

CLÉMENT VIGUIER

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

ABSTRACT

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 new conditions. Moreover, individual variation has large effects on community responses to external condition 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 level , the model *MountGrass* was developed. It is designed around two main components: (1) a closed strategy space allowing a 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 studied. In a second part, the effect of plasticity is then studied at the scale of the community.

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

ACKNOWLEDGEMENTS

I LOVE YOU ALL, BUT I LOVE YOU MORE MOM.

CONTENTS

I Introduction	VII
1 Context	1
1.1 Global change: how to describe the future of alpine ecosystems?	1
1.2 The need for new mechanistic models	5
2 Aims, Objectives, and Overview	8
2.1 Aims: understanding and prediction	9
2.2 Objectives: a new agent-based model for plant community dynamics	9
2.3 Thesis overview	10
II Background: community dynamics, traits and phenotypic plasticity	15
1 Understanding community dynamics and properties: drivers and theories	17
1.1 Community assembly and coexistence	17
1.2 The complexity of diversity	21
2 How to represent plant community	22
2.1 The continuity of functional ecology	23
2.2 How trade-offs make strategy space	25
2.3 How traits link to ecosystem properties	28
2.4 Modelling diverse plant community	31
3 The importance of phenotypic plasticity as a specific case intra-specific variability	33
3.1 Intra-specific variability change the rules	33
3.2 Phenotypic plasticity: a specific case of intra-specific variability	36
3.3 Toward an integrative framework of plant strategy and phenotypic plasticity	41
3.4 How phenotypic plasticity affect ecosystem properties and dynamics	43
III Modelling alpine grasslands with MountGrass, a generic framework integrating phenotypic plasticity	53
1 Alpine environment: conditions, resources, and perturbations	55

1.1	The scales of alpine grasslands	55
1.2	Resources: light and water	56
1.3	Perturbations: frost, grazing, and mowing	56
2	Multi-dimensional strategy space, carbon pools, and trade-offs	57
2.1	Multi-dimensional strategy space and allocation pools	57
2.2	Craft a trade-off: active and structural tissues	60
3	Modelling phenotypic plasticity	61
3.1	Plasticity as a strategy: between species memory and individual experience	62
3.2	Driving rules of allocation	64
4	ODD description of the model <i>MountGrass</i>	66
4.1	Model overview	66
4.2	Design concepts	70
4.3	Details	72
4.4	Limitations and problems	82
IV	Individual performance: strategy and plasticity	85
1	Model properties and individual responses	89
1.1	Parametrisation and sensitivity analysis	89
1.2	Individual level behaviour and properties	99
2	Individual performance, plasticity and variable conditions	103
2.1	Individual performance: between strategy, memory and plasticity	104
2.2	Plasticity and variability of conditions	113
2.3	From model behaviour to competition and coexistence in the real world	119
V	Community dynamics	121
1	Community level simulations: non plastic community	123
1.1	Parameter filtering	123
1.2	Non plastic communities	124
2	Plasticity: impact on species fitness and diversity	124
2.1	Plasticity and diversity	124
2.2	Strategy	125
VI	Synthesis & Outlook	127
1	Synthesis	129
1.1	Modelling diverse community	129
1.2	Effect of plasticity of mountain grasslands properties	129
1.3	On plasticity modelling	129
1.4	The limit of the species.	130

2 Outlook	131
2.1 Competition and feedback	131
2.2 Extend to climate change effects	132
3 Extensions	133
3.1 Ecology of plasticity: plasticity as a trait	133
3.2 Include nitrogen: source of trade-off	133
3.3 For more interaction	134
Glossary	137
4 Index	137

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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

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 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_value_1997** to capture the value of **ecosystems**. It encompasses the benefits humans extract from ecosystems. It enables a categorisation of services and their quantification (that can go to the monetisation), and therefore allows them to be taken into consideration in the global logic of capital, investment and value.

A NEW LOGIC

The notion of ecosystem services aims to capture the value of ecosystems, but what is this value? In other words, what benefit do nature provide us? If ones 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.

SERVICES

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 and theoretical.

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

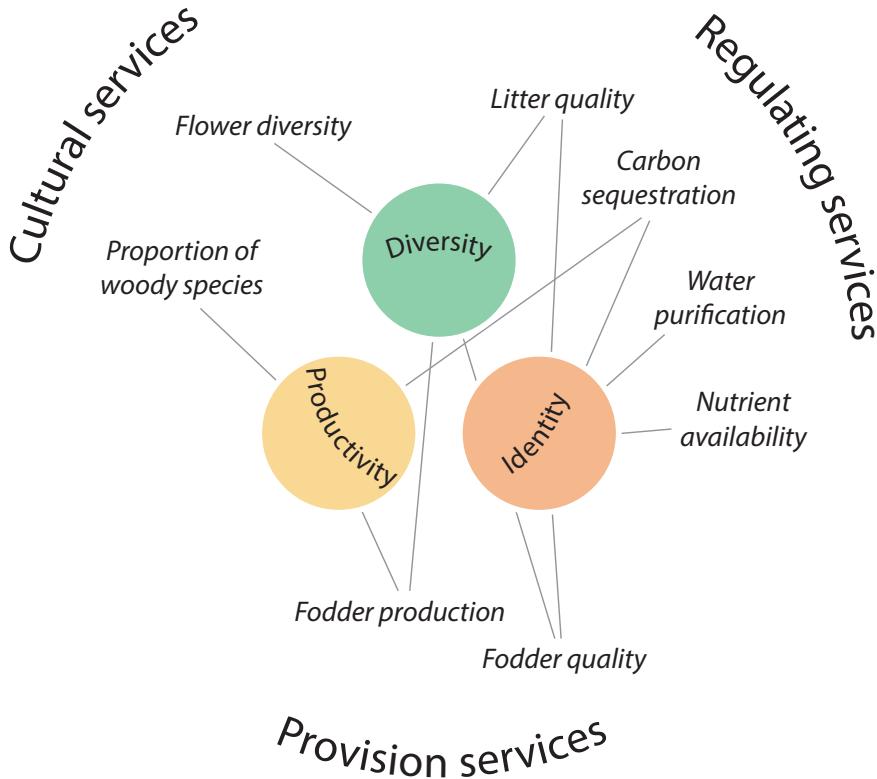


Figure 1.1: Three forms of plasticity in models.

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 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 of primary production, and the fact that vegetation community informs on the properties of the abiotic and biotic conditions. Moreover, most of studies on services from terrestrial ecosystem are interested in plants and soil invertebrate [de_bello_towards_2010](#) 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 production. All these arguments support the interest of studying the vegetation dynamics for the assessment of ecosystem services.

The ecosystem services are tightly related to the **ecosystem properties** (as illustrated in figures 1.1) (S. Lavorel and Garnier 2002; Díaz, Sandra Lavorel, 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:

PROPERTIES

- **identity:** the identity of the community refers to 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 (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 species¹;

- **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 term of species richness or functional diversity², and by a wide range of indexes that are not discussed here. Despite a lot of nuances between these notions, they are often tightly correlated and diversity will be discussed in term of the number of species or functional volume in the rest of this document.
- **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, ones can take advantage of this link and assess levels of ecosystems services 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. 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).

The evaluation of ecosystem services relies on a precise description of the ecosystem abiotic and biotic properties. In mountain ecosystems, the plant community is the most dynamic and complex driver of ecosystem services, but direct links can be drawn between 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. Plant communities are complex interconnected systems. In order to evaluate ecosystem services, 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 in opposition to variables that are related to a system, e.g. diversity cannot be expressed for a species alone

² each measure depending on the functional space that is considered

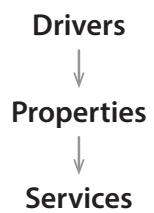


Figure 1.2: Link between abiotic drivers, community properties and ecosystem services.

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 frequent grazing or cutting perturbation regimes that strongly limit the growth woody species and favour low stature species or rapid growth herbs (Díaz, Sandra Lavorel, McINTYRE, et al. 2007). But these drivers are changing at alarming rates with negative consequences on levels of ecosystem services [schroter_ecosystem_2005](#). Moreover, mountain grasslands are suspected to be very vulnerable ([schroter_ecosystem_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.

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 known and easily observable phenomenon (see figure 1.3). But mountain grasslands will also suffer from more frequent and severe drought event, but also precipitation events ([beniston_climate_1997](#); Solomon, Change, and I 2007; Intergovernmental Panel on Climate Change 2014). They will also experience longer growing seasons and stronger invasive pressure from alien species and species from a lower altitude.

CLIMATE CHANGE

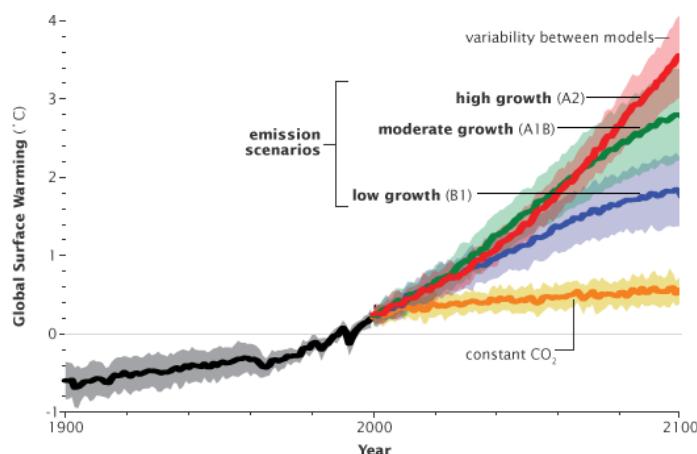


Figure 1.3: Historical models and projection scenarios for global mean temperature from Solomon, Change, and I 2007

In this context, the aptitude to 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).

In addition to changes in climate, land use is also modified. Land-use, mowing or grazing in alpine grasslands, is a great 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](#)).

LAND-USE MUTATIONS

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 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 their attributes and services they provide.

Mountain grasslands provide numerous services, that can be assessed thanks to the main attributes of the plant community. But global change threats 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

The world is changing at a fast rate (**butchart_global_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 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.

A NEW WORLD

To answer this challenge, large-scale experiments are conducted such as Cedar Creek experiment in the United-States, or 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 (example for SLA response Scheepens, Frei, and Stöcklin 2010, or see **debouk_functional_2015** for an increase in productivity and decrease in diversity, as well as a shift toward more acquisitive species).

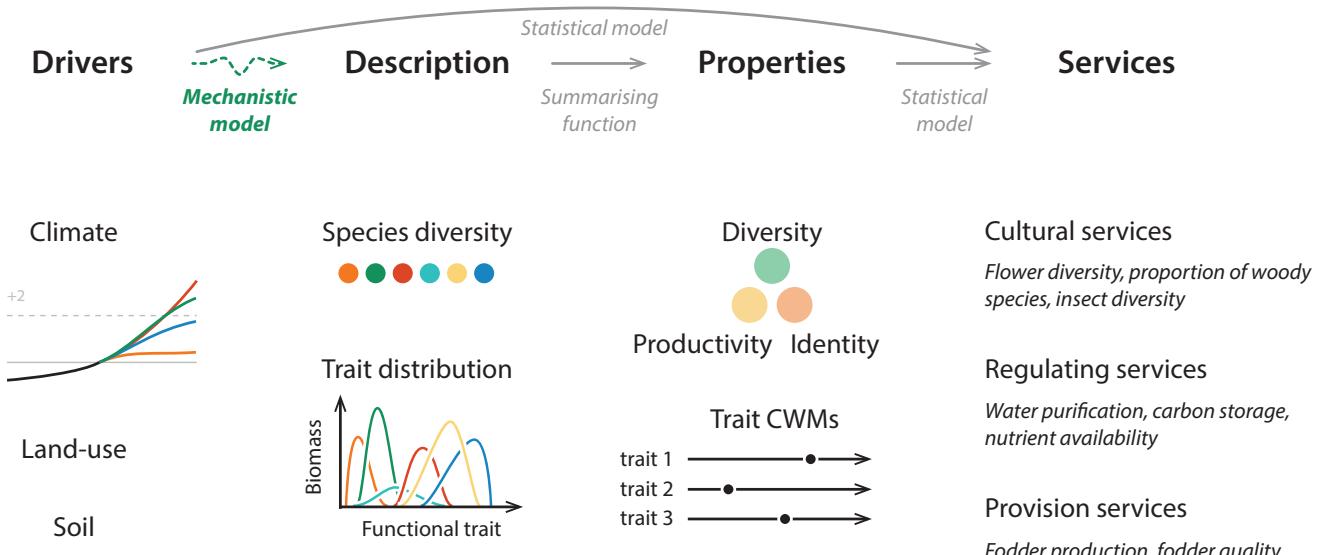
FIND BALANCE

But these common garden or transplant experiments also show contrasting response, that can come from opposite responses between 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 approaches need to use.

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

we are capable of changing our dependency to 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).



Mechanistic approaches allow better linking of drivers with community dynamics. This link can then be used to assess the level 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_comparing_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.

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 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.

1.2.3 The rise of individual-based approaches

Individual-based-models (IMBs) let the complex behaviours of systems made of numerous interacting agents emerge from individual functioning. 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 hypothesis. Most of these hypothesis 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 depends on the focus of the modelling exercise, and the importance of the given variables for the dynamics of the system.

