CLÉMENT VIGUIER

MOUNTAIN GRASSLANDS DYNAMICS: INTEGRATING PHENOTYPIC PLASTICITY IN A NEW AGENT-BASED MODEL

ABSTRACT

potential ~~the~~ a underlying

Mountain grasslands provide numerous ecosystem services that need fine understanding and characterisation to be assessed and predicted. The vulnerability to climate change and the complexity of mechanisms ~~driving~~ alpine community dynamics require the development of new tools to predict the dynamics of these communities ~~facing~~ under new conditions. ~~Moreover~~, individual-level variations have large effects on community responses to changes in external conditions ~~changes~~, ~~as shown by~~ multiple empirical studies, but often overlooked in modelling approaches. In addition to these effects, intra-specific variability has contrasting potential impacts on coexistence mechanisms that need to be disentangled.

To answer both the need for a dynamic model of species-rich communities and the integration of individual Variation ~~level~~, the model `MountGrass` was developed. It is designed around two main components: (1) a closed strategy space allowing an efficient representation of high species diversity, and (2) a plastic allocation mechanism integrating trade-offs between active and structural tissues, as well as between shoot and root tissues. In a first result part, after a parameter filtering step, the combined effects of allocation rules, species strategy and phenotypic plasticity on individual plants ~~are~~ were studied. In a second part, the effect of plasticity ~~is~~ was then studied at the scale of the community.

This work demonstrates the importance of phenotypic plasticity both at the individual scale and its role in community dynamics. While further work is needed to fully capture plasticity mechanisms, the model provides a sound starting point to further explore the role of intra-specific variability in coexistence mechanisms, the resistance and resilience (of what?) to drought events, or the detection of regime shifts in this type of systems.

The model was analysed at two levels of organisation:

~~The model is parameterised at two levels~~ with

a) ~~indiv~~ growth of individual plants ~~in isolation~~

b) community dynamics

in a first step, growth parameters individual-level values ~~are~~ were ~~identified~~ filtered using published ~~growth~~ experimental growth data.

add some results.

Aknowledgements

I love you all, but I love you more Mom.

CONTENTS

I

INTRODUCTION

1 CONTEXT

1.1 Global change: how to describe the future of alpine ecosystems?

1.1.1 The value of ecosystems: from properties to services

A NEW LOGIC

unclear

Everyone has a particular relationship with nature. The vision we put behind this word depends on the way we experienced nature, it ~~can~~ be temperate or tropical forests, mountain rivers or cliffs on the ocean littoral, bird songs or wind between stones. Anyone who ~~that~~ shares one of these visions wants to preserve natural systems. But facing this emotional perception and inner desire to see these ecosystems ~~be~~ preserved, there are other forces that push in opposite direction. The reduction of biodiversity is increasing at dangerous rates, the deforestation threatens the largest forest systems, insects are less and less presents and animals are repelled to fragmented and diminishing habitats. Logics, other than emotional attachment and will to protect nature, impact all natural systems around the world because they are driven by other interests. To be protected, the natural systems needed a way to be integrated within these strong driving logics. The notion of **ecosystem services** was developed by Costanza et al. 1997 to capture the value of **ecosystems**. It encompasses the benefits humans ~~extract~~ derive from ecosystems. It enables a categorisation of services and their quantification (up to the level of ~~that can go to the~~ monetisation), and therefore allows them to be taken into consideration in the global logic of capital, investment and value.

at some level / too strong

will likely

need citations here. or you put the whole thing in a foreword, what you can be scientific

does the highlighting mean something?

SERVICES

The notion of ecosystem services aims to capture the value of ecosystems, but what is this value? In other words, what benefits does nature provide us? If one could be tempted to answer that the value of an ecosystem cannot and/or should not be measured, it is clear that all ecosystems do not benefit ~~to~~ humans in the same way, and that these differences could be quantified. Facing the diversity of ecosystems, and the diversity of services they provide, we can try to develop a short answer for the object of study to this document: mountain grasslands.

The term **mountain grasslands** designates, in this document, all grasslands, below and above the treeline, that have short growing seasons delimited by snow-covered periods and experience high variations in temperature and water availability. This term is intentionally generic as the scope of this work is relatively broad rather ~~and~~ theoretical.

→ related to existing definition? Körner?

