plant species richness recovered 150 years after cultivation abandonment, but plant community composition was still different (Jaunatre *et al.* 2014). Those findings are similar to my study on the experiment at Schynigger Platte (Spiegelberger *et al.* 2006a) where I observed the same pattern.

Besides ecological diversity, theoretical and experimental work suggest that resilience is further affected by **nutrient fluxes** (DeAngelis *et al.* 1989; Moore, Ruiter & Hunt 1993). The "resilience – productivity hypothesis" posits that the time required by an ecosystem to regain equilibrium after a disturbance is similar to the turnover time of nutrients in the system (DeAngelis *et al.* 1989; Moore *et al.* 1993), suggesting that resilience may be particularly low in ecosystems with harsh environmental conditions, like alpine and arctic ecosystems. Plant species growing in such environments are characterized by a set of traits that promote the tolerance to environmental stresses (Körner 2003). The same traits are associated with low growth rates and are therefore predicted to be associated with low rates of resilience (Leps *et al.* 1982; MacGillivray *et al.* 1995).

Consequently, resilience to perturbations and in particular to changes in key ecosystem properties (pH or P) of grassland ecosystems under harsh environmental conditions may be particularly low (Spiegelberger *et al.* 2006a) and may even be irreversible (Semelová *et al.* 2008). While intensive forms of land use are essential for humans to obtain natural products such as food and fibre, they have contributed to the transformation of ecosystem patterns and processes (Foley *et al.* 2005). In particular, human activities have altered the rate, pathways and efficiency of the movement of nutrients within and between the various biotic or abiotic ecosystem compartments. These changes in nutrient cycles do not only affect today's ecosystem functioning but may also result in long-term legacy effects on ecosystem processes, thereby changing the resilience of ecosystems and their adaptive capacity to sustain ecosystem services in the face of uncertainty and global change (Folke *et al.* 2002; Elmqvist *et al.* 2003). We showed such long-term effects of agriculture use in a water-constraint ecosystem: 150 years after the abandonment of cultivation in the La Crau, France, soil chemistry became similar to a a several thousand year old grassland used as reference area, while plant species richness or diversity indices recovered after 150 years, but plant community composition was still different even 150 years after cultivation abandonment (Jaunatre *et al.* 2014).

Thirdly, the **connectivity** of the above-standing elements strongly contributes to ecosystem resilience. Early after the introduction of the concept of resilience, first analysis of real world data sets indicated that resilience was more likely if the interactions within selected food webs were not randomly choose (Yodzis 1981). Mathematical approaches show that increasing connectivity by increasing the number of connections or "nods" increases stability (Rozdilsky & Stone 2001; Jansen & Kokkoris 2003). Experimental studies in food webs have demonstrated that – as above – food webs with higher species richness were more resilient compared to species poor food web, but the numbers of "nods" or connection points was even a better predictor for the stability of the food web (Dunne, Williams & Martinez 2002). As for the biological diversity, ecological redundancy which seems to play an important role, as "overlap species" may re-establish novel trophical linkages after random loss of predating species; the increase of such overlap species is highly correlated to the resilience of food webs (Staniczenko *et al.* 2010).

These elements become more and more recognized as essential to any kind of complex systems, as they provide stability in time and thus a high resilience against unexpected changes. As a consequence, the concept of stability and resilience of complex systems has become an ecological "export bestseller" towards for example monetary and financial systems (Lietaer, Ulanowicz & Goerner 2009). Increase the resilience of coupled SES and consequently reduce the vulnerability of ecosystems and people may be achieved by both, the flexibility of ecosystems and the ability of social systems to learn in response to disturbances (Turner *et al.* 2003a). Resilience also encompasses the ability of an ecosystem to reorganize and renew itself under change and how much it expresses a capacity for learning and adaptation (Carpenter *et al.* 2001). This concept on which a variety of interdisciplinary research focuses implies the use of novel management options adapted to the new challenges for society and ecosystems, called "adaptive management" of socio-ecosystems.

By studying the long-lasting effect of liming of mountain grasslands, I showed that small-scale human and natural perturbations might cause long-lasting changes in nutrient cycling and hence influence below-ground and above-ground community composition in mountain grasslands (Spiegelberger *et al.* 2006a). Concerning a sustainable use of these ecosystems, our results indicate that the widely used practice of soil liming might have long-lasting effects on plant and soil microbial biodiversity as well as on the chemical composition of soils (pH, Ca and Al content), at least for several decades or even centuries. Long-lasting legacies of human activities might be particularly common in mountain ecosystems, which are characterized by low rates of nutrient cycling (DeAngelis *et al.* 1989). The management of mountain ecosystems should therefore be based on a thorough understanding of the interrelationships between the legacy effects of historical land use, ecosystem resilience and the sustainability of socio-ecological systems in order to sustain or restore desirable ecosystem patterns and processes in the face of global change (Folke *et al.* 2002).