These models are used to investigate the effect of climate change in the study of Rodriguez, Van Oijen, and Schapendonk 1999 with the model LINGRA-CC and show an increase in productivity. 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 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 present also numerous implementations of individual-based models (see Falster et al. 2016; Maréchaux and Chave 2017 for recent forest model examples).

BETWEEN CLIMATE AND LAND-USE

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

1.2.4 Gaps to fill

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 hypothesis 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 ratio (RSR) or strategic traits like SLA). (2) if the non-modelled process has a great impact on the dynamic of the system.

Among models that target grasslands ecosystems (or more specifically) there is a dichotomy between growth models that are mainly interested in individual processes and species dynamics [lohier_analyse_2016](#); Soussana et al. 2012; Taubert 2014, 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 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 highlight the lack of integrative models that support community dynamics at long time scale 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 facets of mountain grasslands communities (diversity, productivity, and identity) that can integrate both management practices and climate scenarios.

DICHOTOMY BETWEEN MODELS

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_statistical_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 generic framework must be adopted to avoid the calibration of individual species. Such diversity is observed in DGVMs that integrate trade-offs and multiple strategic axis ([kleidon_global_20000](#); Pavlick et al. 2013).

WHERE IS THE DIVERSITY

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.

BUILDING BRIDGES

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 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.

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

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 specialisable thanks to parameters or simple equation changes.

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, intra-specific 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.

As multiple services derive from the main properties of the vegetation of mountain grasslands, it is crucial to establish how phenotypic plasticity specifically impact 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, the final chapter discusses the outcomes of this work and possible paths to follow from the presented conclusions. Extensions to develop on the model are also proposed.

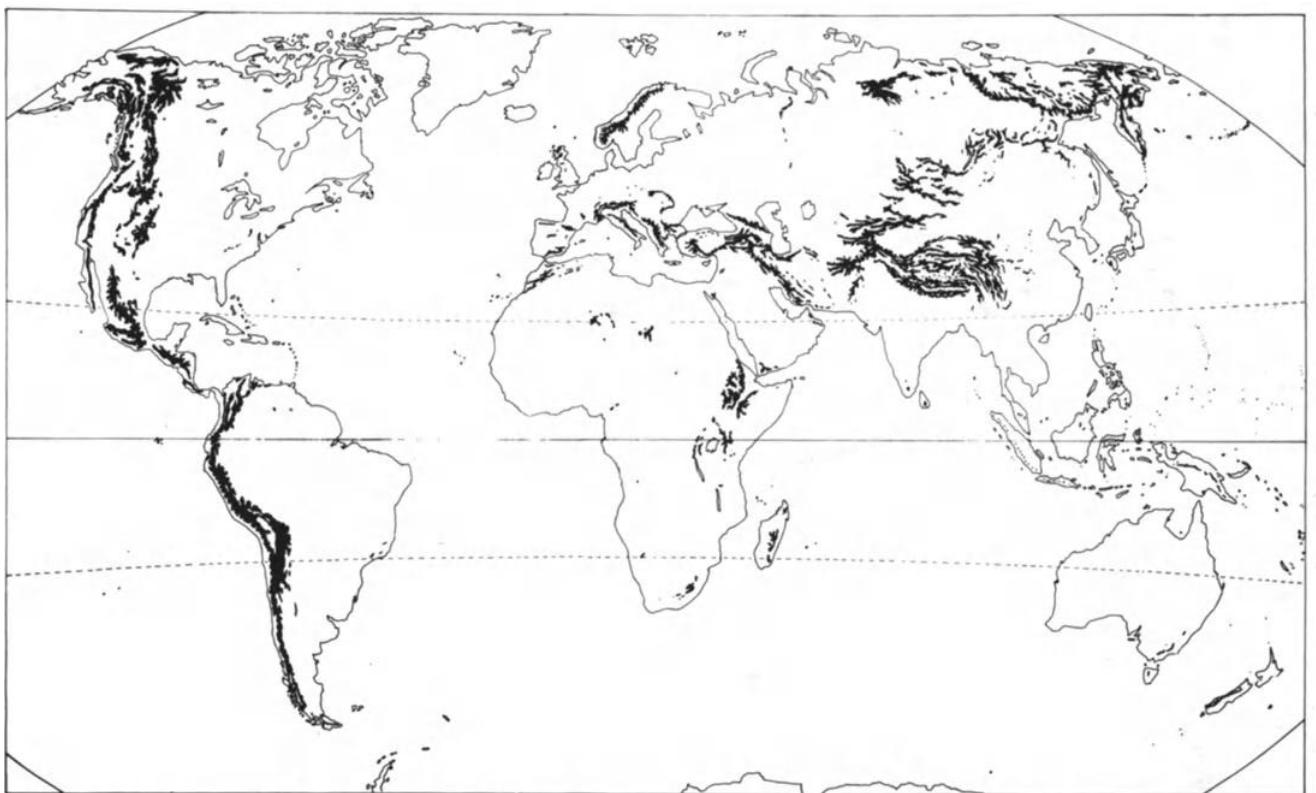


Figure 2.1: Distribution of alpine habitats. Alpine habitats shelter unique and rich ecosystems providing numerous services to human populations. Climate change and mutations of land-use practices threaten these dispersed and fragile habitats. From [korner_alpine_2003](#)

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II

BACKGROUND: COMMUNITY DYNAMICS, TRAITS AND PHENOTYPIC PLASTICITY

This chapter is dedicated to the review of the literature and aims to introduce the concepts and hypotheses used and interrogated in following chapters. A link between properties of the community and the ecosystem services is first drawn, then I examine the use of functional traits to represent plants, plant functioning, and communities. Finally, the impact of intra-specific variability, in particular phenotypic plasticity, on community properties is interrogated.

While this thesis is a modelling thesis, it is not a modelling textbook, and rather than an exhaustive description of the different types of models the focus will be given to selected modelling examples close to the context of this work.

1 UNDERSTANDING COMMUNITY DYNAMICS AND PROPERTIES: DRIVERS AND THEORIES

1.1 Community assembly and coexistence

1.1.1 Filtering processes: from potential to realised niche

A community is defined by the ensemble of species that coexist within the same space and time intervals. Communities were first viewed as a group of species that have evolved together to survive within specific conditions. To maintain itself within the community, each species need to grow during the vegetative phase, survive and reproduce. These steps of the life cycle result from the coordination of multiple physiological processes, supported by the extraction and use of essential resources: light, water, and nutrients. A part of community ecology sees communities as discrete entities with specific characteristics. This view is particularly practical for management as the community type can be associated with certain properties and services, or even particular dynamics and management systems. This view is the base of phytosociology as it is still used. While a discrete approach to community ecology provides practical categorisation, it ignores the fundamental dynamic nature of living systems. In a context of global changes, considering the dynamics of plant communities is crucial to predict how these systems will react to conditions never experienced. Another approach to community ecology considers that communities emerge from the distribution of individuals of a species, distribution controlled by its genetic and physiologic characteristics and its interactions with other species (Gleason 1926, Whittaker 1975). The distribution of individuals depends on how it is affected by abiotic conditions and interaction with other species or biotic conditions. The joint effects of the abiotic and biotic environment are captured by the concept of niche ([elton_1927](#)). The **niche** of a species is defined by how a species population reacts to abiotic and biotic conditions (resource, competition, predation, survival) and how it impacts its environment. Defining the niche of a species is primarily defining the barriers that constraint the distribution of the individuals of the species.

PLANT COMMUNITY

The **abiotic filtering** designates the non-biological variables that prevent the establishment of a species in a habitat. This term generally refers to climatic conditions and resource availability because temperature, water, nutrient and light availability are the main variables that constrain the plant development. Other abiotic factors can be considered, such as salinity L. Poorter and Bongers 2006 or soil properties (pH). These variables determine if a plant (depending on its specific properties) can establish a given habitat without any biotic interactions. These filters define, for a given habitat, the pool of species (or individuals if genetic variations are considered) that can grow and reproduce in this habitat without interaction. The ensemble of habitats a species can invade if only the abiotic factors are considered is called the **potential niche** (see figure 1.1).

ABIOTIC FILTERING

In addition to this large scale filters, another barrier may prevent a species to invade a habitat: its access. Indeed, dispersion plays a major role in the geographical extent of a distribution area of a species. Dispersion barriers such as mountains, seas or ocean prevent uniformisation of vegetation and reduction of global diversity. Such limits explain the existence of endemic species that grow only in a few locations, despite a larger potential distribution area (defined by potential niche).

DISPERSION FILTERING

Finally, the main factor that can affect the ability of a plant species to establish, is living interactions. For plant species, herbivory and competition are the most important factors, but other forms of interaction can affect the potential niche. The resulting niche, after all filtering processes, is called the **realised niche**. Competition affects the growth of the focal plant indirectly by reducing the availability of resources, increasing the stress of the plant and reducing its niche (see the interaction between species 1 and 3 in figure 1.1). Competition interactions are major factors shaping vegetation community and are extensively studied both with theoretical (Chesson 2000a; Amarasekare 2003) and empirical approaches ([kunstler_plant_2016](#)).

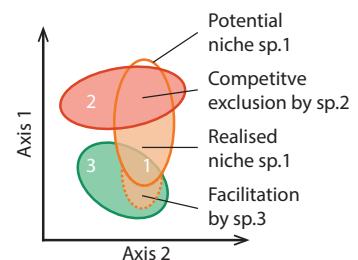
BIOTIC FILTERING

Figure 1.1: The potential niche of the **focal** species is reduced by competition interaction with **species 2**, but extended by facilitation interaction with **species 3**. This representation of the niche requires the knowledge of the effects of both abiotic factors and all pairwise interactions with other species. A more mechanistic approach of the niche should be considered in IMBs.

Similarly **facilitation** interactions also affect indirectly the levels of resources experienced by the focal plant, but in a way that is positive for the focal plant. So they widen the realised niche outside the potential niche (see the interaction between species 1 and 3 in figure 1.1). There are hypothesised to be larger along a stress gradient, where competition interactions are filtered out because they do not allow species maintenance and only positive interactions remain. Such relationships are dependent on the pair of species considered and may change depending on conditions (Callaway, Pennings, and Richards 2003).

FUNDAMENTAL NICHE

From the point of view of the focal plant, these interactions only exist through the changes in resource availability (even if plants are able to identify their neighbours). In this sense, we can see potential and realised niches as displacements of the fundamental niche (niche defined in term experienced conditions, stresses and resources) within spaces defined by abiotic variables or biotic variables. From this framework, the fundamental niche, or conditions experienced by the focal plant, is the stronger representation of the species niche and the realised niche (abiotic and biotic filters on the niche) emerge from the effects of external factors on this experienced environment.

This point of view should be adopted in models (Berger et al. 2008) because it allows the representation of both abiotic and biotic factors in a shared and generic framework. This is an improvement in comparison to models requiring

a matrix of interaction coefficient between species. Such matrix, in addition to being hard to parametrise, cannot be used in a framework of dynamic strategies. Modelling effort should instead be on explicit temporal and spatial dynamics of resource dynamics. Plant interactions would be captured by the effects of plant functioning (reduction of resource levels in relation to plant growth and resource use) on these dynamics ([morin_comparing_2009](#); Berger et al. 2008).

The concept of ecological niche serves as a great tool for theoretical research on coexistence. It encompasses in a convenient way both abiotic and biotic filters of one species distribution. While traditional view of the niche requires considering both abiotic filters and pairwise interaction, fundamental niches and resource dynamics modelling offer an alternative to model realised niche as an emergent property of the model.

1.1.2 The complexity of coexistence

If ones want to better understand and predict dynamics of complex systems, they first need to understand how such complex is assembled. Niches can be used to characterise a range of habitats a plant can live in, but because of complex inter-specific interactions, determining the final composition of a community from the list of species that can live in this habitat is not easy. If it is easy to observe diverse ecosystems (from bacteria to plants, insects or algae), it is challenging to determine the processes that 1) group the entities together (in time and space), 2) maintain an apparent stability in the group composition (at least at a certain spatial and temporal scale). We can imagine biotic filtering as a physical filter, the same way the abiotic filter is often illustrated, but this image does not translate the dynamic and complex nature of underlying processes. Biotic filtering emerges as the result of all the interactions between the entities that make it through the other filters. And how these interactions, direct or indirect, play together determines the stability of the diversity.

THE QUESTION OF COEXISTENCE

To predict the outcome of competition interactions multiple theories have been developed. Among these theories, we can cite two that have a different perspective on the same question: how do species sharing essential resources coexist in a homogeneous environment?

Chesson 2000b tends to have a population dynamic view of the system and identifies two types of processes that promote coexistence: (1) stabilizing mechanisms, (2) equalizing mechanisms. The former are required to stable coexistence as it a condition of invasibility. In other words, plants can coexist only if one species can invade the other. The condition to such invasion is that the species at low-density growth better than the species at high density. This is the case if intra-specific competition is higher than the inter-specific competition. Equalizing mechanisms are processes that diminish the fitness differences between the species, without ensuring stable coexistence. This framework is extended by [adler_niche_2007](#) in the modern coexistence theory. It states that niche differences (Levine and HilleRisLambers 2009) and fitness differences are the two mains axis of species coexistence. They make the assumption that niche differences define the relative strength of inter-specific versus intra-specific competition. The larger the differences between niches, the thinner is the overlap, and the weaker the inter-specific interactions. Therefore, this can be related to

stabilizing mechanisms in Chesson 2000a. On the other end, fitness differences also impact coexistence. The lower the differences, larger are the chances species coexist. The importance of niche differences required for stable coexistence decrease with the decrease in fitness differences.