Mountain grasslands provide numerous services, that can be divided into multiple categories such as provision, cultural, and regulating services (see figure 1.1). Provision services are related to the quantity and quality of primary resources the grasslands provide. Fodder production and quality are the main

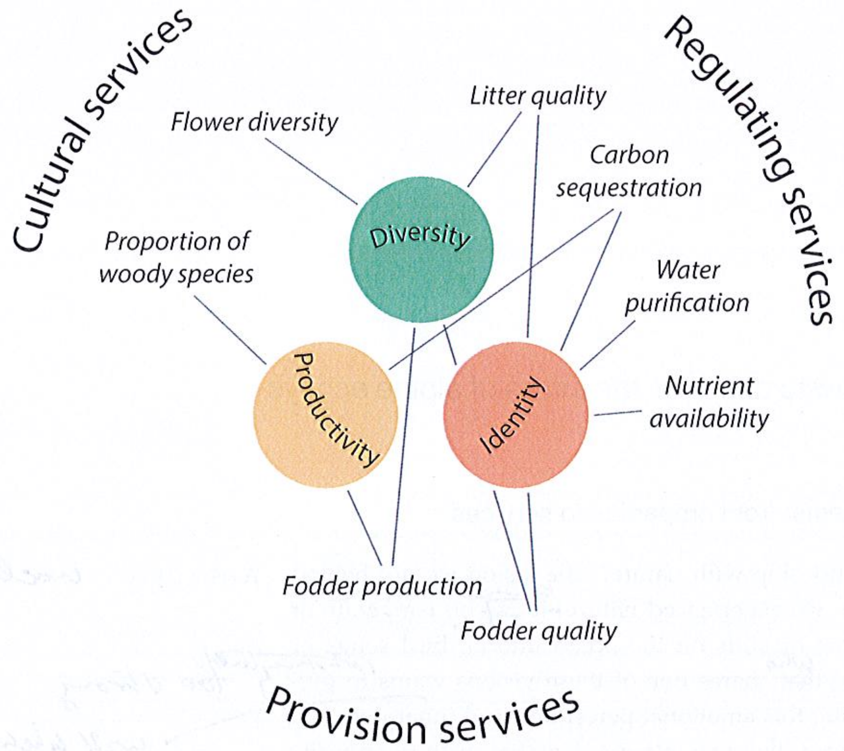

Figure 1.1: Three forms of plasticity in models.

Title does not match content

(and honey)

measures of provision services. Other services can be included in this category: diversity of flowers and phenology for flower production for instance. Productivity is also ~~interesting~~ relevant to assess carbon capture, a regulating service. Soil nutrient availability and water filtering are other regulating services impacted by the identity and diversity of species populating mountain grasslands. Finally, cultural services, related to tourism activity and landscape appeal are also related to grasslands species diversity.

In case of terrestrial ecosystems, vegetation cover is often central because of its role in primary production, and the fact that vegetation community informs ~~on~~ about the properties of the abiotic and biotic conditions. Moreover, most of studies on services from terrestrial ecosystem are interested in plants and soil invertebrates **de_bello_towards_2011** revealing the importance of vegetation in the provision of ecosystem services. In addition, in alpine habitats plant communities are susceptible to be the first impacted by the global change because they cannot escape changes in conditions and are the target of management practices linked to fodder productions. All these arguments support the interest of studying the vegetation dynamics for the assessment of ecosystem services.

PROPERTIES

~~The~~ Ecosystem services are tightly related to the **ecosystem properties** (as illustrated in figures 1.1)(S. Lavorel and Garnier 2002; Díaz, Sandra Lavorel, F. d. Bello, et al. 2007) that can be extracted from the description of the grassland communities. Ecosystem properties are features of the community that characterise it and arise from the characteristics of all parts of the system or how they combine. The main properties of a plant community are captured in the following concepts:

- **identity**: the identity of the community refers to its ~~the~~ dominant species (or directly its characteristics) ~~of the community~~ that transfers its traits to the whole community. It can also refer to mean traits (with community-weighted mean measures) of a community. In this document, identity will often be used to talk about the resource use strategy i.e. whether it is (more or less exploitative). While this notion can encompass multiple traits and measures, it is practical to use one term to identify components of the community description that can be attributed to a species[1];

Add a phrase to explain what exploitative strategy means

[1] in opposition to variables that are related to a system, *e.g.* diversity cannot be expressed for a species alone