While stocking rate will need to be reduced in open and nowadays intensively used pastures exposed to drought and productivity collapse (Gavazov *et al.* 2013), it will become crucial to enhance stocking rates in more encroached areas in order to maintain a diverse pasture-woodland mosaic in the light of climate change. The biodiversity of wooded pastures depends on landscape structures (mosaics and interconnecting ecotones), which emerge from extensive grazing and cannot be easily reproduced by direct human intervention (logging, shrub-cutting). The segregation between grassland and forest, which is predicted for moderate climate warming, comes with a drastic loss of open pastures and their ecotones to forest (Peringer *et al.* 2013). Both can be mitigated with enhanced browsing pressure and possibly with various grazers, even cattle behaviour being different for cows and for heifers. While the historical landscape dynamics in Planets-Cluds shows that segregation is not reversed but promoted by intense cattle grazing, browsing animals are able to thin forests to densely wooded pastures and clear sparsely wooded pasture to open grassland. Thus adapted management options might be a) extended stocking periods adapted to enlarged future vegetation periods and b) the (re-)introduction of horses, sheep and goats. Both constitute an opportunity to maintain the desired heterogeneous landscapes and indeed, this calls also for reforms in policies (Huber et al. 2013a).

In summary, our results clearly show that adapted land use offers an opportunity to mitigate climate change impacts on mountain grass- and woodlands, even though inevitable shifts in landscape structure cannot be compensated. Policy development should aim on the provision of favourable socio-economic constraints for the future practice of diverse management options including livestock breeding in mountain pastures.

Conclusion

My works on the resilience of mountain ecosystems through the assessment of climate and land use changes suggests that the fine-grained, patterned pasture woodland landscape may be aggregated in larger spatial units or completely homogenised depending of the underlying climate change scenarios. In both case, these processes may lead to a more vulnerable ecosystem and a loss of biodiversity in the long run. In consequence, management (longer stocking periods, diversification of grazers) has to be adapted to the new challenges.

2.5 Exploring the limits - will mountain grasslands change in the future?

As shown in the previous chapters, mountain ecosystems are not an exception compared to other ecosystems and will undergo in the future important changes. I'll therefore introduce in a concise manner, several concepts and ideas which seems to be worth exploring in the future.

2.5.1 Critical thresholds and early warning systems

Positive feedbacks are widespread in ecosystems, which leads to alternative stable states (May 1977; Scheffer *et al.* 2001). A critical threshold is an intermediate stage at which ecosystems can shift abruptly from one stable state to another. This shift is seen as a consequence of a loss of resilience of the ecosystems.

The idea of the existence of thresholds appeared in the 1970ies simultaneously to the emergence of the concept of resilience (cf. paragraph above). Today, it becomes more and more clear that many complex systems have critical thresholds (also called "tipping points") at which the system abruptly change its quality and consequently shifts from one stable state to another. First disruptive effects where a continuous change in a control variable can have discontinuous effects on a response variable have already been described some years after that the concept of resilience was introduced (May 1977). To date the threshold concept is applied in ecology mainly in three contexts (Groffman *et al.* 2006): the analysis of dramatic and surprising shifts in ecosystem quality (Scheffer *et al.* 2001), the determination of critical loads (Bobbink & Roelofs 1995; Bowman *et al.* 2006), and the analysis of extrinsic factor thresholds where changes in a variable at a large scale alter relationships between drivers and responses at a small scale.

While the concept of thresholds is largely acknowledged, the use of only a single threshold between alternative regimes is criticised as such shifts often lead to a "cascading effect" in which multiple thresholds across scales of space, time, and social organization and across ecological, social, and economic domains may be breached (Kinzig *et al.* 2006). Therefore it is recommended to define accurately the characteristics of the system under study in particular the questions "resilience of what?" and "resilience to what?" (Carpenter *et al.* 2001) what consequently results in a single threshold.