In the other hand, Tilman elaborates a theory [tilman_resource_1982](#); [tilman_plant_1988](#) around resource use more in line with the idea of fundamental niche expressed in the previous paragraph, the contemporary niche theory. Species are characterised by the impact they have on the resource, and they use the resource for growth. Competition is in favour of the species with the lowest requirement for the resource because competition leads to resource deprivation it can survive. But coexistence if there is more than one limiting resource. In this case, coexistence can be achieved if species have a stronger impact on the resource from which they benefit the most (and intersecting zero net growth isolines).

These two theories give strong conditions for stable coexistence, however, they required simplifying hypotheses (all other things being equal, homogeneous environment) that are not met in natural environments. Despite their different approaches, these theories can be united as demonstrated by [letten_linking_2017](#) if the impact and benefit coefficients from contemporary niche theory are translated into niche and fitness differences. Despite this unified theory, they applied to a too limited range of situation to be applicable in the context of diverse mountain grasslands.

Plant community requires strong coexistence mechanisms to maintain species richness. Single theories fail to predict high diversity observed in plant communities such as natural mountain grasslands. However, high dimension coexistence processes and complexity seems to be an answer to the biodiversity paradox. In addition to niche based coexistence processes, other mechanisms that promote coexistence must be considered.

1.1.3 Variability and dynamics: driven by the resource

Resource dynamics, even with constant influxes, seems to be the key to understanding plant interactions and dynamics according to Tilman [tilman_plant_1988](#). Can the resource distribution in time and space explain coexistence?

In Tilman's perspective, resources are driven by two things, external influx and internal (to the system) consumption or cycle. The system structure and composition is responsible for resource dynamics as much as external influx. And these dynamics alter the structure of the community and change the hierarchy within the community. This cycle is well illustrated by the cycles we can observe in forest systems and gaps models. Mature forests produce big trees that fall down and create perturbation within the system. The resulting hole in the canopy allows for pioneer species to invade this space without competition. While they grow, other slower species are in shadows and must tolerate this competition, and grow enough to out-compete first established species. Because there is a trade-off between potential growth and shade tolerance allowing this cycle to set up, there is a succession dynamic after each perturbation of the systems. These local events of perturbation support coexistence at a large scale, a coexistence that can be captured by spatially explicit models Jérôme Chave 1999; Falster et al. 2016.

COMMUNITY DYNAMICS

Such drastic dynamics do not exist in mountain grasslands communities. But the natural temporal variability of resources due to contrasted seasons also drives diversity in growth strategies. Coexistence comes to the existence of multiple climatic contexts at the same place (but not the same time). As plants cannot be the most competitive species for any given condition in the whole range of conditions experienced in mountain habitats, there is a succession of species at the top of competition hierarchy (Adler et al. 2006) (see figure 2.5 for illustration). The diversity of flowering periods in figure 1.2 is an evidence of this succession dynamics.

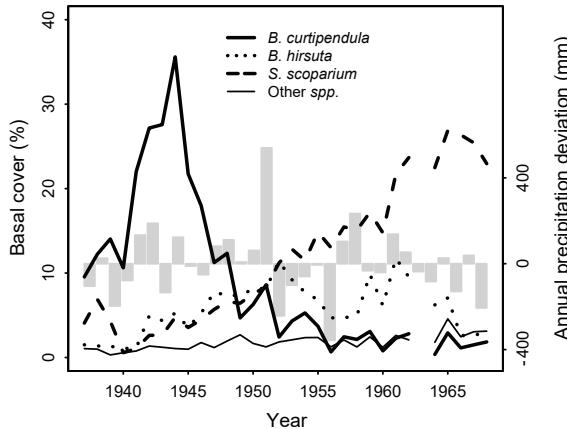


Figure 1.3: Changes in observed basal cover for 3 grassland species. This variation in hierarchy illustrates the succession in grassland communities and the storage effect due to the stabilizing effect of climatic variation promoting coexistence. See details in original study by Adler et al. 2006.

This mechanism promoting coexistence because of succession dominance driven by temporal changes in environmental condition is called storage effect. The species grow when the conditions match their niche and store the gains to wait until next favourable conditions. This term is generally applied to yearly variations, but the idea can be applied for variations within a growing season, allowing growth and storage until next season.

The temporal variations have a stabilizing effect on coexistence [tilman_plant_1984](#) but maybe more intuitively, spatial heterogeneity also promotes coexistence. Indeed, spatial variations of conditions at small scale create multiple niches that allow for diversity if measured at a higher scale. This spatial heterogeneity can be overlooked, but in the context of mountain grasslands, where plants are generally small due to high-stress levels and a very fine scale heterogeneity resulting from the terrain texture, it can play as a strong stabilizing mechanism.

Spatial and temporal heterogeneity play a major role in coexistence maintenance by creating various opportunity, or niches, in a given ecosystem. Internal dynamic variation of conditions also support stable coexistence.

1.2 The complexity of diversity

While resource use strategies and resource heterogeneity are important mechanisms for diversity, dispersal processes and meta-community dynamics should also be considered. Grassland communities are not independent of one another, but there are connected by dispersal vectors such as wind and animals. These connections support diversity but not stable coexistence, but remains crucial for community dynamics. Indeed, the link between the community and the meta-community (all connected communities) is a source a species that can be absent from the focal community. Therefore, in case of transition of environmental

TEMPORAL HETEROGENEITY

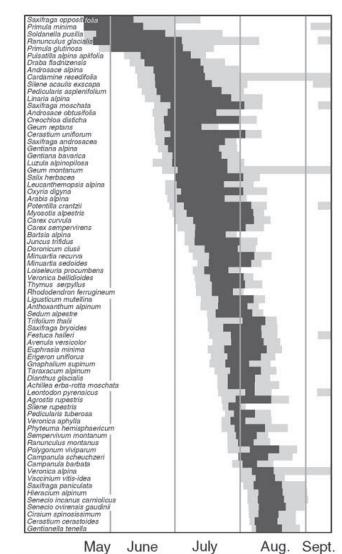


Figure 1.2: Diversity of flowering periods of alpine species. Evidence of succession in grassland ecosystems. From [korner_alpine_2003](#)

SPATIAL HETEROGENEITY

LARGER SCALES DYNAMICS

conditions, these external species can invade the focal community, accelerating species turn-over compared to a closed community. In the context of global change, it is essential to consider mountain grasslands communities as open systems as the question of invasion by lower altitude species is yet to be solved.

Other larger scale dynamics can impact community dynamics such as species-specific interactions (herbivory or pollination) that lead to dynamic equilibriums. However, modelling such processes are demanding, and while it maintains some diversity, it is not expected to be the main driver of grassland dynamics in the context of global change.

Coexistence theory has difficulties explaining high species diversity in communities like freshwater diatoms or mountain grasslands that compete for a limited number of resources in fairly stable conditions. From the previous paragraphs, it seems that these environments are not that stable and that there are numerous mechanisms supporting diversity. Diversity is highly dimensional as it is stated by Clark et al. 2007. This complexity, that we just have scratched the surface here, is too high for theoretical models to handle. That does not mean they are not useful, but they cannot consider all these processes at the same time. To study diverse communities, it is required to incorporate at least parts of this diversity in mechanistic models. While it increases the modelling work, model's complexity, and difficulty to analyse results, it allows a stronger representation of communities, of their diversity and enables the identification of main processes, and possible interactions:compensations:synergies between these processes.

EMBRACING COMPLEXITY

The evaluation of services relies on a good representation of the plant community and its essential properties. To represent complex interacting systems like vegetation communities, descriptive approaches and theoretical models are not sufficient. The main driving processes must be considered and explicitly modelled. Explicit heterogeneity and dynamics of the resources are key to understand and model filtering processes, coexistence mechanisms, and community dynamics. Modelling both community properties and resource dynamics require an understanding of plant functioning and diverse growth strategies. The challenge of community modelling is not to keep simplicity in its structure, but increase diversity in its processes.

2 HOW TO REPRESENT PLANT COMMUNITY

All plants share the same pool of essential resources and similar physiological processes of assimilation and allocation, however, species differ by their growth rates, niches, and competitive abilities. How do such differences emerge from a common functioning wireframe? It seems that these differences can be explained by differences in parameters that characterise this functioning. So considering this diversity is required to represent the diversity observed in mountain grasslands.

The challenge of modern community ecology is to determine the trajectory

ries the existing ecosystems will follow under new environmental conditions. Species centred approaches, because they are limited to the knowledge of existing response patterns to existing gradients, cannot tackle this problem. How can a new representation of plants enable generalisation of the diversity of plant functioning in new conditions?

2.1 The continuity of functional ecology

2.1.1 Shift in paradigm: traits and patterns

Classical use of niche theory can be observed in Species Distribution Models (SDMs) that link the probability of presence of one species to a multidimensional description of a habitat. The environmental variables are literally used as the dimensions of the Hutchinsonian niche, and directly link the species to its fitness in a given environment (see figure 2.1, first row). This method is widely used to model environmental niche, but some can also include species interactions to incorporate an explicitly biotic filter. SMDs have good theoretical support and have a lot of practical applications, however, their strength is reduced at the scale of the community where the biotic filtering processes and fine scales dynamics take the advantage over large-scale abiotic filtering. Also, because they require a lot of data for any given species, they lack generalisation properties to be applied to rich communities. Community dynamics require fine-scale plant functioning processes to capture the effects of small scales variability and plant interactions, drivers of coexistence.

A SHIFT NEEDED

This example of modelling approach based on a species centred framework reveals the weaknesses of this framework. The distribution of a species along gradients, or its niche, while it can be captured by abiotic variables, is primarily determined by the fitness components (and whether or not they lead to a positive fitness): growth, survival, reproduction. These variables are not intrinsic properties of species but emerge from the interaction between physiological processes (carbon assimilation by photosynthesis, water absorption, organic matter allocation, etc...) and the environmental conditions. Only considering these processes allow to explicit and decompose plant functioning, and therefore model it in new combinations of environmental conditions.

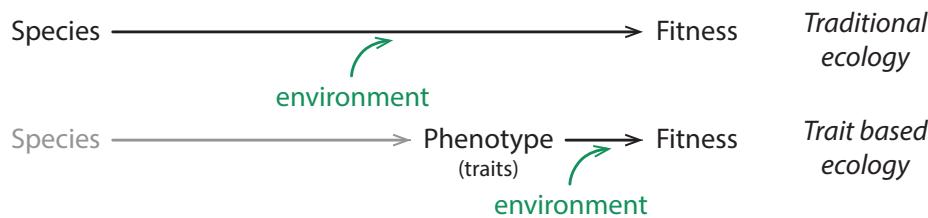


Figure 2.1: The shift toward trait-based ecology allows for the decomposition of the link between species and fitness determined by the environment. On one hand, the link between species and traits is better characterised by standardised protocols and the use of databases such as TRY (TRY). On the other hand, the link between phenotypes (defined by trait values) and fitness can be generalised and the role of environment in this relationship better understood.

Most of plant species share the same growth, survival and reproduction processes, but they still differ in these aspects as a function of the abiotic and biotic environment. The solution to shift from species centred paradigm, and its couple habitats-species (or species-environment-abundance like in SDMs), is to explicit the phenotype of these species. By using functional traits to define the phenotype of a species, ecologist can limit the representation effort to the link

between traits and fitness physiological properties (P. B. Reich, Walters, and Ellsworth 1992), and then link species to traits with simpler data collection procedure ([cornelissen_handbook_2003](#)) (see figure 2.1, second row).

This shift in paradigm allows for a simpler and functional representation of plant species, that can be later linked to physiological or ecological processes.

The functional traits allow the decomposition of the link between species and fitness, to gain general understanding instead of specific relationships between species, environment, and fitness. However, this decomposition also breaks down the species, that can no more be described by one word, but needs instead multiple quantitative values to be described. To the singularity of the species is exchanged the multiplicity of traits. The link between species and fitness, now broken down by traits, can be analysed in a new light, parts by parts.

This decomposition allows the identification of relationships between morphological traits (easy to measure) and physiological traits (more interesting but harder to measure) (D. D. Ackerly and Peter B. Reich 1999; L. Poorter and Bongers 2006; Peter B. Reich 2014). Response patterns along climatic gradients have also been identified (Niinemets 2001) increasing the understanding of the role of the functional traits for the performance of plant species.

This trait-based approach, demanding in data collection effort, benefit from the consistency of the measures [cornelissen_handbook_2003](#) allowing pooling of the data into big databases such as TRY or Glopnet. The standardised collection of data all around the globe is a model of centralisation and collection that can lead to major large-scale pattern enhancing the understanding of the functioning of plant communities.

some interspecific patterns:

along climatic (Niinemets 2001; Ian J. Wright, Peter B. Reich, et al. 2004) ,on nitrogen (Dwyer)

but also correlations and intra-specific change of traits along gradients. Is it interesting?