References

- **diversity**: diversity plays a large role in the provision of multiple services, and is related to other properties of the community. Diversity can be expressed in terms of species richness or functional diversity[2], and by a wide range of indices that are not discussed here. Despite a lot of nuances between these notions, they are often tightly correlated ~~and diversity will be discussed in~~ terms of the number of species or functional volume in the rest of this document.

explanation needed

Citation needed for different strategy: go with two measures complementary

[2] each measure depending on the functional space that is considered

- **productivity**: productivity captures the capacity of the system to produce organic matter in a given timespan. It is an ambiguous term as it can refer to the abiotic environment, to a species or a community property or even to a service. I will try to limit its use to the species or community relative vegetative biomass in a given condition.

Linking ecosystem services to ecosystem properties is essential both for the understanding of processes controlling these services and for an easier quantification of such services. This is particularly important for the prediction of services levels to plan management practices in the context of global change. Some ecosystem services are ~~here~~ linked to the main community properties as illustrated in figure ??. Because services are hard to assess, one can take advantage of this link and assess levels of ecosystems services based on ~~thanks to~~ a detailed description of the community; of both its structure and properties. The structure is defined by the relative abundance of the different species of the community, and properties result from the combination of the structure and the specific characteristics of present species. Multiple drivers affect the relative abundance and characteristics of a given species, from abiotic filtering processes to biotic interactions. Thus ~~So~~, ecosystem services also largely depend on abiotic factors (S. Lavorel and Garnier 2002). Therefore, there is a tight link between drivers, community structure and properties, and ecosystem services (see figure 1.2) that can be exploited to predict changes in ecosystem services (Lamarque et al. 2014).

Drivers
↓
Properties
↓
Services

Figure 1.2: Link between abiotic drivers, community properties and ecosystem services.

The evaluation of ecosystem services relies on a precise description of an ~~the~~ ecosystem is abiotic and biotic properties. In mountain ecosystems, the plant community is arguably the most dynamic and complex driver of ecosystem services, but direct links can be drawn between a ~~the~~ fine description of the community and ~~the~~ ecosystem services. Understanding and prediction the main ~~variables~~ dynamics that capture those links is necessary to efficiently predict changes in ecosystem services levels. of Plant communities are complex interconnected systems. In order to evaluate ecosystem services, plant communities ~~they~~ can be summarised by three main types of variables that capture different dimensions of such systems: the diversity, the productivity, and the identity. But grassland communities are natural systems driven by environmental variables, and changes in these drivers can lead to changes in services because of this link.

1.1.2 Global change: what changes and what consequences

Mountain grasslands are maintained by strong climatic constraints that limit growth rate and lifeforms (**koorner_alpine_2003**), but also by frequent grazing or cutting perturbation regimes that strongly limit the growth of woody species and favour low stature species or rapid growth herbs (Díaz, Sandra Lavorel, McINTYRE, et al. 2007). → check citation But these drivers are changing at alarming rates with negative consequences on levels of ecosystem services (Schröter et al. 2005). Moreover, mountain grasslands are suspected to be very vulnerable (Schröter et al. 2005; Engler et al. 2011) due to higher variations in water availability regimes and specific warming processes (Mountain Research Initiative EDW Working Group 2015), stronger isolation (island effect due to rise in temperature) and reduction of the grazing pressure.

CLIMATE CHANGE

The rise of carbon dioxide in the atmosphere due to human activities has a large impact on climate. The constant increase in mean temperature is the ~~most~~ best known and easily observable phenomenon (see figure 1.3). But mountain grasslands will also ~~suffer from~~ experience more frequent and severe drought event, ~~but also~~ as well as extreme precipitation events (**beniston_climate_1997**; Solomon, Change, and I 2007; Intergovernmental Panel on Climate Change 2014). They ~~will~~ are also predicted to experience longer growing seasons and stronger invasive pressure from alien species and species from a lower altitude. citation