Predicting these undesirable transitions may sound like an impossible task because of the inherent complexity of the underlying system. However, a new field of research starts to emerge which focuses exactly on such "early warning signals" and "critical transitions" (Scheffer *et al.* 2009). Recent works in different scientific fields such as economy, climatology, ecology, medicine on early warning signals suggest that abrupt shifts in stable states are preceded by a critical slowing down of processes in the systems and functioning of the systems in vicinity of tipping points. Most recently it has been observed that the resilience of a system which approaches the near neighbourhood of a tipping point slows down. As a consequence, the recovery time after perturbations of a system slows down when approximating tipping point also leading to changes flux pattern (Dai, Korolev & Gore 2013) and increased autocorrelation (Dakos *et al.* 2008).

2.5.2 Long-term research and sustainability science

In the past few decades, considerable effort has gone into setting up a network of research and monitoring facilities devoted to long-term ecological research (LTER). Started in the USA, the idea rapidly spread out and other countries created their own LTER network or similar observatories. LTER projects initially focussed on documenting, analyzing, and explaining ecological patterns and processes operating over long time spans and broad ecological gradients, and were therefore often situated in areas with no or little human influence. While the first LTER sites were rather small-scaled, the need for finding answers to global challenges such a climate change urged the creation of wider LTER sites or the so-called LTER platforms integrating several sites in one region.

However, rapidly the absence of humans in the majorities of studies carried out in the LTER sites and platforms was regretted. Several currents therefore proposed to study "coupled human environment systems" (Global Land Project; Turner *et al.* 2003b; Dearing *et al.* 2006) or to work on "long-term socio-ecological research (LTSER). LTSER not only investigates changes in the state of the environment, but also analyzes societal pressures on ecosystems and the forces driving them, while proposing measures that might alleviate these pressures. Conversely, the effect of ecological change on society, i.e., socioeconomic impact, is a legitimate subject of research (Haberl *et al.* 2006). LTSER regards society-nature interaction as a dynamic process in which two self-organised systems, society and nature, interact. The way how people are integrated in LTER is often through the implementation of the Integrative Science for Society and the Environment (ISSE) schema (Collins *et al.* 2011).

In the Jura region, the vegetation dynamics in wooded pastures were found to be slow, with strong legacy effects since the development of true wooded-pasture mosaic is quite slow. Climate change since the Middle Ages has contributed to the mosaic structure of these pasture woodlands in the Jura (Peringer *et al.* 2013) and current land use will still influence the landscape patterns even if the management was adapted, e.g. with economic incentives, to increase the maintenance of wooded pastures (Huber et al. 2012a). In this context, time lags in the process of policy making are also relevant. The long time it takes to introduce policy measures far exceeds the normal election and budgetary cycles of the political-administrative system. If changing policies is to be effective, it will be crucial to extend the institutional, structural and policy design-oriented approach with a stronger focus on the temporal dimensions of policymaking and strategy development. Future long-term strategies and policy measures will have to reconcile the long-term goals of sustainable development with individual and collective actions that have a rather short-term focus.

It is obvious that this iterative approach is time consuming and expensive, and can only be rarely achieved in a single project, considering their average duration of one to three years, or by a single person. A proposition (Spiegelberger *et al.* 2012) is that research institutions should pay more attention to the complementarity of scientist's background, so that groups with large and various expertise could be built. Interdisciplinary approaches should be favoured (Likens 1998), even though the communication between different scientific communities could be difficult (Miller *et al.* 2008). It would also be necessary that such groups can work on a common topic for several years. Sustainability science (cf. box 2) which takes into account different disciplines (Turner *et al.* 2003a) could be such an approach.

As an example where sustainability science may play an important role, I'll refer to findings from the Mountland project. Wooded pastures are a specific case in which biodiversity conservation demands a certain level of land-use intensity (see chapter 2.1.2). Not surprisingly, our simulation results reveal a positive relationship between the maintenance of biodiversity and agricultural production (Gavazov *et al.* 2013). Thus, there is a potential win-win situation in food production and biodiversity conservation what may offer an opportunity to achieve a further "greening" of agricultural policy. However, more general policy developments, such as more open agricultural markets, make an implementation of spatially specific economic incentives challenging even though simulation results suggest that new measures could counteract the loss of biodiversity to a degree (Huber et al. 2013b).

Other ways to overcome an individual researcher's incomplete expertise and to excel in several approaches is to bring people together to tackle a common project, as it is done, for example, in the LTER sites (Likens 1998). Such an approach is promoted with the establishment of the Central French Alps long-term socio-ecological research platform (Alps LTER, Lavorel *et al.* 2012). Based on earlier observational studies, a common project was developed which brought together researchers from different disciplines, but also those who used different approaches. This paves the way for more in-depth study of ecological questions. The advantage of such research structures would be manifold and would trigger breakthrough research in deepening the functional approach and also result in increasing individual competences.