The complexity of coexistence and community dynamics processes could not be captured with traditional species centred ecology. The last two decades saw the rise of functional ecology and its ability to capture quantitatively the relationship between vegetation and abiotic gradients. The capacity to

THE RISE OF FUNCTIONAL TRAITS

ARE THERE PATTERNS?

2.1.2 Traits and competition

If traits can describe a species and capture its functioning, it is logical to consider them to assess competitive interactions. Two visions have been developed to capture relative interactions. As mentioned in paragraph 1.1.2, trait distance can be a measure of competitive strength. This interpretation is an extension of the hypothesis of the limiting similarity that states that two species with similar niches cannot coexist. If plant functional traits can be used to define the niche, then, trait dissimilarity should be a measure of competitive interaction: the greater the dissimilarity, the lower the interaction. Because the competition is proportional to the absolute distance between traits, the relationship between distance and competition strength is symmetrical. On the other hand, some argue that competition interaction are not all symmetrical, but hierarchical, and that some traits can capture the competition sensitivity and others the competition impact ([kunstler_plant_2016](#)), therefore the intensity of the competitive interaction is

not symmetrical and dependent on the relative trait difference, but rather on the relative strength of impact traits compared to sensitivity traits. It seems that the form of the relationship depends on the type of competition mechanism considered. It will be hierarchical if they compete for the exact same resource (light, water), and symmetrical otherwise (temperature resistance, specific predation avoidance, pollinator, etc...).

Understanding how competition (or any other interaction) is regulated by traits is important to determine competition outcomes with alternative methods than pairwise coefficients that require empirical data to determine. Linking traits and strength of competition interaction would also allow the intra-specific variations to be considered. In this case, determining the exact relationship between trait distance and the competitive effect is crucial as it would change the effect of intra-specific variability (see Hart, Schreiber, and Levine 2016 for example).

But these interactions are not only symmetrical or asymmetrical, there can be non-transitivity promoting dynamic stable coexistence (Levine, Bascompte, et al. 2017), or be context dependent (Callaway, Brooker, et al. 2002). Moreover, the nature of the competition relationship (dissimilarity or hierarchy) depends on traits considered (Bennett et al. 2016). Due to their complexity, interactions cannot be summarised by single trait value comparison but is multi-dimensional (Kraft, Godoy, and Levine 2015). However, traits can inform competitive interaction by informing the plant functioning and the use and effects on the resource.

Traits can be a good proxy for competitive interaction but the relationship between trait differences and competition intensity depends on the competition process. If the interaction is transitive, a strong asymmetric pattern can be observed between interaction effects and trait differences, while symmetric interaction reveals niche differentiation processes. Despite these observed relationships, the specificity and multiplicity of trait-mediated interactions promote the use of mechanistic solutions to capture the multi-dimensional and context-dependent nature of plant interactions.

The paradigm shift toward functional ecology allowed the shift from discrete to a continuous representation of species. This change makes easier the representation and study of plant communities, especially along conditions or management gradient. Traits are also used to study plant interactions. Trait approaches offer a functional link between morphology and physiology that has great potential in generalising environmental effect on the phenotype-fitness relationship. However, the need for multiple traits to capture plant niche differences or similar response patterns of multiple traits suggests underlying structure within trait assemblage. Understanding this structure and how it relates to community dynamics external drivers is crucial in the representation of diverse communities.

2.2 How trade-offs make strategy space

2.2.1 Trade-offs: capture constraints on species differences

The functional link that is observed between some morphological traits and physiological traits suggests underlying processes that link these traits together. It appears that multiple traits are correlated together at the global scale between species (P. B. Reich, I. J. Wright, et al. 2003; Ian J. Wright, Peter B. Reich, et

al. 2004; Jerome Chave et al. 2009; Peter B. Reich 2014) and within species (Hu et al. 2015). This correlation between functional traits of the leaf was described at a global scale by Ian J. Wright, Peter B. Reich, et al. 2004. The **Leaf Economic Spectrum** (LES), defined by these correlations between multiple traits, draws a continuum of strategies. It spreads from species with high resource acquisition rates and rapid growth rates but low tissue lifespan, to species with longer tissue lifespan but lower growth rates. This is a clear description of a **trade-off** between strategies, opposing exploitative strategies (high Specific Leaf Area (SLA), high Leaf Nitrogen Content (LNC) and low Leaf LifeSpan (LLS)) to conservative strategies.

This axis of differentiation allows ecologists to link quantitative measures to types of strategies that better capture diversity of strategies than discrete typology. These strategies are translated into traits, traits that can be translated into physiological processes parameters, then into components of fitness.

In addition to a quantitative measure of species-strategies, such trade-offs simplify a lot trait-based approaches. While many variables can be measured on one individual, correlations between these variables reduce the number of dimensions to consider. This simplification cannot be better illustrated by the work of Diaz et al. 2004 that demonstrate the existence of two major axes of "evolutionary specialisation" that explain most (41%) of trait variability: size-related traits, and resource use speed traits. Similar evidence is also found on a global scale in addition to evidence for high levels of coordination between axes (Díaz et al. 2016).

Similar correlations could be found in roots P. Ryser 1996; Peter B. Reich 2014 but patterns are generally weaker, certainly because of more fragmented data and interactions with micro-organisms that alter the link between morphology and function of roots.

The existence of such trade-off can be explained by constraints that shape the distribution of trait distributions. Trait-function relationships are often depicted as bell-shape with an optimum (Cécile Hélène Albert, Thuiller, Yoccoz, Soudant, et al. 2010). I rather think that trait and function are linked by monotonous functions, but traits are generally not independent and another monotonous trait-function relationship can constrain the first function. For example, the exchange function of the leaf (and photosynthesis activity), is negatively linked to the thickness of the leave (promoting thin leaves for a higher light capture and photosynthetic activity, but the lifespan and mechanical support of the leaf require denser leaves to be viable. This trade-off in functions, linked by a trade-off in traits (the leaf cannot be both thin and light in one hand, and robust and self-supporting in the other), lead to the emergence of a strong constraint ("hard frontier" in figure ??) on one side of the relationship, while competition processes out-select combination of traits that are not relevant on the other side ("hard frontier" in figure ??).

Trait-based ecology rapidly lead to the observation of trait correlations and trait syndromes between plants. These axes of differentiation emerge from processes that constraint plant strategies. Global characterisation of these constraints should allow a better representation of plant functional diversity.

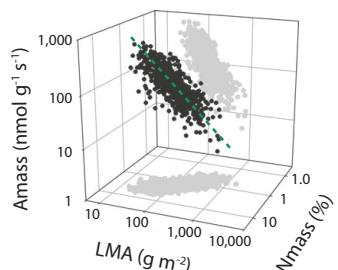


Figure 2.2: Three dimensions of the LES. Correlation of Leaf Mass Area, assimilation rate per mass unit and nitrogen concentration. This correlation reduces three dimensions (more dimensions not shown) into one axis (- -).

STRATEGIES

EMERGENCE

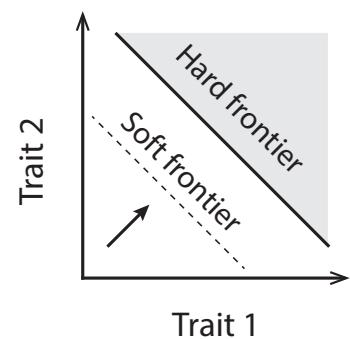


Figure 2.3: Emerge of trade-off between traits because of hard physical-biologival frontiers, and "soft frontier" due to selection.

2.2.2 Strategy-spaces made of trade-offs

Plant diversity is expressed, and visible to anyone, by the variation in shapes and colors, scents and growth forms, but this diversity is the demonstration of the multiplicity of strategies. In an early attempt to make sense of this diversity of strategy Grime 1977 theorise the existence of two type of constraints that shape plant communities: perturbations and stress. The perturbation axis captures the variability of community drivers, while the stress axis captures how conditions facilitate or make difficult plant establishment. They draw a two-dimensional space where three regions can be invaded¹, corresponding to three different strategies: competitive (C) in low stress-low perturbations region, stress tolerant (S) in high stress-low perturbations region, ruderal (R) in low stress-high perturbations region, forming Grime's triangle (see figure 2.4).

Grime's triangle set the basis for strategy space, and the broad meaning of *stress* and *perturbations* terms allow them to be applied to various conditions. However, the diversity of types of stresses (drought, cold, nutrient availability) and perturbations (predation, fire, avalanches etc...) cannot be specifically captured by such wide concepts. Westoby 1998 highlight the difficulty to use such space and its incapacity to explain some patterns. According to him, a strategy space² should:

- "express meaningful differences in ecological behaviour between species";
- allows to "position a plant species from anywhere in the world within";
- be composed of attributes that "require little enough effort to estimate";
- lets "possible to quantify the extent to which the [strategy-space] captures variation in other plant attributes".

He proposes to use functional traits to meet these criteria of functional differences, generalisation, and practicality. Three traits capture the components of Grime's triangle:

- Specific Leaf Area (denoted L): captures the speed of return of investment of carbon in leaf, as latter highlighted in the LES. High SLA is generally associated with competitive species that capture a lot of light and have a high growth rate. At the other end of the spectrum, low SLA species are more stress tolerant. This axis is the practical equivalent to the axis CS in Grime's triangle.
- Height at maturity(H): the race to the light (but not time fixed as the protocol for functional trait measure encouraged it), but also capture ruderal axis (time interval between perturbations)
- Seed mass (S): expresses the capacity of a species to invade freshly disturbed environments or the competitive advantage seedlings possess with a larger starting carbon pool. This trade-off between the competitive strength of seedlings against the chance of invading freshly disturbed environment capture well the CR axis of Grime's triangle.

The LHS strategy space proposed by Westoby has the advantage to be easily measurable and to allow comparison between species all around the globe (Pierce et al. 2013).

FROM THEORY TO TRAITS

¹ high stress and high perturbation regions does not allow establishment

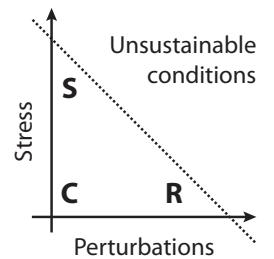


Figure 2.4: Grime's triangle. Competitive (C), stress tolerant (S), and ruderal (R) strategies are dominant in the three regions of the perturbations-stress space.

² called Plant Ecology Strategy Scheme (PESS) in his paper

This approach can be further extended with multiple traits. Indeed, global datasets and databases of functional traits reveal global scale correlations between traits. These correlations, or trade-offs, simplify the representation of plant species (Díaz et al. 2016) and translate fundamental axes of strategy differentiation (**reich_world-wilde_2013**). Yet, plant communities exhibit extraordinary species and functional diversity suggesting that not all traits are correlated. Trade-offs emerge because of hard (physical, chemical or biological) and soft (competitive pressure) constraints on combinations of functional traits (see figure ?? and Shipley et al. 2006). Therefore, for a given couple of traits, the physical independence of traits and the independence of ecological processes they are involved in should ensure the absence of trade-offs between those. While some traits are related to multiple physiological processes (a composite trait like SLA is involved in water regulation, but also light capture and tissue toughness), traits are often specific to one or two processes.

These processes must have an ecological significance, so filtering processes are the best candidate to observe such trade-offs. Against climatic filters, plants can either escape (*i.e.* finish a life-cycle before the filtering event) or avoid/resist (develop specific tissues or strategy to pass the filter). This can be observed for drought (Kooyers 2015) or frost (**korner_alpine_2003**). The resource use strategies and reproductive strategies are also orthogonal (**diaz_global_2014**). From this, a generic principle can be formulated stating that the number of observable trade-off in an ecosystem is close to the number of constraining processes. It is supported by the observation that a limited number of traits (or dimension, or trade-off) is often enough to capture the diversity of vegetation community as in Laughlin 2014.

The independence of strategic trade-off justifies that these trade-offs can be used as independent dimensions of a **strategy space**, defining the diversity of strategies present in a community.

The existence of such low dimensional strategy spaces have been observed at large scale (Pierce et al. 2013; Díaz et al. 2016) but also at smaller scales, where the CSR triangle could be identified in ecosystems where precipitation stress and grazing perturbation are shaping the community Frenette-Dussault et al. 2012.

The multiplicity of processes shaping vegetation systems leads to similarly constrained diversity in plant strategies. These strategies are captured in a strategy space drawn by independent trade-offs tightly related to functional traits. These functional trade-offs have great potential in the representation of a functioning plant diversity, while parameter set allows easy characterisation of species and communities.

GENERALISATION OF STRATEGY SPACES

EMPIRICAL EVIDENCE

2.3 How traits link to ecosystem properties

Now that functional traits, trade-offs and strategy spaces are identified as good candidates to characterised the plant functioning and differentiate species, can we link functional traits to **ecosystem properties** and by extension to ecosystem services.



Figure 2.5: Empirical evidence of the CSR triangle in natural communities. The CSR triangle is created by the translation of a multivariate analysis into a coordinate system (see Pierce et al. 2013 SI for details). "CSR classification of six species of the genus Poa from lowland (left column; P. annua, P. nemoralis, P. supina) and alpine (right column; P. alpina, P. chaixi, P. laxa) northern Italy. Grey circles represent the strategies of individuals, and black circles the mean strategy for the species based on the individuals included in the analysis." from Pierce et al. 2013.