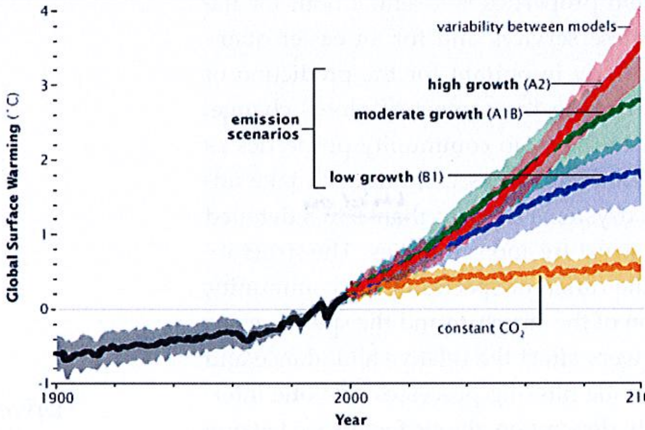

Figure 1.3: Historical models and projection scenarios for global mean temperature from Solomon, Change, and I (2007).

In this context, the ~~aptitude to~~ ability of plants to adapt to such changes and to cope with new competitors, no more filtered out by climatic conditions, will greatly determine the response of alpine communities (Alexander, Diez, and Levine 2015).

LAND-USE MUTATIONS

In addition to changes in climate, land use is also modified. Land-use, mowing or grazing in alpine grasslands, is an ~~great~~ important filter for slow-growing perennial species that try to accumulate biomass over multiple seasons. Because of such asymmetric effects, land-use acts as a strong driver and can cause mountain grasslands communities to shift along service gradients (**schirpke_multiple_2012**). Land-use abandonment is suspected to greatly impact the invasion dynamics as it removes the pressure of biomass removal (**carboni_simulating_2017**).

asymmetric!

Global change is a source of considerable changes, both in mean regimes, but also frequency and amplitude of climatic events. In addition to changes in

the climatic environment and resource availability, ~~mutation~~ changes of management of mountain grasslands will also affect community dynamics and particularly competition hierarchy. These modifications of strong drivers will have large effects on plant communities, and therefore on ~~their~~ the attributes and the services they provide.

Mountain grasslands provide numerous services, that can be assessed thanks to ~~the~~ main attributes of the plant community. But global change threatens these systems, and as consequence, the ecosystem services we take benefit of. We need tools to anticipate the effects of global change on these services and eventually adapt the management of mountain grasslands.

1.2 The need for new mechanistic models

1.2.1 The limit of classic patterns

Citation needed

A NEW WORLD

The world is changing at a fast rate (Butchart et al. 2010; Intergovernmental Panel on Climate Change 2014), but most importantly in ways never experienced by living species in recent history. So, anticipating the effects of new environmental conditions on vegetation community cannot be built on the observation of previous or existing states. Extrapolation of complex system behaviour is generally not a good predictor of its ~~actual~~ current behaviour. ? The complexity of the prediction goes beyond the multiplicity of dimensions impacted by the global change (rising mean temperature, frequency, and amplitude of drought events, reduction of cutting frequency or grazing abandonment, etc...), as the drivers often interact, synergise or ~~negate themselves~~ inhibit. with positive or negative feedback.

FIND BALANCE

To answer this challenge, large-scale experiments are conducted such as the Cedar Creek experiment in the United-States, or the JENA experiment in Germany. These experiments give high-value experimental data for various conditions and a variety of species, where interactions can be studied as well as management effects. Transplant experiments are also conducted to investigate the effects of temperature rise on the productivity, diversity, and identity of the community (as an example for SLA response see Scheepens, Frei, and Stöcklin 2010, or see Debouk, F. d. Bello, and Sebastià 2015 for an increase in productivity and decrease in diversity, as well as a shift toward more acquisitive species).

But these common garden or transplant experiments also show contrasting responses, that can come from opposite responses between the intra-specific level and inter-specific level (Jung et al. 2014), between low and high elevation (changes in identity and contrasting effect in diversity between altitudes, observation data in Rosbakh, Bernhardt-Römermann, and Poschlod 2014) or between effects (see effect of warming and carbon dioxide on phenology in Reyes-Fox et al. 2016).