2.5.3 Where want I go from here?

There are several ways to continue my research. Apart from opportunistic responses to research calls (a necessary evil), I still see my main activities for the next few years in the field of the stability of mountain ecosystems to climate change (increase in average temperature, extreme events, etc.) and/or changes in management (abandonment, increased availability of soil nutrients by liming, fertilizers, increased stocking rates, etc.). However, I whish to develop more research on measuring spatial patterns (autocorrelation) and fluxes of mountain ecosystems to estimate their stability in time and to experimentally disturbing these spatial patterns and fluxes of mountain ecosystems in order to assess their tipping points. On a more wider and international level, I would like continuing working on available data sets from networks such as the Mountain LTER to compare by using directly the original data or by meta-analysis the effects of climate change on vegetation and soil.

In collaboration with researchers and stakeholders, I aim at further investigating the large topic of "sustainability sciences" of mountain socio-ecosystems. Collaborations with other mountain region could be envisagable, but creating a (in)formal working group on a local/regional scale should be a first step.

2.6 Other topics I'm interested in ...

Beside the above described projects, I worked on several others topics during the last years of which I wish to highlight two:

Invasive alien species such as Asian knotweeds (*Fallopia* ssp.) are a particular research subject. A first work was done by F. Dommanget which I co-supervised during her master on the role of the vegetation and light competition in the development of *Fallopia* ssp. at riverbanks. The most prominent outcome was that light availability prevails over soil fertility and structure on knotweed performance expressed as above-ground biomass per square meter (Dommanget *et al.* 2013b). In another study, where my master student S. Bibollet investigated the ecological factors linked to the presence of Asian knotweeds in mountains areas, we analysed our data together with colleagues of the University of Lyon. Light availability was once again an important factor explaining the presence of *Fallopia* ssp. for the lowland region together with anthropogenic parameters and natural components (light penetration, slope, and the presence of a watercourse) while predictors of *Fallopia* spp. presence in the upland area only included anthropogenic elements such as the presence of a road or trail and passing-by rate of humans. We conclude that the spread of *Fallopia* spp. in upland areas was mainly linked to human activity whereas dissemination of the species occurred both through humans and in natural ways in lowland areas, and this may be due to a more recent colonisation in the mountains (Rouifed, Piola & Spiegelberger 2014). Both papers point out that management interventions at an early stage could be a powerful tool to mitigate negative impacts of complete invasion by Asian knotweeds (Rouifed *et al.* 2014) or by focussing on light competition. A way to do so could be planting of rapidly growing willow cuttings (Figure 30), which seem rather resistant against allolopathic effects of Japanese knotweed (*Fallopia japonica*), as we've shown in collaboration with my master

Figure 31: Set-up of experiment on the allelopathic effects of *Fallopia japonica.* on cuttings. By using only leachates from pots with our without *F. japonica*, the confounding effects of competition between target plants and *F. japonica* is avoided. Photo by M. Imbert.

student M. Imbert (Dommanget *et al.* 2013a).

Leaving the area of a single species and going more towards general features, I worked with my master student J. Gay-des-Combes on the assemblage of species in novel ecosystems in Australia (Lai *et al.* 2014). To test this, we examined multiple plant invasions of a single ecosystem by using extensive community data to calculate segregation between six target alien species and all other species. We related segregation to species' positions along community trait hierarchies and identified at least two distinct invasion strategies: "exploiters" which occupy high positions along key trait hierarchies and reduce local native diversity (particularly in nutrient-enriched situations), and "coexisters" who occupy intermediate trait positions and have no discernible impact on native diversity. We conclude that trait hierarchies, linked to measures of competition, can provide valuable insights into the processes driving different invasion outcomes.

Figure 32: Manatee swimming over underwater seagrass pasture. Photo by A. Avampini (US FWS).

Manatees - or "swimming cows" - are another subject from the beginning of my scientific career which allowed me later to switch very gently during my PhD thesis to the study of the impact on the vegetation of "terrestrial" cows. During a field survey in French Guiana, I assessed the forage habitat of manatees and some abotic water conditions, which were similar to other habitats described for the Carribean Sea (de Thoisy *et al.* 2003). Contrary to other habitats in the region, we did not find any submerged aquatic vegetation in the study area which in general represent the main food source. However, a botanical survey along the banks revealed that most plants seem to be potential forage for manatees and it is therefore suggested that manatees graze on the bank vegetation, where feeding traces were found (Spiegelberger & Ganslosser 2005).

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