2.3.1 Mass Ratio Hypothesis, Community Weighted Means, and functional identity

As explained, plant species, based on their identity, provide ecosystem services. Some of these services are direct consequences of the characteristic of the species and their functioning. Because of that, Grime 1998 formulates the **Mass Ratio Hypothesis** that states:

... the extent to which a plant species affects ecosystem functions is likely to be closely predictable from its contribution to the total plant biomass. - Grime 1998

Because functional traits are quantitative variables, they can be manipulated more easily than factors. Therefore, while phytosociology describes vegetation communities with broad types and approximate abundances, trait-based ecology benefit from this continuity to characterise mean properties of community. The **Community Weighted Mean** of a functional trait is the average of species-specific trait values weighted by the relative abundance of each species, and correspond to an extended mathematical application of the mass ratio hypothesis when functional traits are linked to services. These summary variables define the communities in a quantitative way similar to the functional trait for species. In addition to be quantitative, it is functional and responses to disturbing factors can be predicted (Lavorel and Garnier 2002).

According to the **Mass Ratio Hypothesis**, some properties of the community directly scale to the characteristics of the most abundant species. In this hypothesis, the **functional identity**, defined by functional trait values, has more importance than the identity of the species. Community Weighted Mean measures generalise this hypothesis using mean species trait values. While these tools can link community composition to ecosystem properties and services,

they require precise measures of plant functional traits to be reliable.

2.3.2 Benefits of diversity

Certain processes are determined by the most abundant species of a community, but other services and functions may result from the properties of the group. **Diversity** is the most important property of an ecosystem or a community for a wide audience. This measure is peculiar to groups of organisms and plays a major role in its functioning and the services it provides. Diversity can refer to species richness or functional diversity. The former quantifies the number of species present in a habitat and can take into account the relative abundance of the species. Many indexes can be used to measure this variable representing different perspective or aspect of the metrics (see Chalmandrier 2015 for exhaustive information).

Functional traits and functional diversity can be used to estimate certain ecosystem services. For example, the diversity of phenology captured in flowering periods (see figure 1.2) is an indicator of the recreational function of mountain grasslands.

But diversity also supports indirectly functions and other properties of the system. Multiple mechanisms explain this multiplicity contained in the measure of diversity.

First importance of species richness is found in the insurance effect that prevents the loss of a function or a service with the loss of a species by ensuring that multiple species provide such function or service (see • species in figure 2.6). Because insurance effect relies on the redundancy of function, this effect is better captured by species richness than functional diversity. Another way of seeing this notion is the selection effect that states that increasing diversity increases the potential number of services provided by the community (see • species in figure 2.6), as each species added can provide new function/service (or at worst reinforce already present ones). When the function or service is directly linked to a trait value, this selection effect is directly captured by an increase in functional diversity.

Functional diversity is also associated with higher productivity and resistance to invasion or perturbation events due to niche complementarity mechanisms.

Species richness and functional diversity are often strongly correlated, but they do not capture the same services or effect. Functional diversity is a strong indicator of niche complementarity and its benefits.

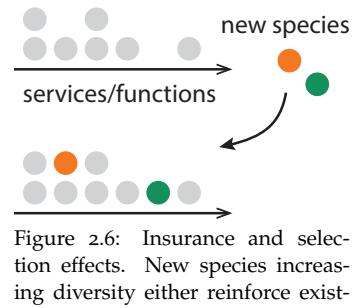


Figure 2.6: Insurance and selection effects. New species increasing diversity either reinforce existing function (•), or provide new function (•)

2.3.3 Productivity: both community property and ecosystem services

Productivity of a plant community is mostly sensitive to abiotic conditions, precipitation, nitrogen, and temperature being the main variables influencing this productivity. Because of that, there is a large contrast between ecosystems in contrasting environmental conditions (tropical forests and mountain grasslands being two extremes). These differences can be observed in the distribution of functional traits of species, size and resource use related traits being the most eloquent ones.

While community productivity depends heavily on environment properties (climate, soil), it is also dependent on the community, its richness, and the domi-

nant species. The abundance of highly productive species, characterised by high nutrient content, fast-growing and exploitative strategies is responsible for most of a community productivity. Nevertheless, it is hard to disentangle the link between the productivity of the habitat and the productivity of the species living this habitat.

The productivity has another ambiguity: it is both a property of the system and a service. It's a property, and is important in ecosystem services assessment as some services will scale with productivity (*e.g.* carbon storage). But it is also a service, it measures fodder production in grasslands, but wood production in forests, etc...

Productivity is at the same time a property of the habitat, of the community and a service. While the role of abiotic factors is prominent, the effect of the dominant species and the community structure on productivity should not be ignored.

2.3.4 Trade-offs in ecosystem properties

Traits can be linked to ecosystem services by statistical framework ([lavorel_how_2014](#)). But, in the same way there are trade-offs between traits, the ecosystem services provided by an ecosystem are also constrained. Understanding these trade-offs and the dynamics of the community dynamics allows to capture these trade-offs between services bundles (Lamarque et al. 2014). This link should encourage ecologist to focus on the development of methods to link drivers of ecosystems to community dynamics, to predict changes in ecosystem services (see figure 1.4 in chapter I).

In addition to facilitate the study of the effect of abiotic conditions and biotic interaction, functional traits can be used to describe the community and its main properties to evaluate ecosystem services. Statistical links that can be used to determine these links, and research effort should better focus on the dynamics of grasslands communities and the changes in main properties.

2.4 Modelling diverse plant community

Modelling mainly consist in deciding what is important considering and worth representing. The choice of how an entity or a mechanism is represented also correspond this decision making. While considering vegetation community the choice can be on the resources needed, the type of perturbation, or the part of the life cycle of most importance. For vegetation models for the study of community properties and dynamics, the representation of the interactions of multiple species is key. The strategy-space concept offers a great solution to both the interactions and the diversity of species, while also informing the modellers of the communities' properties.

2.4.1 How strategy space open vegetation modelling

In a mechanistic model with multiple species, strategy-spaces are simplified ways to define multiple species. Species identity is fully defined by its position in this space of species-specific parameters. This is a great advantage compared to traditional approaches of vegetation models that rely on strong knowledge

THE POSITION MAKES THE SPECIES

of represented species. Because mechanistic models function with shared biological and ecological processes, the differences of behaviours between species emerge not from the functions but from the species-specific parameters. Therefore, to properly model a species behaviour, in addition to having properly modelled the processes, all species-specific parameters for all species must be determined. This step requires a large investment of time and resources and is proportional to the number of species. Strategy space based on trade-offs enable the representation of multiple species, in a closed environment. A greater effort is required to establish such strategy space, as it needs identification of strong trade-offs and the delimitation of ranges along the axes of strategic differentiation. But once established, an infinity of species can populate this robust space without the threat of Darwinian demons. This subject is further discussed in the following chapter (chapter III, section 2). Because of that strategy space are great tools to consider a diversity of species, when the identity of species is not of primary interest.

While I have no knowledge of living species being projected on a strategy space used in a simulation model, it can be imagined with a projection of measured traits on traits used in the model (even if there can be some discrepancies between the two spaces), in the way of Pierce et al. 2013.

Dynamics Global Vegetation Models tend to use such strategy spaces to model high diversity with a limited number of traits. These models, mainly represented by the model of Kleidon and Mooney 2000, and extensions Reu et al. 2011; Pavlick et al. 2013. They use 12 to 15 traits in their strategy space. These traits can be grouped in: allocation traits, tolerance to climatic conditions, resource efficiency, reproduction strategy and tissue turn-over. All these traits are linked to trade-offs in the formulation of the model. A general observation we can make is that these trade-offs often take the form of greater growth or efficiency against greater resistance to stress. This is similar to observed strategies in drought environment (Kooyers 2015). These models (Reu et al. 2011; Pavlick et al. 2013) demonstrate the ability to capture diversity and climatic response patterns, better than plant functional types, with a limited number of traits.

IN DGVMs

Such approaches are also used to study more specific mechanisms like fire perturbations (Scheiter, Langan, and Higgins 2013). In this case, specific traits are included. The adaptive value of the traits in such frameworks thanks to the inclusion of genetic optimisation processes. This kind of approach is a first step in the understanding of the effect of drivers on community property responses. However, the large scale of these models often does not allow to look at small scales interactions and dynamics.

IN IBMs

Individual-Based Models are great tools to model community dynamics incorporating local interactions and small-scale dynamics. Because they are interested in smaller systems, IMBs often do not use strategy-spaces and prefer species-specific parametrisation (lohier_analyse_2016; Soussana et al. 2012; Taubert 2014). This is often explained by the focus on heavily manage grasslands with objectives of productivity that need precise predictions and model a limited number of species. But strategy spaces are used in IBMs to understand diversity patterns in diverse systems such as savannahs (Reineking et al. 2006) or forest (Falster et al. 2016). These approaches successfully describe the diversity and encourage us to use such strategic differentiation spaces.

Higher diversity can be achieved in these models, but numerous species can be discarded. The benefit of a smooth continuum in strategies is that it avoids strong dominance and shifts. Also, the perception of finer changes in the community is possible, while small default in species parametrisation of species centred models could lead to either no shift (one species dominates and is not sensitive to drivers) or drastic responses (the shift in dominance is abrupt because of no intermediary species).

2.4.2 How models inform us on properties and dynamics

reineking: the shift in dominance along a gradient maire : trade-offs
reu ?

schafter: value of a trait context dependant.

The use of strategy spaces in models allows the representation of high diversity in a common plant functioning framework requiring a limited number of parameters. Such approaches are very useful to follow the dynamics of communities in a mechanistic framework. Individual models tend to ignore such simplifications procedure and relies on the direct measure of traits of interest because they generally integrate a limited number of species. IBMS can take advantage of trade-offs and simple strategy spaces to model diverse communities at small scales while keeping biological mechanisms at their core. However, model-based of strategy space tend to consider mean individuals and ignore the individual variations.

3 THE IMPORTANCE OF PHENOTYPIC PLASTICITY AS A SPECIFIC CASE INTRA-SPECIFIC VARIABILITY

3.1 Intra-specific variability change the rules

3.1.1 Increasing interest in intra-specific variations

Trait approaches emergence lead to a better understanding of general patterns of community responses to drivers and of trade-offs in plant functioning. But with the accumulation of large trait databases, the importance of **intra-specific variability** could not be ignored.

The extent of the intra-specific variation is a big question as some ecologists point out because trait-based approaches make sense only if inter-specific differences are greater than intra-specific differences. While this can be discussed, high functional variability within the species would weaken theories and generalisation based on mean traits. Violle et al. 2012 suggest that the extent of within-population variability relatively to within-community variability should be considered and avoid mistakes in the estimation of coexistence mechanisms. EXTEND

Ignoring intra-specific variability lead to underestimation of niche overlapping, plastic response to neighbours or the fraction of resource a species can used. Multiple studies focused on the extent of functional intra-specific variability (Cécile Hélène Albert, Thuiller, Yoccoz, Soudant, et al. 2010; Cécile Hélène Albert, Thuiller, Yoccoz, Douzet, et al. 2010) and how to disentangle this variability from species turn-over (Lepš et al. 2011) in community response. These studies show contrasting results between traits and levels. Cécile Hélène Albert, Thuiller, Yoccoz, Douzet, et al. 2010 demonstrate a within-species variability explaining between 20% and 40% of total trait variance, and Siefert et al. 2015 note similar levels, but this fraction tends to decrease with the increasing community diversity. They also show that the strategic differentiation between exploitative and conservative species is robust to these variations. It appears that all traits are not variable to the same degree and traits like SLA, height, LNC and LDMC are relatively variable while leaf morphology traits variability is lower Siefert et al. 2015.

The variability of multiple traits certainly impacts the functional diversity (Bello et al. 2011; Cécile H. Albert et al. 2012). All indexes are not sensitive to the same degree, with single trait measure being the most sensitive, but should be used carefully to draw an interpretation of ecological pattern linked to functional diversity. To overcome this difficulty and disentangle the effects of the different forms of functional diversity specific indexes are developed (Bello et al. 2011).

The relative extent of intra-specific variability depends on the trait, spatial extent, and species richness, but not on climatic conditions (Siefert et al. 2015) suggesting general mechanisms

The fact that some traits are variable, while others are not, implies that some mechanisms structure this variability. A way to identify such effects is to look if variability is structured along environmental gradients, suggesting adaptation mechanisms.

Along such gradients trait variability for traits like SLA (H. Poorter, Niinemets, et al. 2009) of leaf mass fraction (LMF) (H. Poorter, Niklas, et al. 2012) follows similar patterns as inter-specific response (Niinemets 2001), with increasing SLA along precipitation and temperature gradient, and decreasing SLA along radiance gradient (leaf mass fraction shows similar responses). These responses suggest strong constraints (similar to the ones that shape inter-specific differences) shaping this variability. However, species may vary in their response (Kichenin et al. 2013). This contrast can be explained by differences in position around a bell-shaped response curve around the optimum (see Cécile Hélène Albert, Thuiller, Yoccoz, Soudant, et al. 2010 for more details). Kichenin et al. 2013 argue that it is not the case because alongside a wide altitudinal gradient the response curves observed for any trait or species are not bell-shaped.