To accurately predict the future dynamics of grasslands communities, we need to be able to find the balance between dominant effects and eventually identify the interactions. For such complexity, empirical studies provide required and fundamental knowledge of processes and basic differences between effects, but no consensus can be made (Merilä and Hendry 2014) and ~~new~~ additional approaches need to be ~~use.~~ ~~developed~~ used. unclear unclear

An additional argument for the use of alternative approaches is the uncertainty around ~~the~~ climate scenarios (see figure 1.3). Indeed, the future of the ~~planet~~ atmosphere, and by consequence climate, ~~is~~ mainly ~~depending~~ depends on how humans

we are capable of changing our dependency ~~to~~ on fossil energy (Intergovernmental Panel on Climate Change 2014). The will to adjust management scenarios to the future of vegetation community (**schipe_multiple_2012**) also require extensive experimentation (Rodriguez, Van Oijen, and Schapendonk 1999; Martin et al. 2012; Deléglise et al. 2015).

this comes a bit as a surprise given that you talk about climate

Nice!

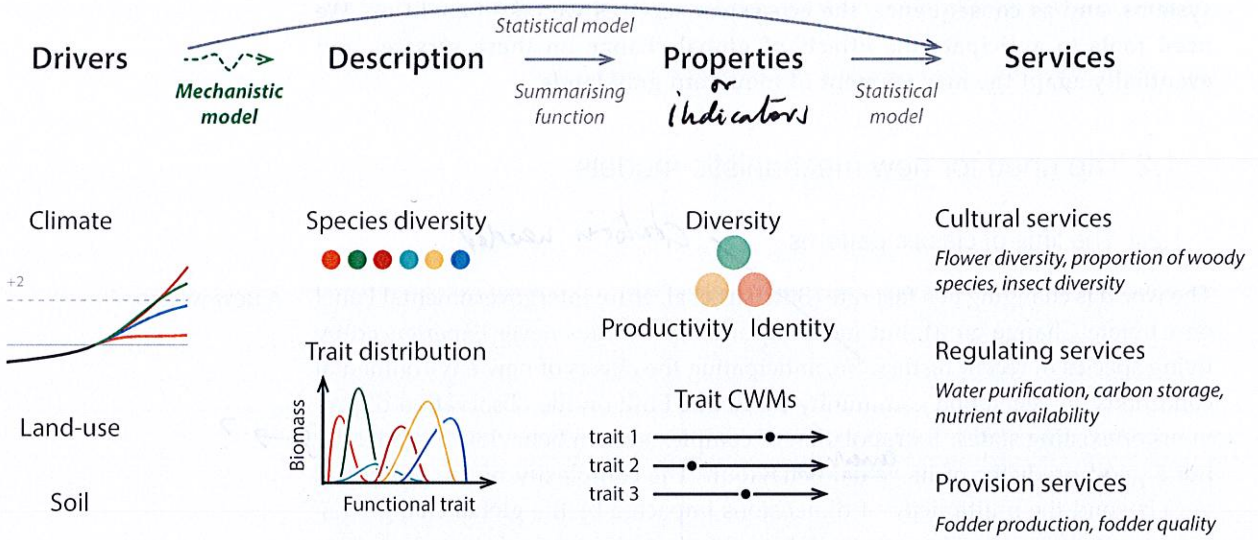

Figure 1.4: From drivers of community dynamics to ecosystem services. The effects of main drivers (climate and land-use) on grasslands dynamics is captured ~~thanks to~~ by mechanistic approaches to predict the composition and structure of the community. This description can then be used to assess the levels of ecosystem services through statistical models, to evaluate climatic scenarios or alternative land-use practices.

Mechanistic approaches allow better linking of drivers with community dynamics. This link can then be used to assess ~~the~~ levels of ecosystem services as illustrated in figure 1.4.

1.2.2 When phenotypic plasticity makes things complicated

Within the context of climate change, the ability of species to adapt has a great influence on the response of the community. Indeed, the capacity of species to adjust to variations in drivers, via genetic variability and mutations, or thanks to plastic mechanisms, will certainly buffer the response of the community to changes in climate or land-use. Morin and Thuiller (2009) highlight stronger responses to climate change from vegetation communities within niche-based distribution models than within process-based models that capture adaptation mechanisms. More mechanistic processes should be included in these approaches (**evans_toward_2016**) to take into account adaptation mechanisms and interactions between species (Gilman et al. 2010). Plasticity can also change the competition intensity that increases negative effects of climate change (Hänel and Tielbörger 2015), while it can in other cases shift interactions from competition to facilitation (Callaway, Pennings, and Richards 2003).

Phenotypic plasticity adds another level of complexity to the dynamic of communities and the interacting drivers. Statistical or expert based prediction cannot handle such complexity and mechanistic approaches have great potential to model complex systems.

easily

You need to make clear the difference between phenotypic plasticity in particular and other forms of intraspecific variation (e.g. genetic variation). Either here or elsewhere. If elsewhere, make reference to that place already here

1.2.3 The rise of individual-based approaches

Individual-based-models (IMBs) let the complex behaviours of systems ~~made~~ composed of numerous interacting agents emerge from individual ~~functioning~~ behaviour. This type of modelling is extremely well adapted to the modelling of plant communities as we have a fairly good understanding of plant functioning, and parameters are relatively easy to measure. The dynamics of essential resources is also relatively easy to compute. Yet, this apparent simplicity is relative (to animal modelling for example) and numerous models have been developed with various simplification hypotheses. Most of these hypotheses deal with the essential resources: light is often ignored in grasslands, while forest models focus on this aspect of resource competition. ~~These hypotheses~~ are most of the time justified, and the choice of model simplifications depends on the focus of the modelling exercise, and the importance of the given variables for the dynamics of the system.

IBMs of plant communities have been ~~These models are~~ used to investigate the effect predicted of climate change in the study of Rodriguez, Van Oijen, and Schapendonk 1999 with the model LINGRA-CC and show an increase in productivity with climate change. But the link to land-use practices is always questioned, and in this example, the increase in productivity allows a higher cutting frequency. Alternative scenarios of what? are also explored in other grassland models Taubert, Frank, and Huth 2012; Taubert 2014; Maire, Soussana, et al. 2013; Maire, Gross, et al. 2009. Forest modelling presents also numerous implementations of individual-based models (see Falster et al. 2016; Maréchaux and Chave 2017 for recent forest model examples). → why these? physiologically oriented; with strategy spaces (at least for Maréchaux)

BETWEEN CLIMATE AND LAND-USE

unclear

This list is somewhat arbitrary.

Other models based on processes can be used to study long terms dynamics in the context of climate change in mountain ecosystems. It can be used to study patterns of diversity (**isabelle_fate-hd_2014**) or the impact of evolutionary processes on adaptation to climate change (Cotto et al. 2017).

1.2.4 Gaps to fill : plasticity

A wide range of models has been developed to better understand biological processes involved in plant growth and population dynamics and the impact of climate change and land-use on these dynamics. They spread from organ-based models to functional types approaches. As the scale increases, the resolution diminishes and the verticality of processes is rarely ~~taken into consideration~~. This is rarely a problem in stable conditions because the lower levels are implicitly integrated into the grain of larger processes (like the leaf gas exchanges regulation processes are ignored at the scale of the population). But two aspects can limit such simplification: (1) if the process is ignored instead of being integrated into higher level function (*e.g.*: stomatal regulation is often not modelled because it is assumed that it is correlated to photosynthetic activity, either because it is limiting the photosynthesis when the vapour pressure deficit is high, or it is down-regulated to avoid water loss when photosynthesis is limited by other factors). However, phenotypic plasticity is often ignored but not translated into the hypotheses of the model. Moreover, variables that are directly impacted by this process are explicitly represented (unlike stomatal conductance with stomatal regulation processes) leading to a misrepresentation of these variables (especially root:shoot ratios (RSR) or strategic traits like SLA); (2) if the non-modelled process has a great impact on the dynamic of the system.

unclear

DICHOTOMY BETWEEN MODELS

Among models that target grasslands ecosystems (~~or more specifically~~) there is a dichotomy between growth models that are mainly interested in individual processes and those interested in ~~species dynamics~~ Soussana et al. 2012; Taubert 2014; Lohier 2016, and models interested in species-level processes and community dynamics (**boulangeat_fate-dh_2014**; Cotto et al. 2017). The former focus on the individual growth of a limited number of species. They take into account fine-scale resource dynamics and interactions driven by explicit strategies and precise plant functioning. These models are on the side of the spectrum of the development models that often focus on a single species. The productivity of the system is often the primary concern and questions relative to the management of these systems are privileged over questions concerning climate change (but see Rodriguez, Van Oijen, and Schapendonk 1999, but still with the perspective of productivity). The latter is more interested in larger scale dynamics driven by the climate and evolutionary processes. The questions investigated ~~interrogated~~ with these models are therefore more often relative to climate change and adaptive dynamics of the communities and the effects on community diversity and identity. These models are closer to DGVMs despite finer scale interactions. This dichotomy highlights the lack of integrative models that support community dynamics at long time scales with modelling of processes at the individual scale, based on explicit resource dynamics. The explicit modelling of the link between plant strategies, plant functioning, resource dynamics and plant growth allows a solid integration of plant interaction and external drivers (via the effect of resource dynamics and plant growth). Moreover, phenotypic plasticity can be integrated at the plant level, while its complex effects are emergent. Finally, considering the growth of individuals, the strategies of species and the dynamics of the population is required to ~~build~~ predict ~~of all~~ many facets of mountain grasslands communities (diversity, productivity, and identity) that can integrate both management practices and climate scenarios.