This additional level of variability is not always in the same direction as community response driven by turn-over (Cécile Hélène Albert, Thuiller, Yoccoz, Soudant, et al. 2010; Kichenin et al. 2013; Jung, Cécile H. Albert, et al. 2014) leading to difficulties to predict the response of the community. These levels must be disentangled, in order to do that, mechanisms underlying intra-specific variability must be understood. This is particularly important because they have multiple effects on how we model community dynamics and understand coexistence mechanisms Bolnick et al. 2011; Viole et al. 2012.

After the emergence of trait-based ecology and its high potential, the re-

cent focus on intra-specific trait variability questions the strength of mean species approaches. While intra-specific variability does not negate numerous conclusions from previous work, because of its large extent and how it alters functional diversity, its effects on community dynamic processes must be interrogated, and underlying mechanisms investigated.

3.1.2 Contrasting effects of intra-specific variations

Intra-specific variability impacts coexistence mechanisms and community properties in multiple ways. The following paragraphs are not an exhaustive list of all ways intra-specific variations affect community properties or coexistence mechanisms, but a few contrasting examples to emphasise the need for better identification and understanding of underlying mechanisms.

Hart, Schreiber, and Levine 2016 use a mathematical model to investigate the impact of intra-specific variations on coexistence. They demonstrate the negative effect of intra-specific variations by the intermediate of Jensen inequality effects, that leads to an under-estimation of competitive dominance because of the non-linearity. I argue that this problem is partially solved if the estimation of the mean parameter is empirical, in this case, the variability is taken into account. Moreover, this certainly applies to genetic variations. Indeed, the plastic response would emerge if there are changes in conditions, changes that certainly affect the competitive interactions. Such change (justifying a change in phenotype), is likely to alter the competition relationship as modelled. This supposition is supported by the fact that variations away from the mean are generally due to a distance from the optimum of the niche, and therefore, certainly a lower fitness and lower competitive ability.

JENSEN INEQUALITY

ISV also effect of abiotic filtering

NICHE

effect on realised niche

neighbours: avoid or increase competition

specifically on diversity

CONTRASTING EFFECTS

callaway 2003 from competition to facilitation.

Bolnick et al. 2011 (Hart, Schreiber, and Levine 2016) (Courbaud, Vieilledent, and Kunstler 2010) (Turcotte and Levine 2016) (Roscher et al. 2015) (Valladares et al. 2015) ([barabas_effect_2016](#)) (Jung, Violle, et al. 2010)

The intra-specific variability has been observed to be an important part of community functional diversity, but also a way the community responds to changes in conditions. In addition to the empirical evidence of this importance, theoretical approaches support contrasting effects of such variations on coexistence mechanisms, evolutionary processes and community responses to climate event or invasion. It is crucial to disentangle different sources of intra-specific variability in order to understand potential effect on ecosystem dynamics.

3.1.3 Beyond the mean and the bell-shape: towards more mechanisms in representing intra-specific variability

There is a difference between how we observe ISV, and why it emerges. What is random? Therefore it is ... not good ... to apply such simplification of random effect onto theoretical models to predict the effect of intraspecific variability

...

with strong assumptions (observed on the functional trait in wide spatial range, applied to interactions in homogeneous context) on how they translate onto interactions (done in Halt, check Bolnick) Cécile Hélène Albert, Thuiller, Yoccoz, Soudant, et al. 2010 bell shape intra-specific response pattern along gradient, but doesn't stand according to Kichenin et al. 2013. Depends on trait and gradient... cannot assume that, need real quantification. ok if not a gradient response (or gradient is not known). Bell shape can emerge from non-measured gradient with linear response.

Dewitt and Barabas.

The same way the neutral theory is simplifying and brings little understanding to underlying processes and relies on strong hypothesis, considering intra-specificity as a purely random mechanism is insufficient.

Bell shape does not appear in altitude gradient... inconsistencies between theory and empirical data

Strong theoretical hypothesis

refer to asymmetric and symmetric competition

If most of the changes are plasticity or selection: it changes the effects on interactions and niche.

What are the possible effects? probably it does not affect interaction like (Hart, Schreiber, and Levine 2016) supposes (even if they talk about variations, their conclusions may not be extendable to plastic variations). May change a lot the balance between abiotic filtering and biotic filtering.

– go to individual mechanisms, evolution could tackle genetic variations, physiology and ecology on ontogeny, and evolution and ecology on phenotypic plasticity

Simple approaches to intra-specific variation constitute an improvement over mean approaches as they highlight processes ignored until now. However such approaches overlook the structure of the variability and underlying processes, leading to simplistic representations and potentially misinterpret the role and effect of this variability.

Ecology shifted from species to traits syndromes with great success, but the intra-specific variability constitutes a great challenge for generalisation of observed patterns. By overlooking the processes that structure intra-specific variations, we might lose the capacity to properly interpret the role of variability and refine our understanding of community functioning. The complexity of living communities requires to go further down and consider the individual scale. This is made possible by the accumulation of more and more numerous and detailed data, the improvement of statistical and new simulation tools. The question of the sources and drivers of intra-specific functional variability seems crucial to rise to the challenge it issues.

3.2 Phenotypic plasticity: a specific case of intra-specific variability

Until now, the processes at the origin of intra-specific variability has not been discussed, but to understand how it can alter community properties it is necessary to differentiate the different sources of intra-specific variations as they work

in different ways.

3.2.1 The different sources of intra-specific variability

Intra-specific variation can be caused by two mechanisms: genetic variation and phenotypic plasticity. Genetic variation occurs when individuals from the same species have different genotypes, leading to different phenotypes. On the other hand, phenotypic plasticity implies that the same genotype can lead to different phenotypes. Plasticity can involve epigenetic mechanisms (beaman_evolution_2016; Zhang et al. 2013; Adrienne B. Nicotra et al. 2015) that blur the frontier between the two forms of intra-specific variability as epigenetic is an inheritable form of plasticity. It is transmitted to descendants but unlike genetic mutation is reversible. To keep things simple, epigenetic phenomena will not be discussed here.

Genetic variability (as well as epigenetic) can be detected in case of origin specific response, while if the variability is explained by the treatment, it is a plastic response (Frei, Ghazoul, and Pluess 2014), and a large fraction of the variability observed in grasslands species is a plastic response rather than genetic variation alone (Frei, Ghazoul, and Pluess 2014; Merilä and Hendry 2014).

A. B. Nicotra et al. 2010 provide a good review of plasticity mechanisms and the importance for the adaptation to climate change. They advocate plasticity in functional traits should be considered in mechanistic models as they may play a central role in the speed and adaptiveness of community response to climate change.

Intra-specific variability can be decomposed in two main types: genetic variability that seems to be closer to random processes envisioned in simple models of intra-specific variability, and phenotypic plasticity that specifically links variations of phenotype to differences in external conditions. These mechanisms of variations are under the control of both evolutionary and molecular processes, that need to be better understood to be disentangled and to better predict their effects on community dynamics.

3.2.2 What is phenotypic plasticity?

Plasticity is a source of intra-specific variability, but biological processes leading to changes in phenotype can be complex. These paragraphs try to disentangle the different forms of plasticity and the underlying mechanisms.

Molecular basis of phenotypic plasticity

Phenotypic plasticity lies both in the perception of external conditions through sensor organs and signaling pathways (auxin pathway, root system for gravity ...), and the integration of this information to alter the development plan. This integration must be coordinated at the scale of the plant according to rules or objectives, which partly explore in this work, but ultimately is applied at the cell levels. Because of the complexity and our partial understanding of these mechanisms, we will not attempt to model them. However, I hope that this little overview of molecular mechanisms at the scale of the cell will give the reader an idea of the processes behind the abstract concepts used in this manuscript.

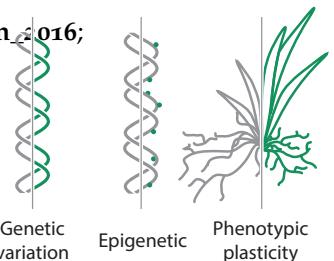
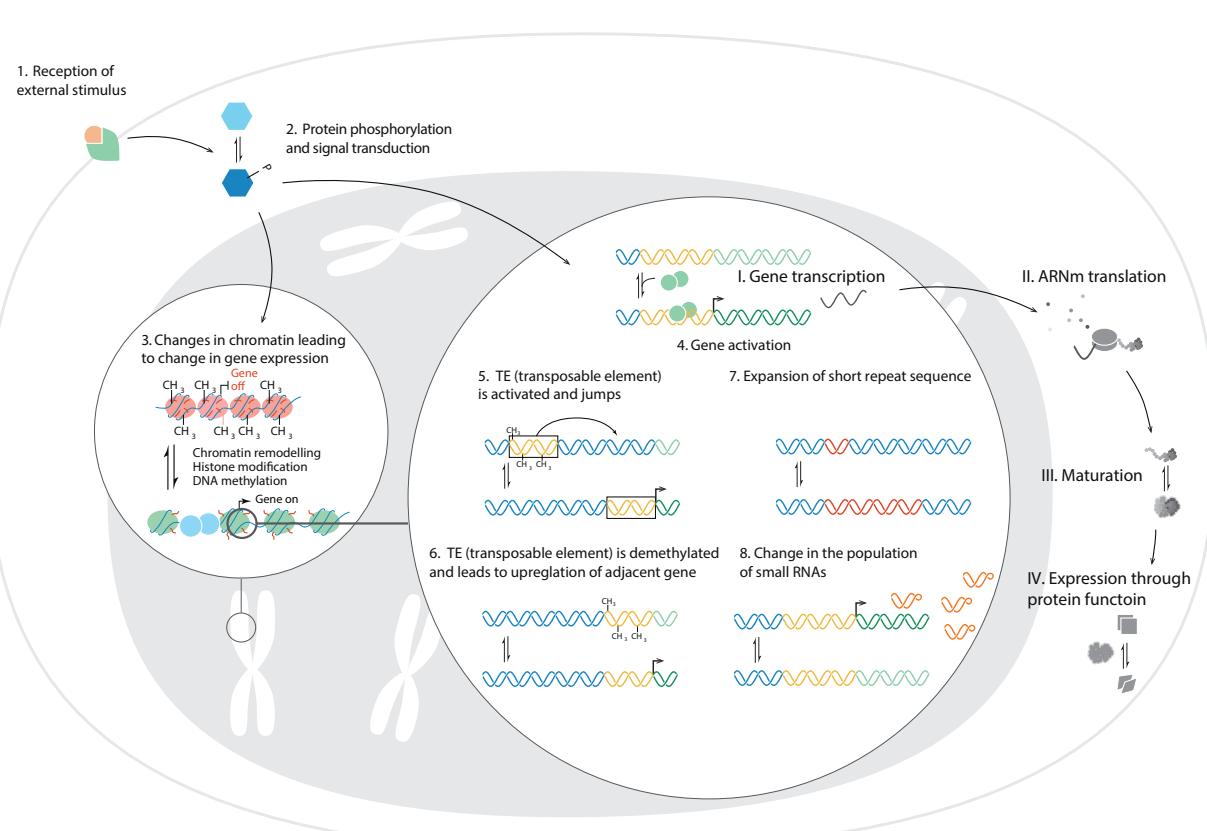


Figure 3.1: The three main sources of intra-specific phenotypic variability: genetic, epigenetic and phenotypic plasticity. Phenotypic plasticity can involve epigenetic mechanisms.



The diversity of mechanisms and scales (both spatial and temporal) these processes can act inside of plant gives an idea of the diversity of strategies a plant can deploy to face changes in its environment. Considering this complexity, only a small fraction can be explored in such model as *MountGrass*, but hopefully, it will help make progress in our understanding of the role of these molecular mechanisms at the scale of the community.

Phenotypic plasticity is the capacity of a species to produce individuals with the same genotype but different phenotypes. This difference in phenotype should be an active process, not the results of direct alteration of the phenotype by external factors without changes in internal functioning. This change in internal functioning process has the objective¹ to match the phenotype with expected future conditions to maximise the individual fitness. The expression "expected future conditions" is key here, as it is this projection that drives the plasticity.

Active plasticity is used for predominantly anticipatory, and often highly integrated, phenotypic changes in response to some environmental cue or signal, and reflect modifications of developmental pathways and regulatory genes. Forsman - 2014

FORMS OF PLASTICITY

¹ in the sense it has been selected because it provides this capacity

Passive plasticity, on the other hand, may stem from direct environmental influences on chemical, physiological and developmental processes, and is generally not considered anticipatory, but a mere consequence of the environment, such as stunted growth owing to low resource levels.