first use? explain abbreviation

WHERE IS THE DIVERSITY

Because models have often practicality objectives, it is easier to develop a model that can be calibrated with species-specific empirical data. They can also be calibrated with Bayesian procedures and pattern-based approaches (Hartig et al. 2011) As a consequence, these models often integrate a limited number of species or functional types. This requirement of calibration limits the number of species simulated. To model diverse communities and evolutionary processes, this species diversity is required and a generic framework is attractive in order ~~must be adopted~~ to avoid the calibration of individual species. Such high species diversity is observed in DGVMs that integrate trade-offs and multiple strategic axis (**kleidon_global_20000**; Pavlick et al. 2013).

Models

BUILDING BRIDGES

Mechanistic models are great tools and can be used to explore the uncertain future of mountain grasslands ecosystems. Bridges between individual-centred and generic community dynamics approaches must be built to take into account the complexity of population dynamics emerging from fine-scale interactions and plant functioning, driven both by ~~the~~ environmental conditions and species strategies. Considering both levels is compulsory to capture the complexity of responses of vegetation communities exposed to diverse drivers.

2 Aims, Objectives, and Overview

2.1 Aims: understanding and prediction

Global change is probably the biggest challenge humanity has to face at the beginning of this millennium. Actions are urgently needed to reduce the release of carbon dioxide but also to mitigate the effect of climate change on natural and semi-natural systems. While solutions for the former must be found in technology, economics, and sociology, ~~the~~ ecology can help with the latter. But it requires an understanding of how the drivers impacted by global change will impact these ecosystems. The multiplicity of environmental drivers impacted by global change - whose effects can synergise or balance themselves -, in addition to complex structure and dynamics of natural systems make this understanding hard to build and to summarise.

To go beyond traditional pattern-driven ecology and overcome the difficulty of combined causes leading interacting effects, mechanistic approaches ~~should be privileged~~ are promising.

The functioning of individuals living in these communities and the dynamics of the resources should be at the core of the new approaches to better understand the trajectories of the ecosystems.

2.2 Objectives: a new agent-based model for plant community dynamics

~~fully integrate~~ quantitatively explore the consequences of the intricate interplay of the multiple processes, in

Traditional empirical approaches of observation and controlled experiments provided valuable information on the functioning of grassland ecosystems. However, they lack the power to ~~understand intricate systems and predict their dynamics~~, especially in case of uncertain scenarios.

Modelling approaches must be used to build understanding and predictions of natural ecosystems dynamics driven by changing environmental drivers. These models should include a diversity of drivers as well as the diversity and the intrinsic complexity of these systems.

In order to compensate a long development time and to extend the reach of simulation experiments, models should try to be generic in structure and flexibility at use, while being specialisabled thanks to parameters or simple equation changes.

citations! Too often you state apodictically something that is hotly debated, without reference to the literature

2.2.1 Generic framework for multi-species and plastic plant modelling

In the context of mountain grasslands, showing unique levels of diversity despite strong environmental drivers, species diversity cannot be ignored to predict the response of the community. This diversity must be translated into species-specific functioning differences leading to diversity in niches and possible responses. In addition to species level dynamics driven by these differences, intraspecific responses cannot be ignored, and a phenotypic plasticity mechanism is needed.

2.2.2 Effect of phenotypic plasticity on plant growth, community properties, and dynamics

Intra-specific variations are expected to play an important role in the response of mountain grassland communities to global change. The effects of phenotypic plasticity and other sources of variations must be disentangled. Explicit integration of species-specific phenotypic plasticity in a plant community model will help identify and understand these effects.

too strong

As multiple services derive from the main properties of the vegetation of mountain grasslands, it is crucial to establish how phenotypic plasticity specifically impacts these properties. Because these properties depend both on properties of the individuals and the relative abundance and diversity of species, effects on processes at both individual and community scales must be investigated.

2.3 Thesis overview

The rest of this thesis is divided into five chapters. The following chapter II, in the form of a literature review, introduces the concepts and knowledge that support the approach developed in later chapters. The chapter III develops the generic framework for plant functioning and phenotypic plasticity from the concepts established in chapter II ~~and further extended~~. Chapters IV and V present, respectively, individual and community scale results of simulations made with the developed model `MountGrass` on the effects of phenotypic plasticity on main plant community properties. ~~Finally, t~~The final chapter discusses the outcomes of this work and possible paths to follow from the presented conclusions. Extensions to d~~evelop on the model~~ are also proposed.

further model developments

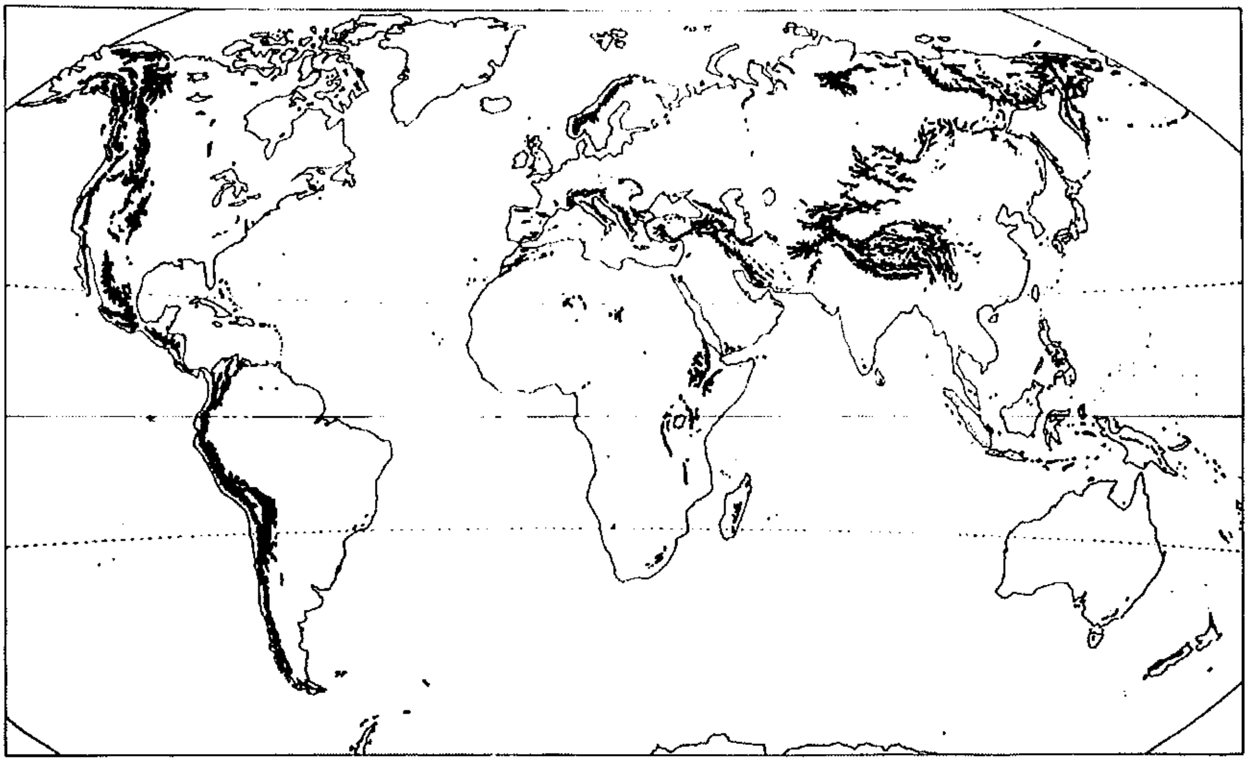

Figure 2.1: Distribution of alpine habitats. Alpine habitats shelter unique and rich ecosystems providing numerous services to human populations. Climate change and mutations of land-use practices threaten these dispersed and fragile habitats. From Körner 2003.

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