Active and passive plastic response can be discriminated by the position of the control: internal for the active plasticity, or external for the passive response. In the case of active plastic response, the signal from environment must be inte-

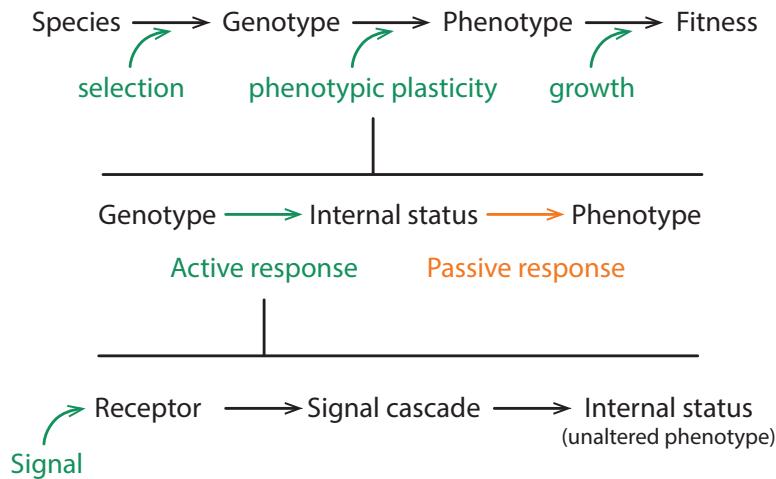


Figure 3.2: Decomposition of phenotypic plasticity as a step between the genotype and the fitness. Phenotypic plasticity is the effect of environment on the link between genotype and phenotype. Plasticity can itself be decomposed in active plastic response that change the internal status of the individual (under genetic control) and passive response that results from the inevitable effect of the environment of the traits on the individual.

grated (from physical or chemical to information) then transferred to response organs. These organs respond to the integrated signal by changes in their expression levels (*internal status* in figure 3.5) as summarised in figure 3.3.

Changes in phenotypes are controlled mainly by complex development processes. These processes involve numerous proteins and signalling pathways. Genes expression of proteins (transcription factors, enzymes, signalling proteins...) is controlled by specific mechanisms with various degrees of speed and duration (instantaneous regulation response, to inherited epigenetic adaptation). Some of these molecular processes are detailed in box ?? in relationship with gene expression pathway (see also A. B. Nicotra et al. 2010).

Active phenotypic plasticity is an integrative process at the scale of the individual that aims for an improvement of plant fitness by the adjustment of its morphology according to environmental cues. It often relies on multiple regulation processes. Modelling the extent and the rules of such mechanism is not an easy task that might depend on the context and the framework used.

3.2.3 How to model phenotypic plasticity

A plastic response can involve numerous genes interaction in networks of regulatory pathways. The objective of an ecological model is not to reproduce this complexity, but the basic behaviours emerging from this biological complexity¹. The basic components of the active plastic response are the perception of the external signal, its integration into meaningful information and the transformation into phenotype modification.

Every growth model is plastic. Every growth model predicts different phenotypes for plants sharing the same phenotype (often just defined by the species affiliation) growing in different condition. But most of this plasticity is passive, and it could be encompassed in this personal definition of the notion of **growth function** (see figure ??). However, among vegetation models only some of them claim to include phenotypic plasticity (Maire et al. 2013), why so? What criterion can be used to distinguish active from passive plasticity in the context of plant modelling?

The use of information from the environment to change the phenotype in or-

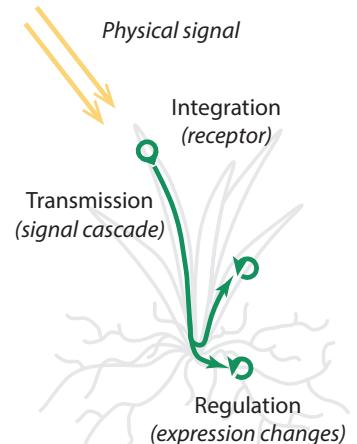


Figure 3.3: Mechanism of active plasticity. Integration of a physical (or chemical) signal, transmission and regulation of phenotype through regulation of gene expression, or post-transcription regulations.

¹ this biological complexity can be explained by the simplicity and a limited number of basic biological units living organism are made of, and the emergence through a simple mutation-selection operation. This complexity can be mimic by simpler and freer mathematical design.

der to have a better fitness is active plasticity. But in practice (in models) (Maire et al. 2013), often nothing really separates the two as plasticity is often modelled as a general mechanism shared by all species (but see [jablonka_adaptive_1995](#) for discrete strategies in clonal plants) and local environmental variables are used to determine the phenotype of a plant in both cases. Only the justifications and the forms of the linking functions are different, and they may involve different traits. This idea is illustrated in figure 3.4, where the phenotype is first defined by the genotype then controlled by the growth function as a function of current phenotype and environment (see figure 3.4, left column). There are no differences between plasticity of two species if two species have the same phenotype, then in a similar environment, they would express the same plastic response. I argue that plasticity, to be considered as an active process, should be under a genetic control (*i.e.* species-specific parameter). This means that, despite a shared rule and similar phenotype, the plastic would be different and would depend on a species-specific parameter.

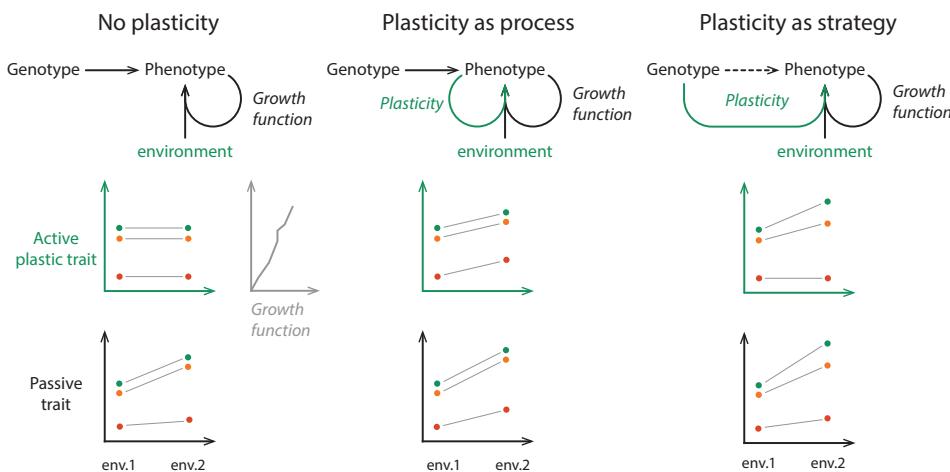


Figure 3.4: Three forms of plasticity in models.

Moreover, no integration function,

Two questions emerge from this: if growth function and plastic response are different (conceptually), how to determine each of these functions? How the genetic control affect the phenotypic response? Or why would it be beneficial to have multiple rules - non-discrete perspective on plasticity?

we want active plasticity, what's distinguish plasticity types is not the frame of reference, but the strategy: it's a choice: determine by another trait that characterises the response.

what makes it plastic: find the invariance. Laughlin? (what's invariance anyway)

defined by variable (ref plasticity is good in variable) and limiting variables (resource, temp, perturbation) = drivers

functions: reaction norms (Feller et al. 2015) thickness and light. Nice, but doesn't work with multiple drivers and composite traits

Or general rules : give an optimum phenotype. More deterministic approach. But optimum = general rule. Conceptually, if there is an optimum: why do something else ? Empirical studies: can be maladaptive, plasticity is a bet, and often ignore

PLASTICITY RULES: A QUESTION OF DRIVERS

resources, but also risks (frost, grazing): alter cost and gains. Multi-process plasticity, with relative weights. see chapter VI, section 3.

Or perfect optimisation with perfect estimation of conditions.

3.3 Toward an integrative framework of plant strategy and phenotypic plasticity

Adaptive plasticity in models is often a layer on top of the species strategy, it acts more like a new mechanism, rather than a strategy within the already existing growth process. To interrogate the plasticity as a dimension of plant growth and an evolutionary process (Bradshaw 1965) (see also work of Scheiner ([scheiner_genetics_2002](#) ; Scheiner and Lyman 1989; Scheiner and Holt 2012)), or better understand the cost and limits of plasticity DeWitt, Sih, and Wilson 1998; Callahan, Maughan, and Steiner 2008; Auld, Agrawal, and Relyea 2009, or the effect of plasticity on coexistence and community dynamics Hart, Schreiber, and Levine 2016, plant strategies and plasticity need to be blended together in an integrative framework.

3.3.1 Plastic strategies

Resource-use and allocation strategies have been related to environmental conditions in both empirical (Ian J. Wright and Westoby 2002; D. Ackerly 2004; L. Poorter and Bongers 2006), conceptual (Grime 1977; Westoby 1998) and modelling(Kleidon and Mooney 2000; Scheiter and Higgins 2009; Reineking et al. 2006) studies. Moreover, functional traits show evidence of intra-specific changes along environmental gradient (Kichenin et al. 2013) and intra-specific economic spectrum (Hu et al. 2015), and constraints that shape main ecological trade-offs are certain to also constrain individual traits. Therefore, if strategies vary between and within species along environmental gradients, it makes sense to imagine that plasticity as changes in strategic traits. This goes beyond changes in spatial allocation(Schapendonk et al. 1998), or parameters not identified as strategic traits Lohier et al. 2014; Feller et al. 2015. Considering strategic traits is not common practice because it blurs the limits between species that are not well identified by these traits any more¹.

However, while this interpretation makes sense, the species and the individuals do not have the same constraints, and plasticity cannot be as large as intra-specific diversity as there are limitations to plastic development (DeWitt, Sih, and Wilson 1998; Auld, Agrawal, and Relyea 2009). Moreover, it seems that rules that drive plastic may not be the same as the ones that drive intra-specific genetic variations and inter-specific differences(Peter Ryser and Eek 2000), explaining contrasting response along gradient or between experimental drought treatment (Kichenin et al. 2013; Jung, Cécile H. Albert, et al. 2014). This difference is probably more important for grass species than trees (Franklin et al. 2012) because of a lower scale difference between growth and selection processes.

¹ especially when a relatively low number of species-specific traits are considered

Phenotypic plasticity tends to maximize resource acquisition and growth rate in the short term, whereas the higher tissue-mass density and the longer leaf lifespan of shade-tolerant species indicate reduced loss rates as a more advantageous species-specific adaptation to shade in the long term. - Peter Ryser and Eek 2000

3.3.2 Plasticity as a strategy

Most models consider plasticity in traits or carbon partitioning as a general behaviour that is present or absent for all considered species. While this discretisation of the phenomenon is not problematic, and rather informative for a single plant or monoculture simulations Maire et al. 2013, it ignores the question of the adaptive value of plasticity and does not allow a continuous representation of plasticity.

Intuitively phenotypic plasticity is a mechanism that increase fitness and has a positive adaptive value (increases the chance to be selected). However multiple **costs** and limits have been identified, both biological ([dewitt_cost_1998](#); Auld, Agrawal, and Relyea 2009; Callahan, Maughan, and Steiner 2008) and ecological ([dewitt_cost_1998](#); [scheiner_genetics_2002](#) ; Auld, Agrawal, and Relyea 2009; Scheiner and Lyman 1989; Scheiner and Holt 2012; Van Kleunen and Fischer 2005), limiting the extend of plasticity observed in nature and differences between species (in grasslands see Peter Ryser and Eek 2000).

...

These limitations, in addition to indicating the processes that should be included in dynamic models involving phenotypic plasticity, show that plasticity should be continuous. Indeed, costs of plasticity can increase with the amplitude of the plastic response and/or the complexity, therefore reducing the adaptive value of plasticity. Because non-linearity can be expected between the amplitude of plastic response and both fitness increase and cost, the adaptive value of plastic response can switch from positive to negative depending on its amplitude. Such behaviour would justify a non-discrete plastic response (or variable sensitivity for polyphenism) to be captured in a model.

As mentioned, ecological processes can favour or limit the selection of plasticity as any other trait. The idea of plasticity as a trait under genetic control is not new. Anthony Bradshaw was probably the first to defend this idea of genes controlling the variability of phenotypes.

But it is rarely implemented in individual or community growth model. This can be explained by the fact that plasticity is often seen as a process, rather than a strategy (see the previous paragraph). In individual-based models, plasticity as a process is often considered because of the relatively low number of species, and scientific question not focusing on ecological aspects. In models that consider the dynamics of diverse communities under drastic changes, integrating the plasticity as a strategy is crucial. This can be done by the use of species-specific traits that control the amplitude and/or direction of the response (see more details in chapter III). In population models, plasticity is often considered as a source of variation equivalent to intra-specific genetic variations and is modelled by a distribution function. DeWitt 2016 proposes approaches with higher moments and environment dependent distribution to integrate plasticity into such models. In development models, Bayesian models offer a unifying framework to combine inherited information and environmental cues (Stamps and Frankenhus 2016).

This shift is also important because if genes control plasticity, plasticity can also alter evolutionary process and therefore the response to climate changePfennig et al. 2010; Matesanz, Gianoli, and Valladares 2010; A. B. Nicotra et al. 2010.

Plasticity is a complex matter, both a growth process that alters strategies

COST AND LIMITS

CONTINUOUS PLASTICITY

FROM PROCESS TO STRATEGY

and a strategy itself. New simulations tools for understanding community dynamics should try to both include multiple coexistence mechanisms and plant strategies, and focus on individual level mechanisms of competition, growth, and survival. This can only be achieved in a constraint high dimensional strategy space based on physical and biological trade-offs. Individual-level modelling allows the integration of multiple sources of intra-specific variability: genetic diversity and phenotypic plasticity. Phenotypic plasticity being driven by the perception of the environment, it cannot be simply described by normal random distribution and should receive more attention. This focus is particularly important considering both the lack of understanding of this phenomenon and the consequences for plant communities.

3.4 How phenotypic plasticity affect ecosystem properties and dynamics

The difficulty to model phenotypic plasticity, more precisely to integrate multiple aspects of the complexity of phenotypic plasticity in the context of community dynamics, is limiting the current knowledge of the impact of this mechanism on community composition, properties, and dynamics under global change. In this paragraph, I try to identify the mechanisms by which phenotypic plasticity impacts plant communities, and to determine if there are unresolved questions or paradoxes, or incomplete conclusions. The focus will be given to the main properties of the grassland communities: diversity, productivity, and identity.

3.4.1 Contrasting effect on diversity

Diversity is a complex subject as discussed earlier in section 1, resulting from various processes and measured by many indicators. Therefore, there are many ways the plasticity can affect diversity. Also, the scope at which diversity is considered may change the effect of plasticity as the balance between may driving mechanism is shifted (see Chalmandrier 2015 for the importance of the scale of diversity). I will try to keep it simple and focus on measures of diversity at the scale of the community.

Species diversity is driven on two levels, at large scales by abiotic conditions and filtering, and at a lower scale, within this large potential niche defined by abiotic conditions, by competition and facilitation interactions. From this point of view, plasticity certainly increases the potential niche both along environmental conditions axis, but also along variation axis (species might be more or less sensitive to changes in conditions), therefore enlarging **niche** superposition (Violle et al. 2012). This effect should, in theory, increase potential diversity as more species can potentially live in any given environment (Lepik, Liira, and Zobel 2005; Jung, Cécile H. Albert, et al. 2014), but the effect of biotic interactions must be considered before drawing any conclusion of the effect of plasticity on realised diversity. The effect of plasticity on interactions is much harder to predict. According to **adler_coexistence_2007** increase in niche difference and decrease in average fitness differences would increase stable coexistence.

SPECIES DIVERSITY

The impact of plasticity mechanism on stabilizing effect is also hard to an-

ticipate. It will likely be negative because established species may better fill any potential gap and prevent low-density positive effect and therefore invasion (Berg and Ellers 2010). On the contrary, reduction of fitness difference due to plasticity could lead to stronger coexistence between species. Yet, the reduction of fitness differences is not guaranteed and in case of asymmetric gain (relative to strategies), plasticity could reduce realised diversity by increasing competitive exclusion. There are here multiple effects (figure ?? on species diversity that needs to be disentangled. Recent review (Turcotte and Levine 2016) of these effects show no consensus on the effect of phenotypic plasticity on stable coexistence.

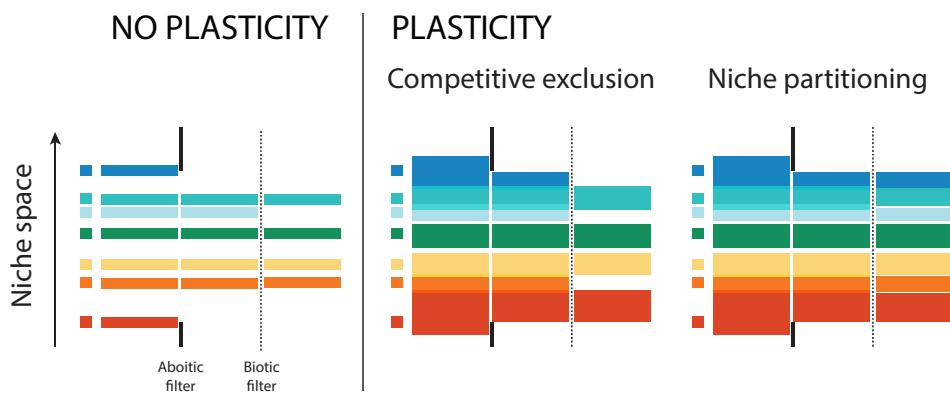


Figure 3.5: Phenotypic plasticity can affect filtering processes in diverse ways, making difficult the understanding of the role of plasticity in diversity maintenance.

But plasticity responses not only depend on abiotic condition, but also on the neighbourhood that affects local environment (Sultan 1995) at a fine scale. Because of plasticity, these interactions can even shift from competition to facilitation Callaway, Pennings, and Richards 2003. A novel difficulty arises with the evidence that the identity of the competitor affects plastic response (Callaway, Pennings, and Richards 2003; Abakumova et al. 2016), but it is likely that such interaction is related to traits and therefore impact on resource (Callaway, Pennings, and Richards 2003).

Species diversity often comes with functional diversity, however, phenotypic plasticity affect plant traits and is likely to affect functional diversity (Cécile H. Albert et al. 2012). Plasticity can lead to a convergence or a divergence of functional traits, decreasing or increasing functional diversity. In an experiment with legumes species Roscher et al. 2015 observed these two phenomena on different types of traits, between monoculture and mixture. The convergence of canopy filling and vertical growth traits suggests that competition stresses the different species on light competition, leading to a reduction of working strategies along these dimensions. Whereas, relatively, the other aspects of plant development are less constraint, or species experience diverse and contrasting conditions in mixtures than in monocultures.

FUNCTIONAL DIVERSITY

Phenotypic plasticity is expected to increase the potential niche of species and reduce the filtering effect of abiotic conditions. However, the effect on biotic interaction makes no consensus and is likely to vary depending on the identity of the competitors, and the relative effect on trait differences. The balance between stabilizing niche differences and average fitness differences is crucial to determine the final impact on stable coexistence. The effects on

functional diversity are also diverse but mainly depends on the plastic rules leading to convergence or divergence of traits.

3.4.2 Productivity always improved?

There is still debate on the effect of phenotypic plasticity of mechanisms driving species diversity, but is the question of the effect on productivity solved?

Plasticity is a mechanism that emerges in a situation where the plants can increase their fitness in response to environmental conditions. This increase in fitness is often due to higher resource use or resource foraging efficiency and therefore better growth rate (observed in models (Maire et al. 2013) and empirical studies (Hamann et al. 2016)). This leads to higher individual productivity. It is especially true when resources are varying and these variations can be anticipated Richter et al. 2012.

STABILITY

However, has mentioned earlier, plasticity comes with inherent costs, related to the biological machinery needed to sense and process the signals and alter the phenotype. This costs, if the plant does not take advantage of the plasticity (no variability, in its niche) to increase (or maintain) growth rate will impact the productivity.

COSTS AND LIMITS

The unreliability of environmental cues is a limit of plasticity, and it can lead to maladaptive changes in phenotypes, but this is a marginal behaviour, and maladaptive plasticity is expected to be eliminated by an evolutionary process in fairly constant conditions. However, in the context of climate change, the reliability of these cues may decrease and leads to maladaptive responses.

If unnecessary costs and unreliable cues can impact overall plant efficiency, adaptive plasticity can also hurt productivity while increasing fitness. Indeed, as evolutionary models and game theory predict, competition can lead to lower efficiency than optimum arrangement. Competition leading to lower resource availability, plastic species may have an aggressive plastic response leading to a stronger competitor but with less effective resource use.

Biodiversity - productivity

DIVERSITY AND PRODUCTIVITY

3.4.3 Community identity shift

The third main property of grassland communities is the **identity** of the dominant species (or average species if CWMs are considered). Phenotypic plasticity can impact community identity in two ways: (1) by shifting the identity of present species, (2) by altering the output of filtering processes in favour of different traits.

The first effect makes sense only in the context of a change in condition. Drought experiments in mountain grasslands show an intra-specific shift toward higher LDMC and lower SLA (Jung, Cécile H. Albert, et al. 2014). Other empirical studies show uncoupled response between above- and below-ground organs, shifting the strategy of the species ([freschett_plasticity_2014](#)).

A modelling experiment shows that the phenotypic plasticity is required to correctly model the dominance pattern along cutting frequency gradient (Maire et al. 2013), illustrating the second effect.

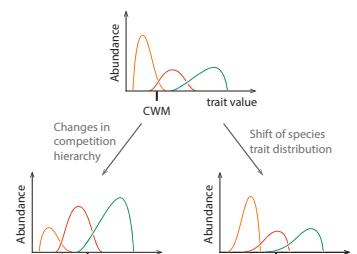


Figure 3.6: Phenotypic plasticity effects on community identity. Phenotypic plasticity can modulate community-identity response to a change in conditions by two distinct but non exclusive mechanisms: altering the competitive hierarchy and species abundances (left) or shifting the individual species identity (right)(Dwyer, Hobbs, and Mayfield 2014).

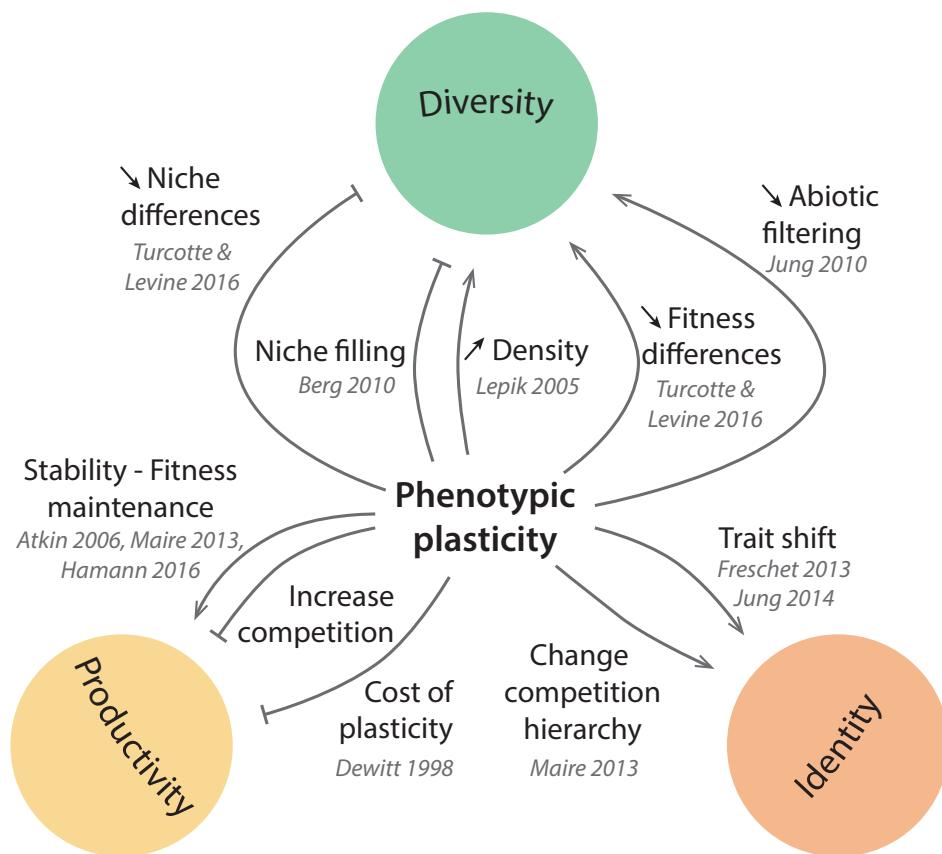


Figure 3.7: Effect of phenotypic plasticity on the three main community properties. Phenotypic plasticity can impact these properties through multiple processes that may have contrasting effects. To determine the overall effect of plasticity on community response to changes in drivers (climate and land-use) we need to integrate all these effects.

3.4.4 Phenotypic plasticity effect on individuals and communities

Plasticity is a complex matter, both with a growth process that alters strategies and a strategy itself. New simulations tools for understanding community dynamics should try to both include multiple coexistence mechanisms and plant strategies, and focus on individual level mechanisms of competition, growth, and survival. This can only be achieved in a constraint high dimensional strategy space based on physical and biological trade-offs. Individual-level modelling allows the integration of multiple sources of intra-specific variability: genetic diversity and phenotypic plasticity. Phenotypic plasticity being driven by the perception of the environment, it cannot be simply described by normal random distribution and should receive more attention. This focus is particularly important considering both the lack of understanding of this phenomenon and the consequences for plant communities.

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III

MODELLING ALPINE GRASSLANDS WITH MOUNT- GRASS, A GENERIC FRAMEWORK INTEGRATING PHE- NOTYPIC PLASTICITY

IV

INDIVIDUAL PERFORMANCE: STRATEGY AND PLASTICITY

V

COMMUNITY DYNAMICS

VI

SYNTHESIS & OUTLOOK

GLOSSARY

active plasticity Change in phenotype controlled by internal regulation processes. Opposed to passive response. *i.e.* change in SLA when light is limiting is an active plastic response.

allocation rule The allocation rule is the set of rules that determine the target phenotype of a plant considering its actual phenotype, the biomass available and the projection of external conditions. It can be decomposed in two main parts: the plastic dimensions, and the fitness proxy function (or gain function). Allocation rule is also designated as allocation algorithm, plasticity rule or plasticity algorithm.

Plasticity

4 INDEX

community weighted mean, 29
diversity, 30, 43
dynamics global vegetation models, 32
individual-based models, 32
individual-based-models, 7
leaf economic spectrum, 26
mass ratio hypothesis, 29
productivity, 30
abiotic filtering, 18

costs, 42
diversity, 3
ecosystem properties, 2, 28
ecosystem services, 1
ecosystems, 1
facilitation, 18
functional identity, 29
growth function, 39
identity, 2, 45

intra-specific variability, 33
mountain grasslands, 1
niche, 17, 43
potential niche, 18
productivity, 3
realised niche, 18
strategy space, 28
trade-off, 26